A Framework for Evaluating *O. mykiss* Juvenile Production and Factors Affecting Anadromy

Photo credit: John Hannon

Suggested Citation

Beakes, M. P., Bilski, R., Brown, H., Collins, A., Ehlo, C., Ferguson, E., Ferguson, J., Goertler, P. A.L., Green. E., Gutierrez, M., Israel, J., Jensen, A., Kurth, R., Mahardja, B., Matthias, B., Nelson, J., Pien, C., Spear, K., and Vick, P. 2024. A Framework for Evaluating *O. mykiss* Juvenile Production and Factors Affecting Anadromy (85 pp.).

Contributing Authors

Author	Affiliation
Michael Beakes	U.S. Bureau of Reclamation
Robyn Bilski	California Department of Fish and Wildlife
Howard Brown	National Marine Fisheries Service
Alison Collins	The Metropolitan Water District of Southern California
Chase Ehlo	U.S. Bureau of Reclamation
Erin Ferguson	California Department of Fish and Wildlife
John Ferguson	Anchor QEA; National Marine Fisheries Service
Pascale Goertler	Delta Science Program
Elizabeth Green	Anchor QEA; National Marine Fisheries Service
Monica Gutierrez	National Marine Fisheries Service
Joshua Israel	U.S. Bureau of Reclamation
Alexander Jensen	U.S. Bureau of Reclamation
Ryon Kurth	California Department of Water Resources
Brian Mahardja	U.S. Bureau of Reclamation
Bryan Matthias	U.S. Fish and Wildlife Service
Jonathan Nelson	California Department of Fish and Wildlife
Catarina Pien	U.S. Bureau of Reclamation
Kate Spear	National Marine Fisheries Service
Page Vick	National Marine Fisheries Service

Table of Contents

Executive Summary ... 7
Introduction ... 9
Central Valley Steelhead Status and Diversity Groups ... 10
Juvenile Production Estimation Framework ... 12
Water Year 2024 Steelhead Loss ... 13
JPE in Concept ... 14
JPE in Practice ... 17
Adult Approach ... 18
Juvenile Approach ... 19
Stepwise Approach ... 19
Surrogate Approach ... 20
Simulated JPE Example ... 21
Accounting of Steelhead Loss ... 23
JPE Framework Implementation ... 23
Value of Information ... 25
Factors Affecting Anadromy ... 27
Historical and Contemporary *O. mykiss* monitoring ... 27
Program Integration ... 27
Knowledge Gaps ... 28
2021 Steelhead Workshop ... 28
O. mykiss Life Cycle and Conceptual Models ... 29
Spawning ... 32
Egg-to-Fry Emergence ... 37
Rearing ... 43
Life-History Expression ... 50
Outmigration ... 56
Ocean Residence ... 63
Returning Adults ... 68
Data Guidance ... 73
Data Management Plan ... 73
Metadata Standards ... 73
Data Accessibility ... 73
Acknowledgments ... 75
Literature Cited ... 76

List of Acronyms

CCV	California Central Valley
CDFW	California Department of Fish and Wildlife
CDWR	California Department of Water Resources
CM	Conceptual Model
CVP	Central Valley Project
CVSMP	Central Valley Steelhead Monitoring Program
DJFMP	Delta Juvenile Fish Monitoring Program
FERC	Federal Energy Regulatory Commission
IEP	Interagency Ecological Program
JPE	Juvenile Production Estimate
LTO	Long-Term Operation
MAST	Management, Analysis, and Synthesis Team
NEPA	National Environmental Policy Act
NMFS	National Marine Fisheries Service
NOAA	National Oceanic Atmospheric Administration
PIT	Passive Integrated Transponder
RST	Rotary Screw Trap
SAIL	Sturgeon Analysis of Indicators by Life stage
SJRRP	San Joaquin River Restoration Program
SMART	Specific, Measurable, Achievable, Relevant and Time-bound
SWP	State Water Project
USFWS	United States Fish and Wildlife Service
VSP	Viable Salmonid Populations

List of Figures

Figure 1: The science plan is focused on JPE methods, monitoring, and special studies in the Southern Sierra Nevada Diversity Group. 11
Figure 2: Conceptual framework of O. mykiss life-stage transitions and estimation of cohort parr and smolt abundance (A) and hypothetical life-stage timing (B) at years one through three......15
Figure 3: Boxplot (top) and density curve (bottom) summarizing results from 200 simulations of each JPE calculations method. 22
Figure 4: Depiction of the O. mykiss life cycle by life stage domains developed into conceptual models. All boxes represent a stage for which monitoring and directed studies can be implemented to develop parameters necessary to support JPE development and estimation. The arrows represent transition rates (e.g., survival, life history expression) to the next stage. Stages that may last multiple years include a circular arrow, which represents survival within that stage. The conceptual model for life history expression was omitted in the figure (Figure 4) but is represented by the transition of juvenile rearing to either smolt outmigration (migratory strategy) or spawning adults (resident strategy). 30
Figure 5: Spawning conceptual model describing reproduction from spawning anadromous and resident O. mykiss. 35
Figure 6: Egg-to-fry emergence conceptual model linking large-scale processes to management actions, SMART metrics, and desired population responses (i.e., VSP criteria) 40
Figure 7: Juvenile rearing conceptual model linking large-scale processes to management actions, SMART metrics, and desired population responses (i.e., VSP criteria). 46
Figure 8: Life-history expression conceptual model linking large-scale processes to management actions, SMART metrics, and desired population responses (i.e., VSP criteria)...53
Figure 9: Smolt outmigration conceptual model linking large-scale processes to management actions, SMART metrics, and desired population responses (i.e., VSP criteria). 59
Figure 10: Ocean residence conceptual model describing the time prior to migration back to natal spawning grounds. 66
Figure 11: Returning adults conceptual model describing adult migration back to the spawning grounds of natal tributaries. 69

List of Tables

Table 1: A summary of the life stage, and life-stage transition parameters are summarized in table 1 through age 2+ production of parr and smolts. The transition parameters and definitions are the same for older age classes, but abundance estimates, and transition parameter values will differ between older and younger parr and smolts. 16
Table 2: Annual loss of clipped juvenile steelhead at the salvage facilities and total hatchery juvenile steelhead release numbers for brood years 2016 to 2022. From 2016 to 2023, average annual % lost to the facilities was 0.160%. Note that release locations and dates, which vary by year, were not considered for this calculation. Hatchery release numbers were acquired from: CDFW hatchery releases- Calfish.org and USFWS hatchery releases data provided by Kevin Offill, 3/13/2024. Water facility loss data acquired from: SacPAS and reflects Water Year 2017 – 2022..21
Table 3: Summary of surrogate parameters found in the literature and used in JPE calculations 21

Table 4: Stanislaus life cycle monitoring, focal parameters, methods, and organization lead. ...25

Executive Summary

There is significant uncertainty regarding key demographic and life history traits of California Central Valley steelhead (CCV steelhead) *Oncorhynchus mykiss* (*O. mykiss*) populations that complicates management decisions related to state and federal water operations. To address this issue, state and federal agencies are committed to advancing the state of CCV steelhead monitoring and science as part of long-term operational planning. More specifically, these agencies have committed to developing a steelhead juvenile production estimate (JPE), the estimated number of juvenile *O. mykiss* that outmigrate from natal tributaries into the Sacramento-San Joaquin Delta each year, as well as accelerating research and monitoring to better understand CCV steelhead biology and the impacts of water operations decisions on the species.

This document provides a plan (i.e., "science plan") for identifying and prioritizing the monitoring, and science needs for calculating a JPE and filling CCV steelhead knowledge gaps. This science plan outlines multiple methods for calculating a JPE, synthesizes known CCV steelhead information and monitoring efforts, defines a conceptual steelhead life-cycle model, and outlines key data management practices. The overarching goal of this science plan is to provide state and federal agencies with a roadmap for addressing some of the uncertainty complicating CCV steelhead management.

The JPE methods in this science plan will produce a metric of annual population productivity that can potentially replace the metric currently being used to manage steelhead loss at the Sacramento-San Joaquin Delta water export facilities. The current metric is based on historical loss records with limited connection to vitality rates of CCV steelhead populations. The JPE described in this plan will be more directly linked to these vitality rates with the flexibility to incorporate diverse population demographics and multiple diversity groups. This flexibility is important because CCV steelhead are more complex than other salmonids due to the diverse life history strategies the species exhibits.

Well-designed monitoring programs are paramount in assessing and informing management decisions. This science plan provides guidance for monitoring and research that will help address CCV steelhead knowledge gaps related to population demographics and drivers of anadromy. In addition, this plan identifies existing programs that directly or indirectly monitor CCV steelhead and produce valuable information or contain infrastructure that can be leveraged for the monitoring and research needs described in this plan (e.g., acoustic telemetry receiver network).

Developing conceptual models of the steelhead life cycle and factors that affect populations and life-history expression may help identify the necessary core monitoring programs and steps necessary for a steelhead JPE. This science plan contains CCV steelhead conceptual models that were developed for different stages of the steelhead life cycle with one conceptual model focused on life-history expression. Each conceptual model is structured across hierarchical tiers of increasing nuance and complexity with clear hypotheses related to factors that may impact population dynamics and life-history expression. For consistency and familiarity, these conceptual models follow the framework of other conceptual models in the Central Valley, albeit CCV steelhead conceptual models are more generalized to ensure applicability across tributaries.

Lastly, data from monitoring programs and research is the basis of informing the management decisions thus a data management plan is foremost in protecting the value and utility of the data. Datasets should include detailed guidance on discovering, using, and interpreting the data, a sufficient quality assurance and control plan, and include proper metadata to insure the correct use and interpretation of the data. Data should have open access and when possible, should be centralized to allow for integration across multiple monitoring projects and allows for others to utilize datasets.

Introduction

There remains significant uncertainty regarding California Central Valley (CCV) *Oncorhynchus mykiss* (*O. mykiss*) abundance, distribution, productivity, and life history diversity. This uncertainty is driven from limited data on both the resident (i.e., trout) and anadromous (i.e., steelhead) life-history forms of the species. Although there are CCV salmonid monitoring programs that have collected data on *O. mykiss*, the monitoring is not standardized, often designed for Chinook salmon (*Oncorhynchus tshawytscha*) populations, and inadequate for assessing population viability (Lindley et al. 2007). In addition, data collected on *O. mykiss* are primarily composed of information on steelhead because this is the only life-history form protected under the Endangered Species Act (ESA). The lack of information on resident trout adds to the underlying uncertainty of CCV *O. mykiss* populations and further complicates management of the species because both forms affect the species' population dynamics, life-history expression, and evolution.

The uncertainty of CCV steelhead abundance and productivity is particularly problematic with respect to managing and regulating water operations of the Central Valley Project (CVP) and California State Water Project (SWP). For example, the National Environmental Policy Act (NEPA) and ESA consultation for the coordinated Long-Term Operation (LTO) of the CVP and SWP requires detailed assessment of effects to CCV *O. mykiss* populations. When estimates of CCV juvenile steelhead abundance range from as low as 94,000 (Good et al. 2005) to as high as 658,453 (Nobriga and Cadrett 2001), interpreting loss of steelhead at CVP and SWP water export facilities in context of the species population size can be challenging. For example, the average total loss of natural-origin steelhead (i.e., unclipped adipose fin) between 1998 and 2017 was approximately 3,110 fish (NMFS 2019), which equates to 0.5% to 3.3% of the total population based on the estimates cited above. Thus, the proportional population-level effect of loss at the CVP and SWP water export facilities can vary by almost seven-fold depending on the population size estimate. Despite the uncertainty in CCV steelhead population status, the National Marine Fisheries Service (NMFS) is required to set current take limits of wild-origin juvenile steelhead for the CVP and SWP in a population context. As such, improving our ability to quantify *O. mykiss* population status, demographics, and vital rates, or generate an annual *O. mykiss* juvenile production estimate is critical to understanding the effects of water project operations on *O. mykiss* and to evaluating population-level responses to management actions designed to protect and recover the species.

The Bureau of Reclamation (Reclamation), NMFS, the U.S. Fish and Wildlife Service (USFWS), and the California Department of Water Resources (CDWR) committed to advancing the state of *O. mykiss* science and the species' monitoring network as part of the LTO of the CVP and SWP (NMFS 2019). Specifically, these agencies committed to developing a method for generating a CCV Steelhead juvenile production estimate (JPE), an annual forecast of the number of outmigrating natural-origin CCV Steelhead that enter the Sacramento-San Joaquin Delta (Delta) each year. The goal is to develop CCV Steelhead JPE for the San Joaquin and Sacramento River basins that can be used to evaluate loss at the CVP and SWP water export facilities in a population context. In addition, these agencies committed to accelerating *O. mykiss* research and monitoring to improve our understanding of how actions related to stream flow enhancement, habitat restoration, and/or water export restrictions affect biological outcomes including juvenile and adult steelhead abundance, age structure, growth and smoltification rates, and anadromy and adaptive potential in Sacramento- and San Joaquin-origin steelhead.

The purpose of this science plan is to describe alternative methods for estimating a steelhead JPE and the research and monitoring needed to improve our understanding of factors that affect anadromy. The initial effort to develop a steelhead JPE will focus on fish originating from the Southern Sierra Nevada Diversity Group (Figure 1). An expanded effort to include the remaining Diversity Groups will be implemented by 2028. The first section of this plan describes several alternative approaches for calculating a steelhead JPE, identifies critical information needs for each approach, and summarizes the implementation timeline based on the 2023 LTO Proposed Action. The second section focuses on factors that affect anadromy and includes a suite of conceptual models (CM) to illustrate complex interactions between ecosystem dynamics and natural resource management on *O. mykiss* abundance, productivity, spatial structure, and diversity. In combination, this plan will provide the basis for informing research and monitoring needs to generate a steelhead JPE as well as track status and trends of *O. mykiss* populations and factors that may impact anadromy.

Central Valley Steelhead Status and Diversity Groups

The Central Valley Salmonid and Steelhead Diversity Groups include four regions composed of the major watersheds draining the California Central Valley. Current steelhead monitoring efforts are skewed towards watersheds in the Northern Sierra Nevada, and Basalt and Porous Lava Diversity Groups (Figure 1, Appendix A, Beakes et al. 2021). Although there are new monitoring efforts underway in the San Joaquin Basin and Southern Sierra Nevada Diversity Group, these programs have been developed and implemented independent of one another. Further, the data generated from these programs is often difficult to access by the public and/or is unavailable. As such, there is a clear need to develop a plan for coordinating *O. mykiss* research and monitoring in the Southern Sierra Nevada Diversity Group and integrating the data they generate (Beakes et al. 2021).

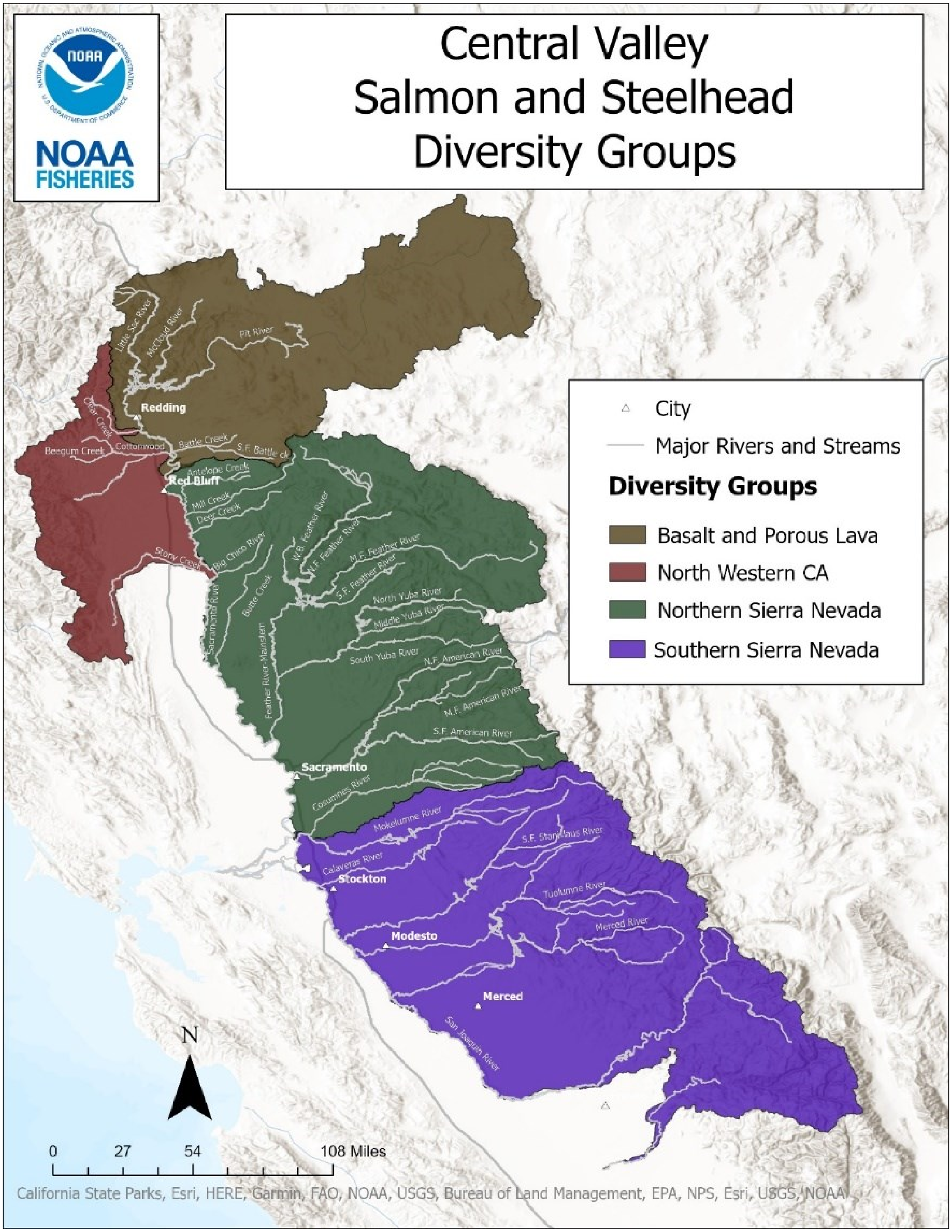

Figure 1: The science plan is focused on JPE methods, monitoring, and special studies in the Southern Sierra Nevada Diversity Group.

This page intentionally left blank.

Juvenile Production Estimation Framework

The 2020 Record of Decision on the LTO of the CVP and the SWP included a program to accelerate steelhead research and monitoring. Phase 1 of this program specifically called for steelhead research and monitoring actions to develop a JPE for steelhead-producing tributaries with CVP or SWP facilities. In this context, the JPE represents the estimated number of juvenile *O. mykiss* that outmigrate from natal tributaries and enter the Delta annually, which is likely a small fraction of the total juveniles produced each year because it excludes resident *O. mykiss*, the non-anadromous form of the species (i.e., rainbow trout).

The primary goal of this effort is to develop a more biologically relevant JPE metric to consider as a replacement to the current steelhead loss metric used to reduce effects of Delta exports on steelhead populations. The current regulatory framework for limiting steelhead loss at the CVP and SWP water export facilities has been set to 90 percent of the greatest annual loss that occurred in the historical record from 2010 through 2018, which equates to approximately 3,000 natural-origin CCV steelhead (NMFS 2019). The primary impetus for replacing the loss limit based on historical CVP and SWP salvage is the recognition that historical loss records have limited connection to Central Valley Steelhead population status, productivity, and the impact on life-history expression of future generations (i.e., adaptation through time based on fitness tradeoffs of anadromy vs. residency). The JPE is intended to incorporate measures of population size, frequency of anadromy, and annual smolt production.

It is important to note that there is desire to have CCV steelhead loss limits that account for the fact that *O. mykiss* in the Central Valley comprise a diverse set of populations and Diversity Groups within the Central Valley Steelhead Distinct Population Segment (DPS), as well as steelhead from Nimbus Hatchery, which are not considered part of the DPS (NMFS 2019). Under the ESA, the CCV *O. mykiss* DPS is the unit listed as threatened and needing federal protection. In addition, hatchery operations have created a mosaic distribution of population genetic diversity in the Sacramento and San Joaquin basins (Pearse and Garza 2015). Thus, in order to better understand the impacts of water export operations on Central Valley steelhead populations, it will also be necessary to generate watershed specific JPEs and assess the potential for assigning *O. mykiss* that are being entrained by CVP and SWP water export facilities to Diversity Groups, or more generally to the Sacramento basin and San Joaquin basin.

Water Year 2024 Steelhead Loss

In water year 2024 (October 1st 2023 – September 30th, 2024), the CVP and SWP water export facilities in the Delta observed unusually high CCV steelhead loss. Loss limit at these water export facilities are separated into to two time periods: December 1st – March 31st, and April 1st – June 15th. The basis for the two time periods is that San Joaquin-origin steelhead are presumed to outmigrate later than Sacramento-origin steelhead based on monitoring data from Mossdale Trawl (NMFS 2019, IEP 2021). CCV steelhead were observed in such high numbers at the CVP and SWP salvage facilities such that the December-March CCV steelhead annual loss threshold was exceeded on February 21st, 2024, which was then quickly followed by an exceedance of the Incidental Take Limit on March 20th, 2024. High numbers of CCV steelhead continued to be salvaged in these facilities into April, and the April-June annual CCV steelhead loss threshold was also exceeded on April 26th, 2024 before loss numbers started to decline in May. Relatively high loss of CCV steelhead continued to occur throughout the spring months of 2024 despite unprecedented pumping restriction. Data from acoustically-tagged wild steelhead from 2024 suggested that San Joaquin-origin steelhead do outmigrate into the Delta prior to April, in contrast to historical monitoring data. However, as of now, we do not yet know what proportion of salvaged steelhead at the export facilities in 2024 originated from the San Joaquin basin. Without a JPE and a population context, it is unclear what these loss events mean for the persistence of CCV steelhead in the system or how it affects the various diversity groups. It is also unknown, due to the diverse life history of *O. mykiss*, whether the loss event was due to a single productive year class or some environmental cue that triggered an outmigration of multiple year classes. The loss event in water year 2024 highlighted the urgent need for the development of a JPE, understanding of outmigration cues, and perhaps an interim alternative method for evaluating the impacts of CVP and SWP operations in the Delta (e.g., see Surrogate Approach section below).

JPE in Concept

Compared to other Pacific salmonids, *O. mykiss* exhibit considerable life-history diversity within and among distinct populations. Past studies have documented over 35 unique steelhead life-history variants throughout watersheds in North America (Moore et al. 2014, Hodge et al. 2016). Much of the observed *O. mykiss* life-history diversity stems from variation in age at outmigration that can occur within the first year of life or several years afterward (Figure 2). The variation in age at outmigration presents an interesting challenge with respect to calculating an accurate JPE that is designed to inform annual water operations. Below we delve into more detail concerning JPE in concept and in practice.

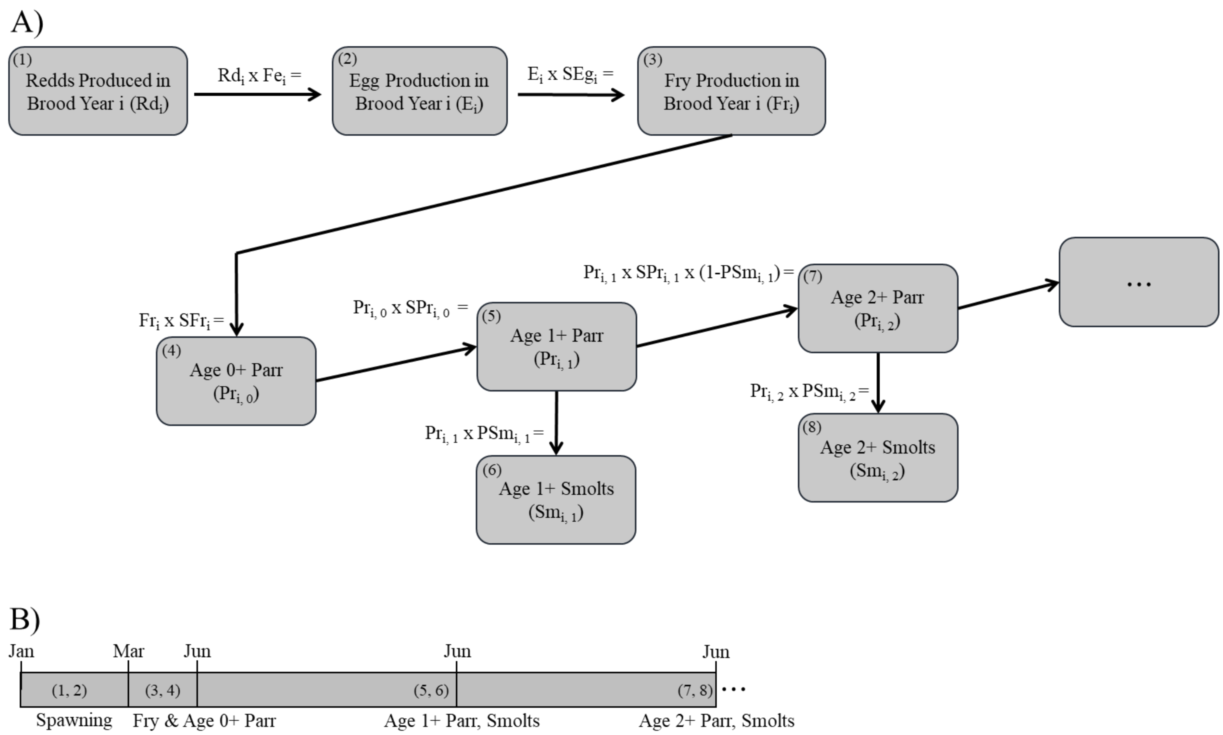

Figure 2: Conceptual framework of O. mykiss life-stage transitions and estimation of cohort parr and smolt abundance (A) and hypothetical life-stage timing (B) at years one through three.

Table 1: A summary of the life stage, and life-stage transition parameters are summarized in table 1 through age 2+ production of parr and smolts. The transition parameters and definitions are the same for older age classes, but abundance estimates, and transition parameter values will differ between older and younger parr and smolts.

Parameter	Description
Rd_i	Count of redds in brood year (i.e., spawning year) i
Fe_i	Fecundity of spawning fish in brood year i
E_i	Egg production in brood year i
SEg_i	Egg to fry survival in brood year i
Fr_i	Fry production in brood year i
SFr_i	Survival probability of fry to age 0+ parr in brood year i
$Pr_{i,j}$	Age j parr produced from brood year i
$PSm_{i,j}$	Probability of smolting by June in the given year for age j parr from brood year i
$Sm_{i,j}$	Age j smolts produced from brood year i
$SPr_{i,j}$	Probability of parr produced from brood year i surviving from age j to age j+1

Using the framework described above for natural-origin *O. mykiss*, the expected life-time juvenile production for a single brood year (i) can be calculated following equation (1):

$$JPE_i = \sum_{j=1}^{n} Sm_{i,j} = Sm_{i,1} + Sm_{i,2} + Sm_{i,3} + \cdots + Sm_{i,n} \quad (1)$$

Here we assume the juvenile production for a brood year (JPE_i) is the sum of smolts entering the San Francisco Bay-Delta that were produced after the first year (i.e., age-1+ smolts, or $Sm_{i,1}$), and years 2 ($Sm_{i,1}$), 3 ($Sm_{i,3}$) or more ($Sm_{i,n}$) after spawning. The number of years *O. mykiss* can spend in freshwater as parr prior to outmigrating as a smolt or maturing subadult depends partly on their lifespan. A maximum age of up to fourteen years was recorded for populations in northern British Columbia (Moore et al. 2014), in which case a single brood year could hypothetically produce smolts over a decade after spawning. However, the lifespan of California *O. mykiss* populations is thought to be much shorter, where one study from the Klamath River reported a maximum age of seven (Hodge et al. 2016). As such, we can assume that the number of smolts produced by a single brood year will typically outmigrate between < 1 to 4 years after emergence.

A similar framework can be applied to estimate the expected juvenile production for spring in a single year y (JPE_y) that includes offspring from multiple brood years. In this case the JPE calculation follows equation (2):

$$JPE_y = \sum_{j=1}^{n} Sm_{y-j,j} = Sm_{y-1,1} + Sm_{y-2,2} + \cdots + Sm_{y-n,n} \quad (2)$$

Here we assume the juvenile production estimate for the spring of a single year (*JPE$_y$*) is the sum of age 1+ smolts from the most recent brood year and smolts produced from prior brood years that outmigrated at age 2+ or older. Although most steelhead in the Sacramento River predominately smolt at age 2 (Hallock 1989), we assume that a single brood year can produce smolts between 1 to 4+ years after spawning. For example, the smolts produced in spring of 2022 would be the sum of age 1+ smolts from BY 2021 ($Sm_{2021,\,1}$), age 2+ smolts from BY 2020 ($Sm_{2020,\,2}$), age 3 smolts from BY 2019 ($Sm_{2019,\,3}$), and age 4 smolts from BY 2018 ($Sm_{2018,\,4}$). Note that the probability of smolting is relatively low for age 1+ and 4+ age classes, and thus likely represent a lower proportion of the total annual smolt outmigrants.

JPE in Practice

Resources managers are often required to strike a balance between utility and technical accuracy of the models used to manage complex species and systems. In almost all cases, a perfectly accurate model can't be created to guide management even if it is desired. Put another way, "all models are wrong, but some are useful" (Box et al. 2005). It should be emphasized that the goal of this steelhead JPE effort is not to develop a technically perfect steelhead JPE, but rather generate a model and metric that is useful for steelhead management. The reason for this is because the annual JPE is likely composed of multiple age classes (i.e., offspring from multiple brood years), and thus the proportional contributions of each age class to the annual outmigration population must be calculated for the JPE to be technically accurate. However, it will likely be infeasible, or impractical, to monitor and estimate the abundance of all age classes and all Central Valley tributaries for the JPE. Therefore, it will likely be necessary to develop a JPE that is simplified, and less technically accurate, but still useful (i.e., biologically relevant) in management applications.

For example, past research has reported up to 70% of outmigrating Sacramento River steelhead spent two years rearing in freshwater before entering the ocean (Hallock 1989), thus hypothetically outmigrating prior to June at age 2+ (Figure 2A, B). If this pattern is still true, and consistent among Central Valley tributaries, focusing the JPE on age 2+ individuals would represent a large proportion of the outmigration population and would be simplified and biologically relevant, but less accurate than an alternative JPE that incorporates younger and older age-class outmigrants.

Similar tradeoffs exist with research and monitoring intensity and the JPE estimate precision and accuracy. Although the precision and accuracy of the JPE may increase as more data and information are collected, resources for research and monitoring are finite. As such, resource managers will have to evaluate tradeoffs in how much data to collect on each *O. mykiss* life stage because implementing complete life cycle monitoring programs in all Central Valley watershed will be cost prohibitive.

To address these tradeoffs, several alternative approaches for calculating a JPE are described below. Each JPE approach relies on data from one or more life stages (e.g., adult, juvenile, etc.), and estimated life-stage transition probabilities (e.g., Figure 2A; $SPr_{i,j}$, $PSm_{i,j}$), to calculate a JPE of age 2+ outmigrants. All JPE approaches focus on what is believed to be the dominant age class (i.e., age 2+, Hallock 1989). The JPE may need to be expanded to include age 1+ fish or older fish if they represent a substantial proportion (e.g., >5-10%) of the annual outmigrant population size. For example, Hallock (1989) reported that up to 29% of outmigrating Sacramento River steelhead spent one year rearing in freshwater before entering the ocean. However, it is worth noting that Hallock's publication is over thirty years old and referenced studies from the 1950's. Current and future research and monitoring will need to provide empirical data on the proportion of the population composed of younger and older age classes that will enable resource managers to determine if basing the steelhead JPE on a single, dominant age class is appropriate.

Adult Approach

An annual steelhead JPE can be calculated based on the estimated number of reproductive adults and the estimated number of redds those fish are expected to produce. Here, the JPE calculation follows equation (3):

$$\widehat{JPE}_{i+2} = Rd_i \times Fe_i \times SEg_i \times SFr_i \times SPr_{i,0} \times (1 - PSm_{i,1}) \times SPr_{i,1} \times PSm_{i,2} \times SO_{i,2} \quad (3)$$

This approach assumes the JPE will be primarily composed of age 2+ outmigrants, and thus we can use redd abundance estimates in the current year (Rd_i) to estimate the JPE more than two years in advance (JPE_{i+3}). The JPE_{i+3} equals the total number of redds (Rd_i) times the average *O. mykiss* fecundity (Fe_i), egg-to-fry (SEg_i) and fry-to-age 0+ parr survival probabilities (SFr_i) in that spawning year, which gives an estimated abundance of age 0+ parr ($Pr_{i,0}$) produced. Multiplying the estimated abundance of age 0+ parr ($Pr_{i,0}$) by the the probability of remaining in freshwater at age 1+ ($1- PSm_{i,1}$), survival probabilities to reach age 2+ ($SPr_{i,0}$, $SPr_{i,1}$), and probability of smolting at age 2+ ($PSm_{i,2}$) and surviving outmigration ($SO_{i,2}$) from the natal tributary yields the expected JPE approximately two years after spawning ($JPE_{i,2}$).

For example, the 2027 steelhead JPE can be calculated by equation 3 using: 1) an estimated redd production, female fecundity, egg-to fry and fry-to-age 0+ parr survival probabilities in 2025, 2) the probability of surviving from age 0+ to age 1+, which spans 2025 and 2026 (Figure 2B), 3) the probability of remaining in freshwater and surviving from age 1+ to age 2+, which spans 2026 and 2027 (Figure 2B), and 4) the probability of smolting at age two and surviving outmigration in 2027.

The primary benefit of estimating a steelhead JPE based on adult *O. mykiss* monitoring is that the estimate can be produced several years in advance. As such, resource managers would have ample time to develop a water management strategy in response to years of relatively high or low juvenile steelhead production. However, estimating the JPE so far in advance will require multiplying a sequence of uncertain survival and outmigration probabilities. The results of this approach would provide a JPE with a likely large amount of error or uncertainty around the mean JPE estimate. The amount of error or uncertainty in the JPE will scale with the variability and uncertainty in the survival and outmigration probabilities and underlying adult *O. mykiss* monitoring data used to estimate it. Some of this uncertainty may be reduced by linking environmental factors to variation in life-stage transitions (e.g., survival, outmigration) if those factors are strongly correlated with observed variation in survival and outmigration probabilities. In other words, we may be able to inform and update the JPE estimates based on correlated environmental conditions rather than monitor subsequent *O. mykiss* life stages prior to outmigration. Note that environmental drivers of *O. mykiss* life stages and life-stage transitions are described in detail in the second section of this plan; "Factors Affecting Anadromy".

Juvenile Approach

An annual steelhead JPE can be calculated based on the estimated number of age 1+ juveniles rearing in natal tributaries. Here, the JPE calculation follows equation (4):

$$\widehat{JPE}_{i+2} = Pr_{i,1} \times SPr_{i,1} \times PSm_{i,2} \times SO_{i,2} \tag{4}$$

Like the 'Adult Approach', this approach assumes the JPE will be primarily composed of age 2+ outmigrants, and thus we can use age 1+ parr abundance estimates in the current year ($Pr_{i,1}$), produced from brood year *i*, to estimate the JPE one year in advance (JPE_{i+2}). The JPE_{i+3} equals the total number of age 1+ parr ($Pr_{i,1}$) times the survival probability to reach age 2+ ($SPr_{i,1}$), the probability of smolting at age 2+ ($PSm_{i,2}$), and surviving outmigration ($SO_{i,2}$) from the natal tributary. This value yields the expected JPE approximately one year after generating the age 1+ parr estimate. This approach could be modified to similarly use the current abundance of age 0+ parr to predict JPE two years later.

For example, the 2027 steelhead JPE can be calculated by equation 4 using: 1) an age 1+ parr estimate generated from monitoring data collected between the spring and summer of 2026 (e.g., from brood year 2025; Figure 2B), and 2) the probability of surviving to age 2+ (spring/summer 2027), smolting at age 2+ (2027), and surviving outmigration in 2027.

The primary benefit of estimating a steelhead JPE based on age 1+ *O. mykiss* monitoring is that the estimate will have less error and uncertainty associated with it compared to the JPE calculated using the 'Adult Approach'. The reduction in error or uncertainty in the JPE is due to reducing the number of terms in the JPE equation and their associated uncertainty. Using this approach, resource managers would have a more precise JPE estimate available a year in advance to develop a water management strategy, but it will leave less time to respond to years of relatively high or low juvenile steelhead production. There will still likely be substantial error or uncertainty in the JPE produced using this method. Like the 'Adult Approach', the uncertainty will scale with the variability and uncertainty in the survival and outmigration probabilities and underlying age 1+ *O. mykiss* monitoring data used to estimate it. Similar to what is discuss above for the 'Adult Approach', some of this uncertainty may be reduced by linking environmental factors to variation in life-stage transitions (e.g., survival, outmigration).

Stepwise Approach

The previous two approaches to calculating a steelhead JPE are based on monitoring a single *O. mykiss* life stage. Both approaches have tradeoffs associated with the degree of JPE uncertainty and the amount of time resource managers will have to plan water operations and/or respond to years of high and low steelhead production. The relative consequence of this tradeoff can be attenuated with additional monitoring if sufficient resources are available. Specifically, a third 'Stepwise Approach' can be used to calculate an annual steelhead JPE that is initially based on the estimated number of reproductive adults and the estimated number of redds those fish are expected to produce, and subsequently updated using the estimated number of age 1+ juveniles rearing in natal tributaries one year after spawning. Here, the JPE calculation uses equations 3 and 4.

As described above, estimating the JPE so far in advance will require multiplying a sequence of uncertain survival and outmigration probabilities. The results of this approach would provide a JPE with a likely large amount of error or uncertainty around the mean JPE estimate. As such, subsequent monitoring of age 1+ parr will provide an opportunity to update the initial estimate. In addition, it may be possible to estimate the updated JPE in a Bayesian framework using the initial age-1+ parr estimate from the 'Adult Approach' as an informed prior, to be updated by subsequent estimates of age-1+ parr abundance from field surveys.

There are several potential benefits of estimating a steelhead JPE using the 'Stepwise Approach' including: 1) two planning windows to provide managers with more time and information to consider alternative water operations scenarios, 2) the output from the 'Adult Approach' may be used to inform parr abundance estimates at a later date, and 3) this approach creates an opportunity to fully integrate adult and juvenile monitoring data (e.g., Conner et al. 2020) which may provide JPE estimates with greater certainty compared to the 'Adult' or 'Juvenile' approaches alone. In other words, the initial JPE estimate can be produced several years in advance leaving resource managers ample time to develop a water management strategy in response to years of relatively high or low juvenile steelhead production. The updated JPE estimate will provide an opportunity to revise that strategy with a more precise JPE estimate, which is still available a year in advance. Although this approach appears to capture the benefits of the Adult and Juvenile approaches, it will come with an increase in resource costs for multiple life stage *O. mykiss* monitoring.

Surrogate Approach

In instances where the origin or exact numbers of Chinook salmon or steelhead cannot be estimated, uniquely marked hatchery-origin fish can be released at a similar time, location, and size as the natural-origin fish. These hatchery fish can then be used as surrogates to represent take of the ESA-listed natural-origin fish. For example, under the NMFS 2019 BiOp for the CVP and SWP, coded-wire-tags are placed in late-fall run juvenile Chinook salmon to evaluate take of yearling spring-run Chinook salmon, an ESA-listed run, at the water project export facilities in the Delta (NMFS 2019). In the absence of a JPE, hatchery CCV steelhead can be utilized in a similar manner where surrogate fish are released at both Sacramento and San Joaquin basins at the appropriate time and size. The number of tagged adipose-clipped steelhead at the Delta export facilities can then be evaluated from each basin to better understand proportional loss (see Table 2 as an example). This approach will not resolve the challenges of estimating juvenile steelhead loss in context with the population size, and it relies on the assumption that hatchery-origin fish survive at similar rates and behave in similar ways to natural-origin fish. However, it can be a cost-efficient approach for estimating proportional loss at the Delta export facilities on an annual basis. It is also worth noting that this approach may be a necessary step in the formation of JPE due to the low abundance of natural-origin fish, which has led to a common reliance on coded-wire-tagged or acoustically tagged hatchery-origin fish to assess monitoring gear efficiency and migration of other ESA-listed salmonids.

Table 2: Annual loss of clipped juvenile steelhead at the salvage facilities and total hatchery juvenile steelhead release numbers for brood years 2016 to 2022. From 2016 to 2023, average annual % lost to the facilities was 0.160%. Note that release locations and dates, which vary by year, were not considered for this calculation. Hatchery release numbers were acquired from: CDFW hatchery releases- Calfish.org and USFWS hatchery releases data provided by Kevin Offill, 3/13/2024. Water facility loss data acquired from: SacPAS and reflects Water Year 2017 – 2022.

Brood Year	Total Hatchery Steelhead Release Number (Brood Year)	Loss of clipped steelhead at the facilities (Water Year)	% Total Hatchery Number Lost to the Facilities	Water Year
2016	1,019,501	164.29	0.016	2017
2017	811,379	2,462.90	0.304	2018
2018	1,264,939	5,777.70	0.457	2019
2019	1,084,899	659.44	0.061	2020
2020	1,853,751	341.69	0.018	2021
2021	1,676,701	639.79	0.038	2022
2022	1,623,483	3,650.30	0.225	2023

Simulated JPE Example

Here, a simulation of mock data is used to illustrate the how uncertainty may differ between the 'Adult' vs. 'Juvenile' JPE approaches. With the exception to preliminary data on egg to fry survival (Zeug et al. 2024), probabilities of life stage transitions included in each JPE calculation are largely unknown in the Stanislaus River and elsewhere in the California Central Valley. Therefore, a literature search was conducted for surrogate numbers to include in this simulation (Table 3). Information on steelhead residency and survival between age 1+ and age 2+ were not unavailable, so estimates from Atlantic Salmon, which exhibit similarly diverse life-history traits, were used as a surrogate (Cunjak et al. 1998; Table 3). Published mean and standard error or a matrix of numbers were used to obtain the mean and standard deviation estimates for each life-stage transition parameter. These parameters were then used to generate a lognormal distribution of 1000 estimates for each parameter using functions built within R Statistical Software (v4.3.1; R Core Team 2023).

Table 3: Summary of surrogate parameters found in the literature and used in JPE calculations

Parameter	Mean	Stan. Dev.	Source
Fecundity	4,170	1,540	Hodge et al. 2016
Egg to Fry Survival	0.34	0.17	Zeug et al. 2024
Fry to Parr Survival	0.26	0.11	Baxter 1997
Parr to 1+ Survive and Remain	0.33	0.20	Cunjack et al. 1998
1+ to 2+ Survive and Remain	0.34	0.09	Cunjack et al. 1998
2+ to smolt survival	0.13	0.06	Cunjack et al. 1998

In order to estimate a JPE from the fecundity and probability estimates between each life stage, a starting number of 1000 redds was chosen. Using this starting number, 200 simulations were first run to estimate a matrix of juvenile abundance estimates by randomly drawing estimates from the parameter distributions and multiplying redd number by fecundity, egg-to-fry survival, fry-to-parr survival, and parr to age 1+ survival respectively. For the adult approach, each estimate from the juvenile abundance matrix was multiplied by a randomly selected estimate within the parameter distributions for probability of age 1+ to 2+ survival and age 2+ to smolt survival respectively resulting in 200 JPEs. For the juvenile approach, the 200 simulations were run once again where the median of the juvenile abundance matrix was multiplied by a randomly selected estimate within the parameter distributions for probability of age 1+ to 2+ survival and age 2+ to smolt survival respectively resulting in 200 JPEs. Finally, the data was visualized in a box and density plots to illustrate the variation between the two methods using R Statistical Software (v4.3.1; R Core Team 2023; Figure 3).

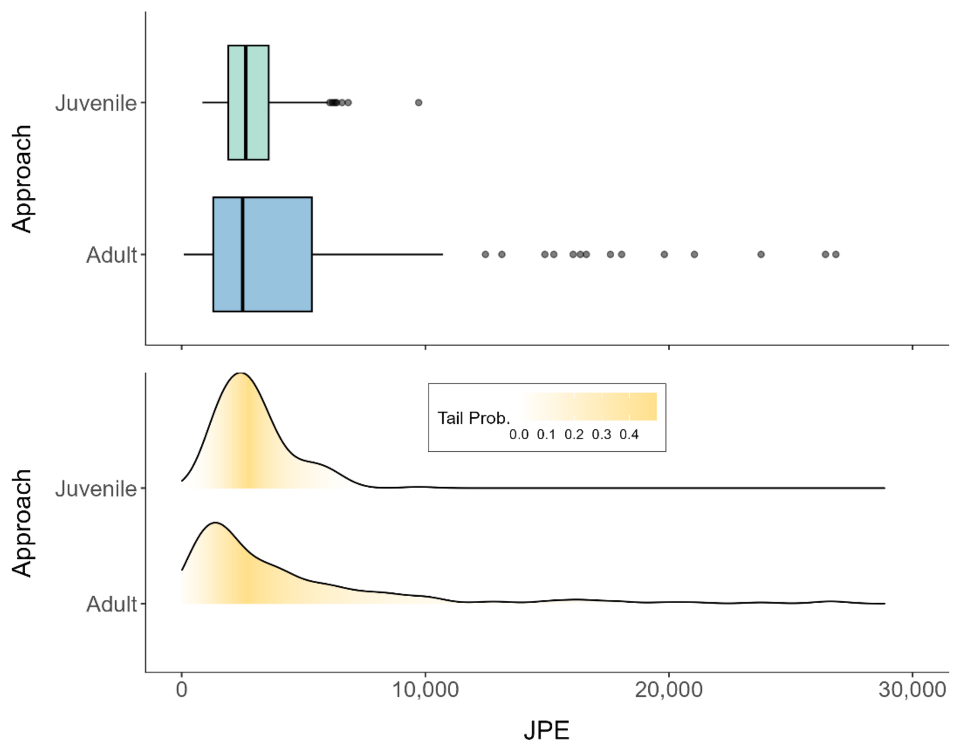

Figure 3: Boxplot (top) and density curve (bottom) summarizing results from 200 simulations of each JPE calculations method.

As expected, there is increased variation in the adult approach compared to the juvenile approach (Figure 3). For the ‘Adult Approach’, estimates ranged from 86 to 26,852 individuals, with 25%, 50%, and 75% quantiles between 1,295, 2,505, and 5,341 individuals respectively. In contrast, estimates from the ‘Juvenile Approach’ approximately ranged from 855 and 9,729 individuals, with 25%, 50%, and 75% quantiles between 1,912, 2,630, and 2,939 individuals respectively.

Accounting of Steelhead Loss

Historically, CVP and SWP loss limits of natural origin CCV Steelhead have been designed to protect populations with unique traits. For example, the NMFS 2019 BiOp on continued operation of the CVP and SWP (NMFS 2019) split steelhead loss limits between two time periods (i.e., December-March and April 1-June 15) to protect San Joaquin origin fish that are hypothesized to outmigrate later in the year compared to Sacramento origin fish. Although this hypothesis has not been formally tested, it is certainly possible that steelhead outmigration timing, and other traits, do indeed differ across populations in Central Valley watersheds. As such, it may be necessary to track the natal origin of fish that are observed at CVP and SWP facilities if regulatory agencies want to apply population-specific protections (e.g., Sacramento and San Joaquin basin populations).

Reclamation executed an Interagency Agreement with the National Marine Fisheries Service in 2023 focused on genetic monitoring of wild-origin juvenile steelhead collected at state and federal salvage facilities. The primary goals of this agreement are to: 1) improve the genetic baseline to enable stock (i.e., population) identification and natal origin of Sacramento and San Joaquin basin steelhead, 2) analyze archived genetic samples of steelhead collected at CVP and SWP facilities and quantify the proportion of fish assigned to Sacramento and San Joaquin basins and their tributaries, 3) evaluate differences in timing of sample collection between Sacramento and San Joaquin origin steelhead and associate differences with targeted adaptive genomic variants, and 4) analyze genetic samples of steelhead collected at CVP and SWP facilities in water years 2024-2026, which should provide annual data/estimates of steelhead abundance originating from the Sacramento and San Joaquin basins and possibly their tributaries.

The primary approach of the monitoring under the Interagency Agreement will be to conduct a genetic analysis to assess the potential for using genetic stock identification to assign *O. mykiss* entrained by the Delta salvage facilities to Diversity Groups, or more generally to Sacramento basin and San Joaquin basin ‘reporting groups’. All analyses will use probabilistic assignments of estimated stock proportions to Diversity Group (Reporting Group) and will assess the accuracy of individual assignment to specific populations. In addition, microhaplotype markers will be genotyped to target known adaptive genetic variants associated with important migratory life-history variation in *O. mykiss* (e.g., Omy05, Greb1L, Six6: Le Gall et al. 2023; Goetz et al. 2024; Pearse et al. 2019; Waples et al. 2022; Waters et al. 2021). Results will illustrate the potential for genotyping to inform weekly water export management based on results across years.

JPE Framework Implementation

Reclamation proposes to develop a steelhead JPE for tributaries with CVP facilities that will focus on the annual production of outmigrating juvenile steelhead. Data used in the JPE will inform the status and trends of Sacramento and San Joaquin basin steelhead and may also help inform actions that will increase steelhead abundance and improve steelhead survival through the Delta. Reclamation and CDWR, in coordination with USFWS, NMFS, and California Department of Fish and Wildlife (CDFW), will create or use an existing technical team to use the Southern Sierra Nevada Diversity Group Steelhead Science Plan, which describes the JPE framework, to identify infrastructure and monitoring needs in tributaries with CVP or SWP facilities and a method for expanding the JPE framework from the tributary to basin levels.

Reclamation and CDWR propose to conduct the first four-year independent panel review (2024) from data generated from the Stanislaus River steelhead life cycle monitoring program (Table 4). Reclamation and CDWR anticipate the independent panel will provide feedback on the scientific merits of the JPE framework and recommendations for improving the JPE framework. Reclamation and CDWR will work with a new or existing technical team to incorporate review panel feedback and recommendations on the JPE framework, as appropriate.

Beginning Fall 2025 and based upon incorporated 2024 review panel feedback and recommendations, Reclamation and CDWR will work with the technical team to consider implementing an expanded JPE framework to the San Joaquin and Sacramento basins. By summer 2026, Reclamation and CDWR will decide to address deficiencies in the JPE framework and/or expand the JPE framework to remaining CVP or SWP tributaries.

Reclamation and CDWR propose to conduct the second four-year independent panel review (2028) from data generated from the San Joaquin and Sacramento basins JPE. Reclamation and CDWR anticipate the independent panel will provide further feedback on the scientific merits of the JPE framework and further recommendations for improving the JPE framework. Reclamation and CDWR will work with the technical team to incorporate review panel feedback and recommendations on the JPE framework, as appropriate.

Table 4: Stanislaus life cycle monitoring, focal parameters, methods, and organization lead.

Input	Description	Methods	Contributing Organizations	Monitoring Years
Rd	Redd number & spawner number	Spawner Surveys Weir Passage Close-kin mark-recapture	CDFW FISHBIO Cramer Fish Sciences	2020 – Present
Fe	Fecundity	Weir Passage VAKI River Watcher Hook-and-line sampling	FISHBIO	2021 – Present
SEg	Egg to fry survival	Egg-basket study	Cramer Fish Sciences	2021, 2022
Fr	Fry production	Seining Electrofishing	Cramer Fish Sciences	2020 - Present
SFr	Fry to parr survival	PIT tag mark recapture Close-kin mark recapture	Cramer Fish Sciences	2020 - Present
Pr	Parr produced	Seining Electrofishing Hook-and-line fishing PIT tag mark recapture Close-kin mark recapture	Cramer Fish Sciences	2020 - Present
SPr	Parr survival probability	PIT tag mark recapture Close-kin mark recapture	Cramer Fish Sciences	2020 - Present
PSm	Probability of smolting	PIT tag stationary antenna Acoustic tagging and tracking	Cramer Fish Sciences NMFS/UCSC/USFWS	2020 – Present 2022 - Present
O	Outmigrants produced	Rotary Screw Traps PIT tag stationary antenna Acoustic tagging and tracking	FISHBIO/PSMFC Cramer Fish Sciences NMFS/UCSC/USFWS	1998 - Present 2020 – Present 2022 - Present
SO	Outmigration survival	PIT tag stationary antenna Acoustic tagging and tracking	Cramer Fish Sciences NMFS/UCSC/USFWS	2020 – Present 2022 - Present

Value of Information

This plan will allow for an iterative evaluation process of the monitoring tools and assessment metrics needed to assess *O. mykiss* and create opportunities to: 1) engage decision makers to reassess management goals and priorities, 2) reassess and update current steelhead biology conceptual models and hypotheses, 3) reassess core monitoring needs and special studies, 4) identify persistent or new knowledge gaps, and 5) identify and adopt new technologies and techniques in the suite of monitoring tools and assessment metrics described below. The monitoring tools and assessment metrics identified in this plan are based on tradeoffs in monitoring needs relative to management goals and priorities (e.g., 2019 Biological Opinion or ESA recovery) and *O. mykiss* biology (e.g., annual recruitment or life-history evolution). New monitoring alternatives may emerge through periodic review of management goals and priorities, improved understanding of *O. mykiss* biology, revised monitoring needs and new directed research based on persistent or new knowledge gaps, and the development and integration of new technology and techniques.

Monitoring alone does not lead to better conservation or management outcomes. Effective monitoring involves the assessment of management actions and adjustment to these actions or decisions as new information becomes available. However, status and trends (i.e., foundational) monitoring are not likely to provide all the necessary information to understand every linkage between management decisions and the viable salmonid population (VSP) parameters (see Conceptual Models). Special studies tackling specific hypotheses as we outlined below may be required to address the uncertainties regarding the JPE. We recommend the use of structured decision-making process and decision tools, such as Value of Information analysis, to provide quantitative values for new studies (Canessa et al. 2015). As any new study will come at a cost, the benefit of reducing uncertainty would need to be considered against this cost and the management decision that uncertainty is affecting. Under this framework, there is no benefit to investing in monitoring and research if the results won't influence management decisions. At its core, Value of Information analysis involves a quantitative assessment of the current state of knowledge, the quality of information to be collected with the new study, and the management outcomes we expect to change as a result of what is learned from monitoring and research.

Factors Affecting Anadromy

Historical and Contemporary *O. mykiss* monitoring

Several efforts to characterize historical and ongoing *O. mykiss* monitoring programs in the CCV have been completed over the last two decades. Eilers (2010) identified a suite of monitoring programs generating data on *O. mykiss*, but determined that monitoring was not standardized, often designed for Chinook salmon (*Oncorhynchus tshawytscha*) populations, and inadequate for assessing population viability (Lindley et al. 2007). Specifically, a total 63 *O. mykiss* monitoring programs were identified during the review, but only eight projects were reported to monitor *O. mykiss* with meaningful confidence, and none could generate abundance or production estimates for juvenile *O. mykiss*. As a result, the Central Valley Steelhead (*O. mykiss*) Monitoring Plan was developed to identify actions needed to provide population data for the assessment of steelhead recovery (Eilers et al. 2010).

A few years after the completion of the Central Valley Steelhead Monitoring Plan, a series of related monitoring projects, identified as the Central Valley Steelhead Monitoring Program (CVSMP), were initiated on the Sacramento River and its tributaries (Fortier et al. 2014). These projects include the mainstem Sacramento River mark-recapture project, Sacramento River tributary mark-recapture monitoring, upper Sacramento River tributary escapement monitoring, and hatchery broodstock and angler harvest sampling. In addition, some population monitoring projects in priority streams outside of the CVSMP were expanded to encompass the entire *O. mykiss* immigration and spawning period.

In the fall of 2020, a group of state and federal scientists initiated a follow-up review from Eilers 2010 (Beakes et al. 2021). This effort enabled the team to characterize new and existing *O. mykiss* monitoring in Sacramento and San Joaquin tributaries, including data compilation from Central Valley hatchery programs. The majority of the new research and monitoring effort stems from the initiatives outlined in the CVSMP in addition to several programs that have been implemented or planned in the Calaveras and Stanislaus rivers. A compilation of past and recent CCV *O. mykiss* monitoring efforts organized by the National Oceanic Atmospheric Administration (NOAA) Diversity Group and regions for the mainstem Sacramento River is described in Appendix A of Beakes et al. (2021).

Program Integration

Some existing Central Valley salmonid monitoring programs within or near the Southern Sierra Nevada Diversity Stratum may integrate well with this science plan. For example, the CVSMP program utilizes a variety of methods including large wire fyke traps, rotary screw traps (RST), Passive Integrated Transponder (PIT) tag arrays, acoustic telemetry monitoring, resistance board weirs, and hook-and-line sampling with the goal of establishing Sacramento River basin-wide adult abundance estimates for wild and hatchery origin *O. mykiss* (Fortier et al. 2014). However, full implementation of the science plan will include expansion into the San Joaquin River. By leveraging the existing tools and infrastructure, including PIT tag and acoustic telemetry arrays, the exchange of information across geographic areas will improve our understanding of *O. mykiss* survival and behavior. It may also be possible to incorporate some monitoring efforts from the San Joaquin River Restoration Program (SJRRP), as pilot scale PIT array and acoustic telemetry projects for juvenile Chinook salmon have already been performed as part of the SJRRP (SJRRP 2013). Other existing programs that may integrate with the science plan include the Delta Juvenile Fish Monitoring Program (DJFMP), which monitors the annual timing, distribution, and relative abundance of juvenile salmonids in the lower Sacramento and San Joaquin rivers, Delta, and San Francisco Bay (McKenzie 2019).

Knowledge Gaps

As stated in the 2021 NOAA Fisheries' Southwest Fisheries Science Center Viability Report, one of the greatest challenges in managing for resilient steelhead populations in our regulated rivers lies in understanding how water management and related changes to habitats and ecosystems promote, maintain, or suppress the expression and survival of the anadromous life history form of *O. mykiss*. It is clear that some river habitats support almost exclusively resident populations, while others support the expression of anadromy (Satterthwaite et al. 2010). In the San Joaquin River tributaries specifically, there is great uncertainty in the extent to which the production of anadromous juveniles from tributaries is low and/or whether mortality of juvenile steelhead is so high during outmigration that it is selecting against anadromy and driving populations towards residency. Recent work has increased our understanding of the genetic basis and maintenance of anadromy in *O. mykiss* populations, which warrants consideration in managing for the anadromous life history for the species (Pearse et al. 2019). More studies are needed to understand the extent to which genes associated with the heritable components of anadromy could be lost from populations with low steelhead numbers, thus placing them at a greater risk of extinction (NMFS 2014; Ellrott et al. 2021).

2021 Steelhead Workshop

Participants in the "Monitoring steelhead populations in the San Joaquin Basin" workshop, held in February 2021 specified knowledge gaps associated with management challenges, a monitoring framework and analytical approaches in three breakout discussion sessions. For example, in the management challenges breakout discussion sessions, participants felt that management needs and potential decisions must be made clear in order to appropriately tailor sampling methods, and to understand what level of "messy-ness" in the data is acceptable. Further, there were logistical difficulties emphasized; there is a need to address how monitoring programs can gain access to private land, design permits for both anadromous and resident *O. mykiss*, approach small populations, and manage the mismatch in timelines between when data is collected and when it is needed to evaluate risk. The need for consistency and coordination was seen as relevant to both addressing management needs and in designing a monitoring framework. In addition to basin-wide coordination and standardization in a monitoring framework, workshop participants spotlighted the need for the development of a life cycle model and a centralized data repository with access to historical data, as well as more information on age structure, adult abundance, juvenile outmigration, the resident contribution to the anadromous spawner population, limiting environmental factors (e.g., mortality bottlenecks and thermal tolerance), and efficiency estimates able to translate catch to abundance.

The workshop participant’s perspective on knowledge gaps associated with analytical approaches called for:

- the establishment of benchmarks and clear goals that incorporate governance structure, funding, decision makers and legal authority (e.g., communication tools, interagency partnerships, clearly defined production and risk to CVP/SWP thresholds in recovery plans, and an adaptive framework with achievable and focused questions),
- a synthesis of our current understanding of status and trends in adult spawning populations, juvenile production, and rates of anadromy
- the reduction of uncertainties through hypothesis development and conceptual models,
- enhancement of current monitoring, and
- data prioritization criteria.

Specific uncertainties included: adult spawning population abundance, drivers of anadromy, juvenile production in NMFS’ core watersheds (e.g., outmigration population and smolt survival thresholds), the spatial distribution of juveniles and effort estimates. Recommended enhancements to the current monitoring framework involved monitoring on the Merced and Tuolumne Rivers (e.g., Core 1 & 2 populations), monitoring that evaluates restoration and Federal Energy Regulatory Commission (FERC) relicensing, enhancements to the Mossdale trawl, the addition of mark-recapture studies, estimates associated with ocean conditions and predation, coordination between *O. mykiss* and spring-run Chinook salmon monitoring programs, the coordinated collection of temporally balanced genetics, scale and otolith samples for life history studies and the integration of emerging technologies (e.g., eDNA, Vaki cameras, acoustic telemetry, and Passive Integrated Transponder tags).

Prioritization criteria for San Joaquin basin *O. mykiss* data incorporated the use of model sensitivity to determine data needs (e.g., delineate biological understanding and regulatory value), evaluating the feasibility and constraints of determining abundance at key locations and life stages, quantifying diversity over space and time, assessing how best to leverage multiple datasets (e.g., otoliths and scales) and exploring the use of legal mandates to set priorities (FERC relicensing vs. Core 1 & 2). For more detail see Goertler et al. 2021.

O. mykiss Life Cycle and Conceptual Models

Conceptual models (CMs) were developed to inform a monitoring and research program to support development of a steelhead JPE and improve our understanding of factors affecting anadromy. Consideration of the VSP parameters is included in the CMs below by representing the *O. mykiss* life cycle with probable application to a variety of management priorities, research opportunities and recovery goals that are important to those managing *O. mykiss* throughout the California Central Valley. The CMs also address needs identified by the “Monitoring steelhead populations in the San Joaquin Basin” workshop, held in February 2021 (e.g., a reduction of uncertainties through hypothesis development and conceptual models).

The CMs developed for this science plan are structured similar to CMs developed for the Interagency Ecological Program Delta Smelt Management, Analysis, and Synthesis Team (IEP MAST 2015, Baxter et al. 2015) and Salmon and Sturgeon Analysis of Indicators by Life stage or SAIL (Windell et al. 2017). Like SAIL, the goal was to develop CMs in a consistent and familiar way to facilitate communication and use in California Central Valley watershed science and decision making (IEP MAST 2015, Windell et al. 2017). The *O. mykiss* life cycle is divided into six CMs by life stage and an additional CM describing life history expression for the resident/migratory strategies (Figure 4). Each CM represents a life stage that can be monitored to develop parameters necessary to support JPE development and estimation. Transitions between and within life stages, when stages may last multiple years, are represented by demographic rates (survival, life history expression, etc.) and can also be monitored to evaluate mechanisms influencing life stage abundances. Similar to the Management, Analysis, and Synthesis Team (MAST) and SAIL CMs, CMs represent each life stage, where arrows link key processes, management actions or metrics to VSP outcomes through effects pathways across different 'tiers' of organization. Hypotheses for linkages within tier three are denoted by 'H' and subscript hypothesis numbers. Similar to SAIL, 'H' number does not denote priority nor does arrow color imply significance nor direction (positive or negative).

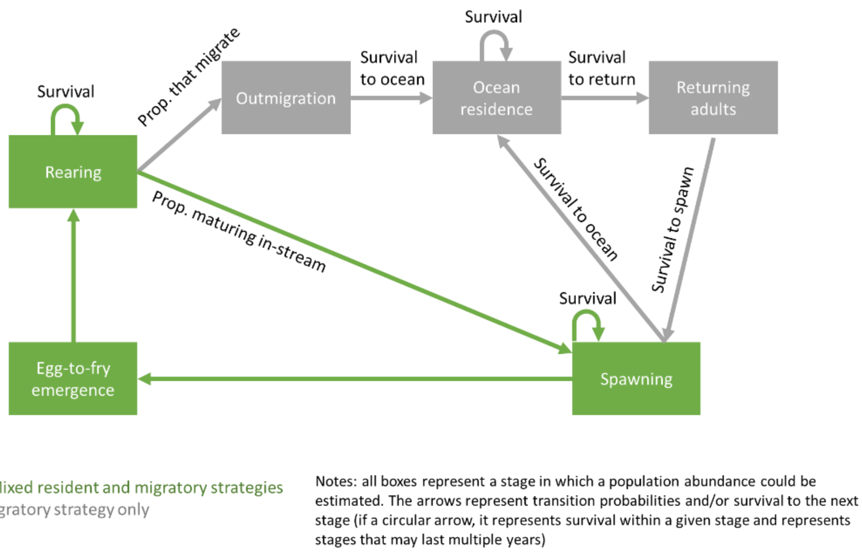

Figure 4: Depiction of the O. mykiss life cycle by life stage domains developed into conceptual models. All boxes represent a stage for which monitoring and directed studies can be implemented to develop parameters necessary to support JPE development and estimation. The arrows represent transition rates (e.g., survival, life history expression) to the next stage. Stages that may last multiple years include a circular arrow, which represents survival within that stage. The conceptual model for life history expression was omitted in the figure (Figure 4) but is represented by the transition of juvenile rearing to either smolt outmigration (migratory strategy) or spawning adults (resident strategy).

Life Stages. The steelhead monitoring plan CMs focus on the following life stages:

- Spawning
- Egg-to-fry emergence
- Rearing

- Life-history expression
- Outmigration
- Ocean residence
- Returning adults

Geographic Scope. Unlike the MAST and SAIL CMs, these CMs are generalized to ensure they are applicable across tributaries within the Southern Sierra Nevada Diversity Group and San Francisco Bay-Delta (Fig 1).

Hierarchical Tiers. Each CM includes the following four tiers. The organizational 'tiers' within the CMs described below differ from those in MAST and SAIL. Tiers range from large-scale ecosystem processes and system states (tier 4), that are largely out of anthropogenic control, to desired population responses in the form of NMFS VSP criteria (tier 1). In between are tiers encompassing a management focus (tier 3) and ecological or biological states (tier 2) that have Specific, Measurable, Achievable, Relevant and Time-Bound metrics (SMART). Thus, the CMs are shaped like 'hourglasses', where concepts are broad on each end with increasing nuance and complexity towards the center.

- **Tier 1 - Large-Scale Processes.** Ecosystem processes and system states such as regional climate, and the underlying geomorphology of the California Central Valley that can have profound impacts on ecosystem dynamics and our ability to manage natural resources.
- **Tier 2 - Management Actions.** Management actions primarily related to hatchery operations, habitat restoration, water operations, and fishing regulation that can influence *O. mykiss* in a significant manner.
- **Tier 3 - SMART Metrics.** Measurable ecosystem and biological characteristics that are hypothesized to impact key *O. mykiss* life stages and life-stage transitions.
- **Tier 4 - Population Response.** NMFS VSP criteria

Factors in Tiers 1 and 2 do not represent every possible environmental or management factor that impacts *O. mykiss*, as CMs are a simplified depictions of complex issues. Further there are four assumptions concerning factors within Tiers 1 and 2, which span all CMs, described in greater detail below.

- Climate controls weather, which has a direct impact on reservoir (e.g., storage and water temperature) and in-river conditions (e.g., flow, turbidity, temperature).
- Contaminants are both naturally and anthropogenically occurring and have accumulated through decades of anthropogenic disturbance (e.g., gold mining, agriculture development). These contaminants can impact in-river conditions that subsequently impact habitat quality and quantity.
- Geologic history and the resulting topography set the physical template that controls how water flows over the California landscape. Further, the geomorphic template controls the potential for what habitat a system can provide. In other words, we realistically lack the capacity to transform the fundamentally characteristics of river systems (e.g., low gradient rivers, to headwaters).

- River discharge and water quality are directly impacted by both water operations and in-river conditions. We assume river discharge, water quality, and habitat restoration actions directly affect habitat quality and quantity.

Spawning

Biology of Life Stage. Spawning and rearing habitat for steelhead is usually characterized as perennial streams with clear, cool to cold, fast flowing water with a high dissolved oxygen content and abundant gravels and riffles. Steelhead use various mixtures of sand-gravel and gravel-cobble substrate for spawning, but optimal spawning substrate reportedly ranges from 6.4 to 101.6 mm in diameter (Reiser and Bjornn 1979). Optimal conditions for steelhead spawning reportedly occur at water temperatures 11°C (Reiser and Bjornn 1979; SWRCB 2003). Steelhead spawning generally occurs from December through April, with peaks from January through March, in small streams and tributaries (NMFS 2009).

Unlike salmon, trout can survive the rigors of spawning and spawn again, a life history pattern termed iteroparity (as in iterative reproduction; Quinn 2005). Steelhead fecundity is high, averaging 4,923 eggs per female compared to 1,648 to 3,654 eggs for smaller-sized salmon (pink, chum and sockeye salmon; Table 15-1 in Quinn 2005). Iteroparity is thought to confer productivity benefits to the population due to the high fecundity. Adult steelhead that attempt to spawn again are termed kelts. These fish migrate to the ocean as adults, feed and rebuild their energy stores, and undertake a second (or third) spawning migration into freshwater and their natal stream to spawn. Literature suggests that repeat spawning is more common in females than males (Quinn 2005). However, scale ageing and analysis work conducted on natural and hatchery origin steelhead scales collected from Central Valley hatcheries suggest that iteroparity is more common in males than females (CDFW Central Valley Tissue Archive, unpublished data). Regardless, Moyle (2002) indicated it is rare for steelhead in California to spawn more than twice before dying.

Hypotheses of factors impacting spawning adult *O. mykiss*

H_1: Life-history mixing
H_2: Age and size structure
H_3: Return timing
H_4: Habitat quality and quantity
H_5: Competition
H_6: Survival

Kendall et al. (2015) found that anadromy and residency reflect interactions among genetics, individual condition, and environmental influences throughout various life stages. Various aspects of spawning habitat can therefore drive life history expression and mixing (**H_1**; Figure 5), which would in turn affect the diversity, abundance, productivity, and spatial structure of a population. There is some indication that residency is more common under conditions of cool, dependable flows during summer, such as conditions found in reaches downstream of large storage reservoirs (Cramer and Beamesderfer 2006, Satterthwaite et al. 2010) (**H_1**, **H_8**; Figure 5). Resident females also prefer smaller spawning substrate than their anadromous counterparts. Meanwhile, anadromous *O. mykiss* is more common in warmer streams, streams that have more variability in flow, and with deeper channels (Kendall et al. 2015). Competition for food and space can reduce growth and survival of individuals in a population. Increased competition thus has been hypothesized to drive higher rates of anadromy in a population (Kendall et al. 2015) (**H_1**, **H_5**; Figure 5). However, density in a population may also be simply reflecting the life history expressed by fish in said population.

Hatchery operations are prevalent throughout California, including within the Southern Sierra Nevada Diversity Group geographic boundaries. Hatcheries can have various significant impacts on *O. mykiss* populations, including the interactions between the two life history types. Hatchery fish are generally associated with higher straying rates and release locations outside of natal streams have been shown to further increase straying (Westley et al. 2013; **H_1** and **H_2**; Figure 5). Unlike wild steelhead, hatchery *O. mykiss* are also often reared on an accelerated growth regime and/or unintentionally select for a particular life history trait (McLean et al. 2005, Tatara et al. 2019), resulting in changes to age and size structure of the species (**H_2**; Figure 5). Because anadromous and resident life history types are partially determined by genetics, hatcheries can also influence life history mixing through stock selection. For example, it has been posited that above-barrier populations may have been subject to strong selection against anadromy (Lindley et al. 2006). Large releases of rapidly grown hatchery fish can also create competitive imbalances between natural and hatchery stocks. Downstream releases of hatchery fish can artificially increase the survival of hatchery fish into adulthood, leading to higher competition in spawning grounds (Sturrock et al. 2019; **H_3**, Figure 5). However, the presence of hatchery fish may help sustain *O. mykiss* populations during periods of low recruitment, though possibly at the cost of masking declines in natural stocks (Johnson et al. 2012).

Water diversions and discharge can also have a sizable influence on the return timing and habitat of spawning *O. mykiss*. Depending on the magnitude, water diversions can affect route selection of returning adults, their stray rates, and in effect, the timing of their arrival to spawning habitat (**H_3**; Figure 5). Suboptimal return time for spawning *O. mykiss* can reduce the abundance and productivity of the population. The return and reproductive timing of fish would also help determine their post-spawning survival (**H_3**, **H_6**, Figure 5). Depending on conditions in a year, early- or late-spawners may be more or less reproductively successful and/or survive spawning. Meanwhile, flow has been shown to generally affect the upstream migration of salmon (Keefer et al. 2008) and appears to also influence migration timing of steelhead in the Columbia River system (Robards and Quinn 2002). It is likely that timing and amount of discharge in San Joaquin tributaries would also affect the upstream migration and therefore return timing of steelhead in the Southern Sierra Nevada Diversity Group (**H_3**, Figure 5). Water releases from reservoirs upstream would also determine when and how much spawning habitat will be available for adult *O. mykiss*, as low flow conditions can lead to dewatering of potential redds (**H_4**, Figure 5).

In addition to flow, spawning habitat is also determined by in-river water quality. Water temperature and dissolved oxygen level can highly influence survival and success of spawning *O. mykiss* (**H_4**, **H_6**, Figure 5). High water temperature can increase spawning adult fish susceptibility to diseases and truncate the spawning temperature window each year. Meanwhile, low dissolved oxygen levels can reduce fitness in spawning adults and may even lead to fish kills when levels are exceedingly low. The constructions of dams have also led to the disruption of gravel supply important for *O. mykiss* spawning. Restoration or augmentation of suitable gravels for spawning habitat should lead to higher productivity given that other needs are met (temperature, depth, etc.). Habitat quality and quantity also influences the availability of food resources (both quantity and quality), which influences the somatic growth and survival of adults, especially the resident form of *O. mykiss*. Additionally, restoration of access to above dam habitat increases the carrying capacity of a tributary, which can reduce overall competition, especially during years of high productivity. Because spawning habitat is finite, increased intraspecific competition for limited resources (food, territory/space, spawning opportunities) would likely lead to reduced abundance and productivity ($\mathbf{H_4}$, $\mathbf{H_5}$, $\mathbf{H_6}$; Figure 5).

Lastly, the survival of *O. mykiss* before and after spawning within the spawning grounds ($\mathbf{H_6}$; Figure 5) is directly affected by the level of in-river recreational fisheries. Impact of recreational fisheries is managed through regulations, which often come in the forms of fish size limits for harvest, seasonal closures, gear type restrictions, and/or daily maximum for number of fish kept per angler. In California's Central Valley, harvest of *O. mykiss* is currently restricted to hatchery-origin fish that are identified by a missing adipose fin, which suggests that harvest impact may be relatively low.

The proportion of kelts that migrate downstream after spawning can be high at many locations. For example, 44 to 55% of wild- and hatchery-origin steelhead pre-spawners in a stream in eastern Washington were re-captured as kelts at weirs upon their outmigration following spawning (Mayer et al. 2008). The age and size of fish likely play a substantial role in determining survival probability to kelt ($\mathbf{H_2}$, $\mathbf{H_6}$; Figure 5), and this relationship may vary depending on environmental conditions. Despite the relatively high proportion of kelts that migrate downstream post-spawning, the number of kelts that survive to return and spawn again is typically low and varies across populations (Narum et al. 2008). The reason for the low survival is the energetic cost for fish of migrating upstream, spawning, and migrating downstream after spawning. Penney and Moffitt (2014a, 2014b) found that between early freshwater entry and post-spawning (kelt) emigration, the lipid content of white muscle was reduced by 94% to levels less than 1% of wet tissue weight.

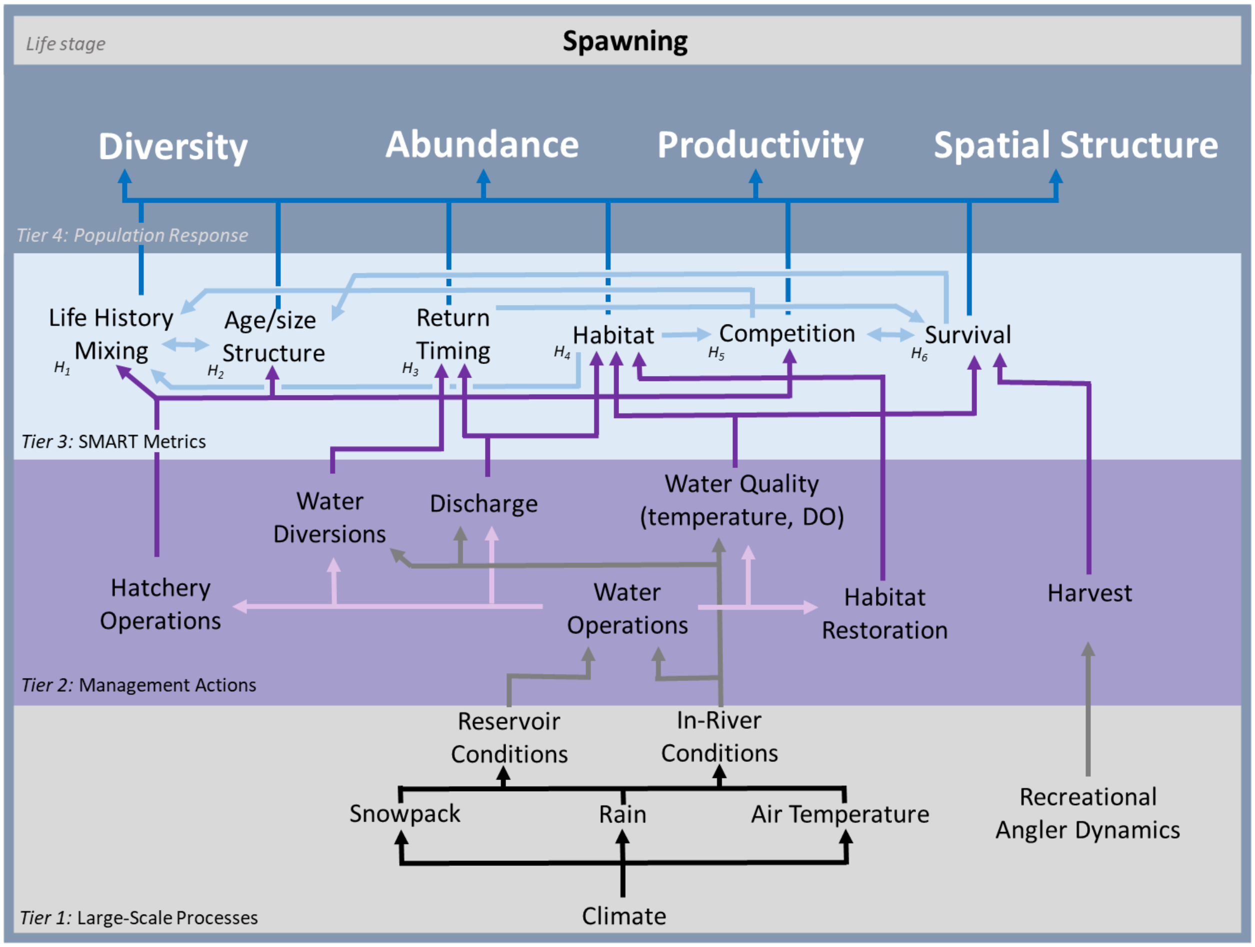

Figure 5: Spawning conceptual model describing reproduction from spawning anadromous and resident O. mykiss.

Monitoring and Special Study Considerations

For the goal of producing a steelhead JPE, assessing the number of spawning *O. mykiss* may not be necessary if fry and smolt counts are sufficiently accurate (Figure 2A, B; "Juvenile Approach"). However, a more comprehensive monitoring of all life stages and life history types of *O. mykiss* can help identify factors or events that limit population growth, their potential causes, and potential recovery actions. Knowing the life stage(s) that is limiting the abundance of steelhead within the Southern Sierra Nevada Diversity Group would be needed to develop the proper management actions to boost population numbers (see Figure 5, Tier 2). Population-level metrics relevant for the spawning life stage of *O. mykiss* include life history mixing (**H_1**), age or size structure (**H_2**), timing (**H_3**), habitat (**H_4**), competition (**H_5**), and survival (**H_6**).

Within the JPE framework, the goal of monitoring for the spawning adult life stage is to understand whether spawner abundance is limiting juvenile production and if so, why and how can it be resolved. Number of redds will be positively correlated to the number of eggs deposited for each year (Figure 2A, B; Table 1, Rd), and egg-to-fry survival may display density dependence due to superimposition during years with high spawner density and low habitat availability (H_4, H_5; Figure 5). Spawner abundance or redd information can also be used to estimate other metrics related to the JPE such as egg production, and as a way to "forecast" fry numbers given available historical data (e.g., egg to fry survival estimates). For example, due to the difficulty of monitoring eggs directly in the field, spawner numbers have been used to indirectly estimate the number of eggs present in the river for other winter-run Chinook Salmon (Voss and Poytress 2020). Note that while this section of the monitoring methods will focus on the period after which *O. mykiss* has conducted their spawning migration into the tributaries. Therefore, we focus on surveys within the spawning grounds of *O. mykiss* during the spawning period. For the counting of adult female steelhead returning into the spawning ground (which can be used in place of redd production estimate under our JPE framework), see the *Returning Adults* section.

Status and trend monitoring

Within the spawning ground, redd surveys are typically the primary method in which spawning adult numbers or redd production is estimated. Depending on stream size, redd surveys can be done by foot or by boat. Redds, identified by clear "tail-spill" resulting from excavated materials as fish construct their nest, are recorded and often uniquely marked electronically or with a flag. Redd surveys are a non-invasive sampling method that can characterize the spatial extent and timing of spawning fairly well depending on the sampling frequency and size of the tributary. Differentiating resident and anadromous *O. mykiss* redds can be challenging, so morphometrics or characteristics of redds (e.g., size, substrate) can be used to predict the size of the spawning *O. mykiss* and therefore estimate the number of eggs produced. However, there are a couple of drawbacks associated with redd surveys that may need addressing through refinement of sampling protocol or additional studies. One, it may be difficult to distinguish *O. mykiss* redds when Chinook Salmon are present in the tributary and overlap in time and space. Another is that it can also be difficult to differentiate between redd produced by a resident *O. mykiss* vs. an anadromous one (Eschenroeder et al. 2022). Redd surveys also do not involve direct capture of fish, and as such, no tagging or collection of tissue for other studies (scales, genetic sampling) can be done. Environmental conditions such as high flow and high turbidity can also pose challenges to field crew and result in incomplete information. Currently, redd surveys occur on three San Joaquin Basin tributary streams, the Calaveras, Mokelumne, and Tuoloumne rivers (Beakes et al. 2021, Appendix A). Expansion of redd surveys to cover each of the San Joaquin Basin streams, including the mainstem river is recommended.

To supplement redd surveys, spawner surveys from a boat or snorkel survey can also be conducted to estimate the number of spawning *O. mykiss*. Information gathered from this additional visual survey can be used to identify whether redds are associated with anadromous or resident fish or to better ensure accurate species identification when other salmonids are present. If collected in combination with redd morphometric data, one can potentially use the information to produce discriminant analysis which can probabilistically assign a redd to either species or life history type. Currently, snorkel surveys occur on four San Joaquin Basin tributary streams, the Calaveras, Stanislaus, Merced, and Tuoloumne rivers (Beakes et al. 2021, Appendix A). Continuation and expansion (if necessary) of visual surveys at the spawning adult life stage in the San Joaquin Basin is recommended.

For tributaries in which carcass survey is conducted for Chinook salmon, *O. mykiss* carcass information can be recorded and sampled opportunistically (e.g., otolith, fin clip, retrieval of tags). Other than the Stanislaus River, San Joaquin Basin tributaries do not currently have carcass surveys conducted on them for *O. mykiss* (Beakes et al. 2021, Appendix A). The implementation of carcass surveys on these rivers would improve the understanding of *O. mykiss* life histories across the San Joaquin Basin, as well as provide the opportunity to collect biological samples from the spawning adult population.

Because of limited resources and river configurations that make certain monitoring challenging, one should consider which tributary within the Southern Sierra Nevada Diversity Group area this information is crucial for, and what spatiotemporal scope and frequency are suitable. Just as with any other life stage, it is also important to concurrently collect information on physical and biological drivers that may affect spawning *O. mykiss* (e.g., temperature, diseases, etc.), especially those that can be affected by management actions (see conceptual model, Figure 5).

Special studies

With visual surveys such as redd and snorkel surveys, care must be taken to ensure that the spatial extent and frequency of sampling are appropriate for the tributary. If deemed necessary, a special study can be done prior to the establishment of a new survey to better understand the most cost-efficient and effective sampling grid and frequency. Once data has been collected over a relatively long period of time, it would also be prudent to assess whether the number of redds observed is highly influenced by survey frequency, as that may indicate insufficient sampling frequency.

To better understand whether spawner abundance is limiting juvenile production, it is also important to address pre-spawning mortality of *O. mykiss* within a tributary. Given that *O. mykiss* is within the southernmost limit of its range in the California Central Valley and global temperature is rising due to climate change, it may be worthwhile to conduct studies to evaluate the aerobic scope and temperature limitations of spawning *O. mykiss*. A study to understand the fecundity of adult *O. mykiss* (Table 1, Fe) by age, length, life history type, or other factors may also be worth pursuing, as it can provide expectation of egg production in a tributary at a given year based on redd numbers (Table 1, E as a product of Rd and Fe). An assessment of age structure for each population may also provide insight into the long-term viability of the Southern Sierra Nevada Diversity Group of *O. mykiss*. Lastly, because proportion of kelts that migrate downstream post-spawning varies across populations and could play an important role in the *O. mykiss* population dynamics in the Southern Sierra Nevada Diversity Group, a special study can potentially be pursued to determine the frequency and drivers of kelts (e.g., using otolith or mark-recapture).

Egg-to-Fry Emergence

Biology of Life Stage. Steelhead spawning generally occurs from December through April, with peaks from January through March, in small streams and tributaries (NMFS 2009). In general, each female steelhead can produce thousands of eggs per spawn, with eggs deposited into gravel nests called redds. Eggs usually hatch within four weeks, depending on stream temperature, and the yolk sac fry remain in the gravel after hatching for another four to six weeks (Eggs usually hatch within four weeks, depending on stream temperature, and the yolk sac fry remain in the gravel after hatching for another four to six weeks (CDFG 1996). Optimal conditions for steelhead spawning and embryo incubation reportedly occur at water temperatures near 11°C (Myrick and Cech 2001; Moyle 2002; SWRCB 2003).

Hypotheses of factors impacting egg-to-fry emergence

H_1: Egg-to-fry survival
H_2: Habitat quality and quantity
H_3: Gene expression and life-history diversity
H_4: Geographic distribution

Egg-to-fry emergence in *O. mykiss* depends on the complex interactions between the environment, the anthropogenic factors affecting the environment, and genetics. Based on past research, we assume that survival, habitat quality and quantity, gene expression and life-history diversity, and geographic distribution have strong direct effects on if or when a juvenile *O. mykiss* successfully transitions from the egg-to-fry life stage. These hypotheses follow:

Egg to fry survival in both regulated and unregulated streams is influenced by habitat quality and quantity, and when added to hatchery production, determines a cohort's abundance and productivity (**H_1, H_2**; Figure 6). In the riverine environment the survival of eggs into emerging fry depends largely on subsurface flow, water quality within the incubation environment, and the composition of substrate. Natural and regulated surface flows in streams must be sufficient to provide water depth and velocity needed to drive intragravel flow during embryo incubation (Kondolf et al. 2008). In more regulated environments, like hatchery settings, water quality conditions such as temperature and dissolved oxygen (DFG and USFWS 2010) are more easily controlled, leading to increased levels of survival from the egg to the smolt life stage when compared to naturally reared salmonids (ODFW and USFWS 1996).

Habitat quality and quantity are major drivers which influence almost all aspects of whether *O. mykiss* eggs survive to the emergent life stage. Habitat quality and quantity influences egg to fry survival and distribution (**H_1, H_4**; Figure 6) as well as gene expression and life history diversity (**H_3**; Figure 6). Habitat quality and quantity is determined by river discharge, water quality within the spawning reaches, habitat restoration projects, and disturbance by trampling (**H_2**; Figure 6).

Salmonid species are poikilotherms, meaning that water temperature can influence processes such as development of embryos and alevins, and freshwater rearing (Carter 2005a). Stream temperature influences the survival of incubating embryos, as water temperatures outside of optimal conditions (5-10°C daily average) are documented to increase mortality rates of *O. mykiss* eggs (Myrick and Cech 2001, WDOE 2002). Adequate intragravel flow through the egg pocket is also required to remove metabolic waste and promote the delivery of oxygenated water (Silver et al. 1963).

Passage barriers such as dams and augmented flow regimes affect gravel accumulation and dispersal below barriers, which then affects the quality and distribution of spawning habitat (Kondolf 1997, Yoshiyama et al. 1998), compromising spawning success (Kondolf 2000). The composition of substrate in the redd is important for facilitating the survival of eggs to fry. The redd may contain a small amount of fine sediment (<1-10mm) to allow for sufficient permeability and successful fry emergence (Jensen et al. 2009). Sediment deposited after redds are constructed and eggs laid may reduce water quality within the egg pocket (dissolved oxygen, metabolic waste removal, etc. (Chapman 1988, Bennett et al. 2003) potentially leading to decreased fry size (Chapman 1988) or prevention of fry emergence all together (Beschta and Jackson 1979). Grain-size distributions also affect the stability of the egg pocket and influence susceptibility to fluvial scour.

Habitat restoration projects such as gravel augmentation, can increase the geographic distribution of spawning habitat in rivers (Zueg et al. 2014). Additionally, spawning gravel enhancements have been shown to increase survival of salmonid embryos by decreasing stream depths and gravel fines, increasing velocities and permeability within the gravel, and by equilibrating the hyporheic zone (Merz et al. 2004).

Trampling of salmonid redds has been shown to decrease survival of eggs within the redd (Roberts and White 1992). However, the extent to which angling pressure and trampling in the San Joaquin basin tributaries will affect salmonid redds is unknown. Generally, fishing regulations and seasonal closures are tools fisheries managers utilize to minimize impacts to spawners and redds.

Hatchery origin embryos/emerging fry and natural origin embryos/emerging fry may exhibit different characteristics (**H_3**; Figure 6). In a hatchery setting, controlled and often optimal conditions may reduce embryo selection and/or positively select for fish adapted to the hatchery environment (Araki et al. 2008). In regulated and unregulated streams, water quality and quantity within the stream channel and incubation habitat may impact the expression of life history characteristics. Variation in stream flow produces fluctuations in water levels and velocities, which may result in dewatering or scour of salmonid redds, and subsequent mortality of eggs and larval fish (Becker et al. 1982, Montgomery et al. 1996). The timing of these events may contract the temporal and spatial selection of embryos in redds. In such cases, the diversity in spawn timing and habitat use may be reduced.

Spatial structure reflects the distribution (occupancy and density) of embryos and emerging fry, which is driven by the water quality within the incubation habitat and quantity of habitat that the flow regime provides in the spawning reaches (**H_4**; Figure 6, reviewed in Malcolm et al. 2012). Stream flow also influences sediment transport, channel morphology, and streambed substrate characteristics which effect spawning habitat quality and availability, as well as determines the hydraulic conditions experienced by individual fish (Merz and Setka 2004, Brown and Pasternack 2008). Ascending baseflows in streams during spawning increases the availability of spawning habitat and may reduce the occurrence of redd superimposition by creating space between spawning habitats (Goodman et al. 2018). Decreasing flows during or following deposition of eggs, can lead to disconnection of redds from the main channel as well as dewatering, which leads to redd stranding and decreases egg survival (Becker et al. 1982, McMichael et al. 2005, Fisk et al. 2013).

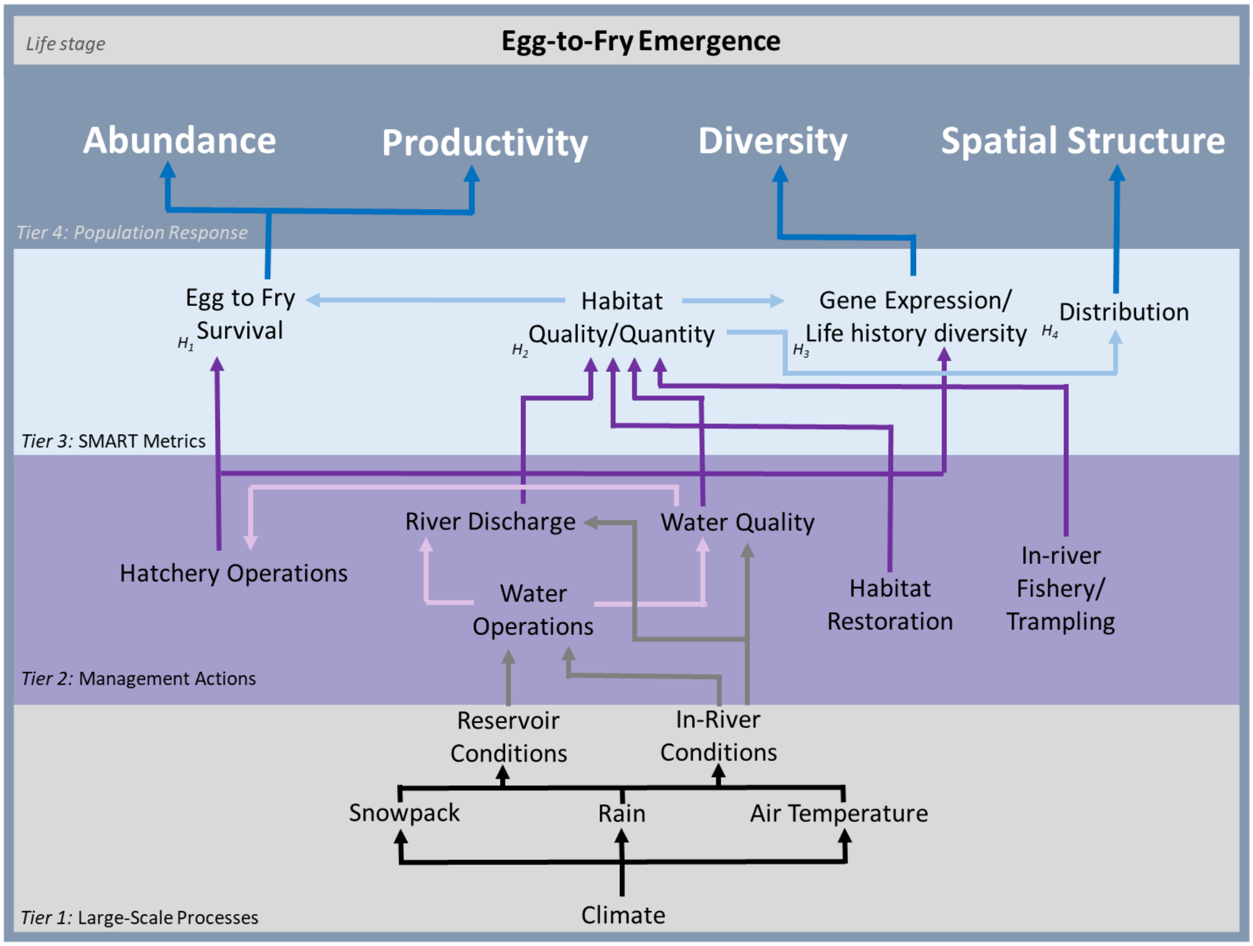

Figure 6: Egg-to-fry emergence conceptual model linking large-scale processes to management actions, SMART metrics, and desired population responses (i.e., VSP criteria)

Monitoring and Special Study Considerations

The primary goal when monitoring the egg-to-fry emergence life stage within the context of the JPE is to estimate the proportion of eggs produced by female spawners that survive to emerge as fry (Table 1, SEg). Additionally, tributary specific juvenile *O. mykiss* production can be estimated through monitoring this life stage (Table 1, Fr) if spawner abundance and fecundity (Table 1, Fr is the product of E and SEg) is also known (Harvey et al. 2020). The egg-to-fry emergence life stage is defined as the transition from an egg until the fry emerges from the gravel. There are four underlying hypotheses driving the transition from the egg to emergence life stage (Figure 6). Survival through the life stage is primarily influenced by habitat quality and quantity (**H_1-H_2**, Figure 6), which influences gene expression and life history diversity (**H_3**) and directly affects the geographic distribution of spawners within a system (**H_4**). Although monitoring needed to estimate survival of eggs to the emergent fry life stage overlaps with monitoring of other life stages (adult spawning and rearing), this section will primarily focus on considerations for monitoring the egg-to-fry emergence life stage (Figure 6, Table 1, SEg and Fr).

To estimate the number of emergent fry produced every year requires monitoring across large habitat areas, as opposed to fixed monitoring locations that are commonly used for later life stages (e.g., rotary screw traps for out-migrating smolts). The abundance of redds and the fecundity of female spawners must be known for Central Valley *O. mykiss* (see Spawning section) to determine how many eggs were deposited by spawning females. Additionally, the spatial distribution of redds, as well as the water quality conditions experienced by eggs in the redds, is needed to estimate the proportion of eggs surviving to emerge as fry. Because stream flow directly influences environmental and water quality conditions within spawning reaches (**H_1, H_2, H_4**), monitoring of the egg-to-fry emergence life stage should consider stream flow, wetted habitat relative to flow, duration of redd inundation relative to flow, water temperature and DO, as well as measures of intragravel flow.

Though hatchery settings control environmental conditions (water temperature, flow, etc.) experienced by eggs and fry during their rearing period (DFG and USFWS 2010), mortality for this life stage transition (egg take to release) for the Mokelumne River Hatchery is only 65% (CDFW 2021b). Hatchery programs monitor survival of eggs to release, as well as water quality parameters on an annual basis (spawning and rearing season). When considering model parameters needed to estimate survival in the egg-to-emergence life stage in natural settings, these annual survival estimates could be included in models as a measure of baseline survival under ideal conditions.

Lastly, if spawning habitat and redd construction overlap spatially and temporally with angling pressure, redd disturbance from trampling may occur (**H_2**). Directed studies could be used to determine impacts of trampling on redds by system relative to flow (flow fluctuations alter water depth and accessibility to fishing grounds/ redds for anglers).

Status and trend monitoring

Long-term monitoring data may include water quality measurements from stream gauges or predictions from water quality models in the spawning reaches of the tributaries. These data may be used to help predict embryo survival to emergence (SEg) during the incubation period (Merz et al. 2004). Model parameters and thresholds may include critical values that indicate when egg survival begins to decline (Hendrix et al. 2017) and how quickly development will occur. Water temperature is a vital parameter that is measured in many of the San Joaquin Basin tributaries (CDEC 2022). These surface water temperature measurements may be used as a proxy for incubation temperatures if there is spatial overlap with spawning habitat and validation occurs through special studies. Predicted water temperatures from models (e.g. HEC5Q; Willey 1986) may also be used if available and serve as an appropriate proxy. Dissolved oxygen may also influence early steelhead embryo development (Silver et al. 1963, Greig et al. 2007) but is not typically measured through long-term monitoring. Currently, environmental parameters such as water quality are used to monitor and predict annual egg-to-fry survival of Winter-run Chinook Salmon, but has not yet been expanded to CCV steelhead monitoring efforts. However, special studies may be used to collect data on dissolved oxygen and other water quality parameters (pH, conductivity) that can be used to help inform and predict incubation habitat quality where spawning occurs, and one such study is currently in the implementation phase on the Stanislaus River (Zeug et al. 2024).

In addition to water quality measurements, stream flow data from surface water gauges or models (e.g. CALSIM) within *O. mykiss* spawning habitat may be used to help inform incubation habitat quality. Hydraulic models of varying resolutions and ages may be available in spawning reaches to predict surface water depth and velocity conditions at range of flows during incubation. In many cases, these models have been used to generate instream flow to suitable area relationships (Gard 2009) and may apply to incubation habitat quality. When higher resolution models (2D) and redd location data are available, site-specific predictions of redd dewatering and scour relative to changes in flow may be available. Substrate mapping data in spawning reaches may be added to model output to further refine habitat quality predictions at a range of flows (Gard 2009). The use of such models will be dependent on availability of recent bathymetry, river stage, and discharge data. The spatial and temporal distribution of *O. mykiss* redds will also be needed. The resolution and accuracy of these data will be important determinants of model uses. Special studies may be needed to validate the use of surface water depth, velocity, and substrate measurements and/or predictions as a proxy for incubation (subsurface) conditions, including how they relate to the direction and magnitude of hyporheic flow through the egg pocket. Implementation of habitat quality monitoring for CCV steelhead are limited to the American River where hydrologic models (Gard 2009) were used to estimate redd dewatering of CCV steelhead at different alternative flow actions as part of the consultation on long-term operations of the Central Valley Project. There are more robust monitoring efforts currently being implemented for Winter-run Chinook Salmon where shallow redds are actively monitored to inform management decisions to minimize negative effects such as redd dewatering (Chelberg 2023).

In a hatchery setting, an estimate of the proportion of eggs that survive to emergence (SEg) may be determined annually during routine hatchery operations (CDFW 2021b). Each year, the take of green eggs is estimated to meet targets that allow for a buffer against mortality or disease during the incubation and rearing phases. The number of eggs taken (E) is typically determined using a count by volume estimate. Once eggs have hatched and fry have reached the swim-up stage, weight counts are typically performed which will provide a baseline measure of fry production (Fr).

Special studies

The accurate identification of egg burial depths is a critical component to understanding and predicting how changes in water quality, flow and substrate quality impact survival and development of embryos. Steelhead egg burial depths proposed for use in scour studies are limited to a small number of older references (Devries 1997). During the steelhead spawning period, special studies may be used to determine the average and maximum steelhead egg burial depths in San Joaquin Basin tributaries. These data may help to identify the range of subsurface depths that are most critical to embryo survival and development.

Studies validating the use of surface water temperature, flow, and substrate as standards for subsurface water temperature, flow, and substrate may also be necessary to understand how incubation conditions correspond to stream conditions. Water quality meters, temperature data loggers, piezometers, standpipes, and sample cylinders are examples of equipment that can be utilized to collect this information (Kondolf et al 2008). Subsurface samples should be collected from a depth in the gravel that is similar to the depth of the egg pockets.

Field-based investigations that provide estimates of eggs that survive to emergence and examine the relationships between hyporheic water quality, subsurface flow, gravel composition and the survival and development of steelhead embryos may also be warranted. Such studies may help identify habitat parameters that limit embryo survival in the spawning reaches and inform predictive models that may be used to estimate embryo survival to emergence. These assessments may place permeable incubators with a known number of fertilized eggs in artificial redds (Malcom et al. 2003) or place caps over artificial redds to capture emerging fry (Philips and Koski 1969, Castle and Jackson 2014). Hyporheic water quality and flow measurements should be collected just adjacent to the embryos.

Gravel augmentation projects are often implemented below dams to increase spawning habitat for salmonids, and to increase survival of eggs to the fry life stage by improving the habitat quality within the spawning reach (Merz et al. 2004, Zeug et al. 2013). While gravel augmentation projects have been implemented in some San Joaquin Basin tributaries (e.g., Mokelumne River, Merced, and Stanislaus rivers), investigations into the feasibility of additional reach-scale projects and maintenance in rivers with existing projects, as well as expansion of projects into other San Joaquin Basin rivers could be conducted. Enhancement projects, when paired with post-project effectiveness studies could inform and benefit the adult spawning, egg-to-fry-emergence, and rearing life stages (Figures 5-87, Table 1, Rd, SEg, and SFr).

Angling effort targeting *O. mykiss* in the San Joaquin Basin is relatively low when compared to other rivers in the Central Valley (Murphy et al. 2001a, Murphy et al. 2001b), but it does exist. There is scant literature addressing the potential impacts to redds from anglers (by walking across or standing on redds while fishing [trampling]), and even less for impacts within the San Joaquin Basin. To more fully understand the extent to which redd trampling by anglers may affect the egg-to-fry emergence life stage, studies that examine the spatial and temporal extent of angling paired with locations of *O. mykiss* redds during the rearing period should be designed and conducted.

Rearing

Biology of Life Stage. Juvenile steelhead rear during most months of the year and typically migrate downstream in the Sacramento River between January and June (Hallock et al. 1961; McEwan 2001). Juvenile freshwater rearing duration is highly variable and poorly documented for populations in the Southern Sierra Nevada Diversity Group. However, the timing of San Joaquin basin juvenile steelhead outmigration is typically later in the spring compared to Sacramento Basin origin fish (NMFS 2019) indicating that freshwater rearing may extend later into the calendar year compared to northern populations.

There is limited published information on habitat suitability criteria specific to California Central Valley steelhead, and less so for populations in Southern Sierra Nevada Diversity Group. However, similar physical habitat characteristics have been reported for populations along the California coast and Pacific northwest. In California's Big Sur River, for example, rearing juvenile steelhead were observed across all mesohabitat types, although the percentage of juveniles observed in run, riffle, glide, and pool habitat types varied by season (Holmes et al. 2014). In all habitat types, the presence and close proximity (<1 m) of escape cover (e.g., boulders, large wood, vegetation) was positively associated with habitat occupancy. Across habitat types, the preferred water depth and velocity varied with fish length. In Holmes et al. (2014) study, juveniles between 60-90 mm were observed in water velocities averaging 35 cm/s (0.91-84 cm/s range) and water depths averaging 0.52 m (0.14 - 1.30 m range), which is consistent with larger juveniles and observations from other watersheds (e.g., Raleigh 1984, Naman et al. 2019).

Hypotheses of factors impacting juvenile rearing

H_1: Survival
H_2: Somatic growth
H_3: Habitat quality and quantity
H_4: Competition
H_5: Geographic distribution

The abundance, productivity, diversity, and spatial structure of rearing juvenile *O. mykiss* can be impacted by numerous factors. Here we focus on several environmental and biological metrics that are likely important for determining rearing survival, somatic growth rates, habitat quality and quantity, competition among juvenile and resident *O. mykiss* and their distribution within rearing habitats. The list of factors and hypotheses described below are not exhaustive, however they do capture important variables that are linked to metrics and actions that are often the focus of habitat and water operations management.

Considerable effort is invested into managing water temperatures in regulated rivers in the California Central Valley, where temperatures regularly meet or exceed stressful temperatures for rearing juvenile *O. mykiss* (Sogard et al. 2012; NMFS 2019). During periods of extreme drought, temperatures can also approach lethal temperatures for *O. mykiss* and other coldwater fishes. Contemporary research provides evidence that temperatures exceeding 22.3°C may cause mortality in *O. mykiss* (**H_1**; Figure 7; Sloat and Osterback 2013). However, it is worth noting maximum tolerable temperatures range from 22.3-33.1°C depending on natal origin and physiological acclimation (Sloat and Osterback 2013). Even without acute mortality due to exposure to higher water temperatures, protracted exposure to sub-lethal temperatures can weaken *O. mykiss* immune systems and increase relative risk of infection and vulnerability to pathogens that can lead to mortality or reduced fitness (Bratovich et al. 2005).

The recommended temperatures for optimal growth of juvenile steelhead ranges from 14°C to 19°C (**H_2**; Figure 7). However, one study did find that juvenile steelhead could achieve average growth rates exceeding 1mm/day in the American River with abundant food availability and limited competition when summer water temperatures regularly exceed 20°C (**H_1**, **H_2**; Figure 7; Sogard et al. 2012; NMFS 2019). As such, it's possible that optimal temperatures for juvenile steelhead growth increase as relative food availability increases similar to other salmonids (Perry et al. 2015, Manhard et al. 2018). Similarly, *O. mykiss* may have the ability to capitalize on variability in water temperatures to optimize bioenergetics during foraging and energy assimilation (**H_2**; Figure 7; Armstrong et al. 2013, Brewitt et al. 2014).

Habitat quality and quantity can directly impact survival, somatic growth, competition and the geographic distribution of rearing juvenile *O. mykiss*. The presence of physical structure (e.g., large wood, boulders, etc.) can provide refuge from avian and aquatic predators including large resident adult *O. mykiss* ($\mathbf{H_1}$, $\mathbf{H_3}$; Figure 7; Holmes et al. 2014). Habitat quality, quantity, and type (e.g., floodplain, pool, riffle, etc.) can impact both prey production, availability, and the energetic costs of foraging (e.g., water velocity), movement and growth of rearing juvenile *O. mykiss* ($\mathbf{H_2}$, $\mathbf{H_4}$, $\mathbf{H_5}$; Figure 7; Grantham et al. 2012, Myrvold and Kennedy 2016). Habitat limitations can increase competition for prey resources increasing competition for food and/or antagonistic behavior among conspecifics can affect foraging behavior and success, thus leading to movement to alternative habitats ($\mathbf{H_4}$, $\mathbf{H_5}$; Figure 7; Keely 2001, Ebersole et al. 2001, Beakes et al. 2014).

Competition among juvenile *O. mykiss* and habitat availability can affect their geographic distribution (Figure 7). As fish grow over time their territory size needs increase and competition for suitable habitat may subsequently increase ($\mathbf{H_4}$; Figure 7; Imre et al. 2004) leading to movement when suitable habitat is limited ($\mathbf{H_4}$, $\mathbf{H_5}$; Figure 7; Grantham et al. 2012, Myrvold and Kennedy 2016). While most hatchery reared *O. mykiss* are expected to outmigrate upon release, a percentage of each cohort may rear for days to weeks post release or fail to outmigrate and complete their life cycle in freshwater (Hausch and Melnychuk 2012). Hatchery origin *O. mykiss* that do not outmigrate can exacerbate competition and density dependent effects on growth and survival ($\mathbf{H_4}$; Figure 7; McMichael et al. 1997, Harnish et al. 2014).

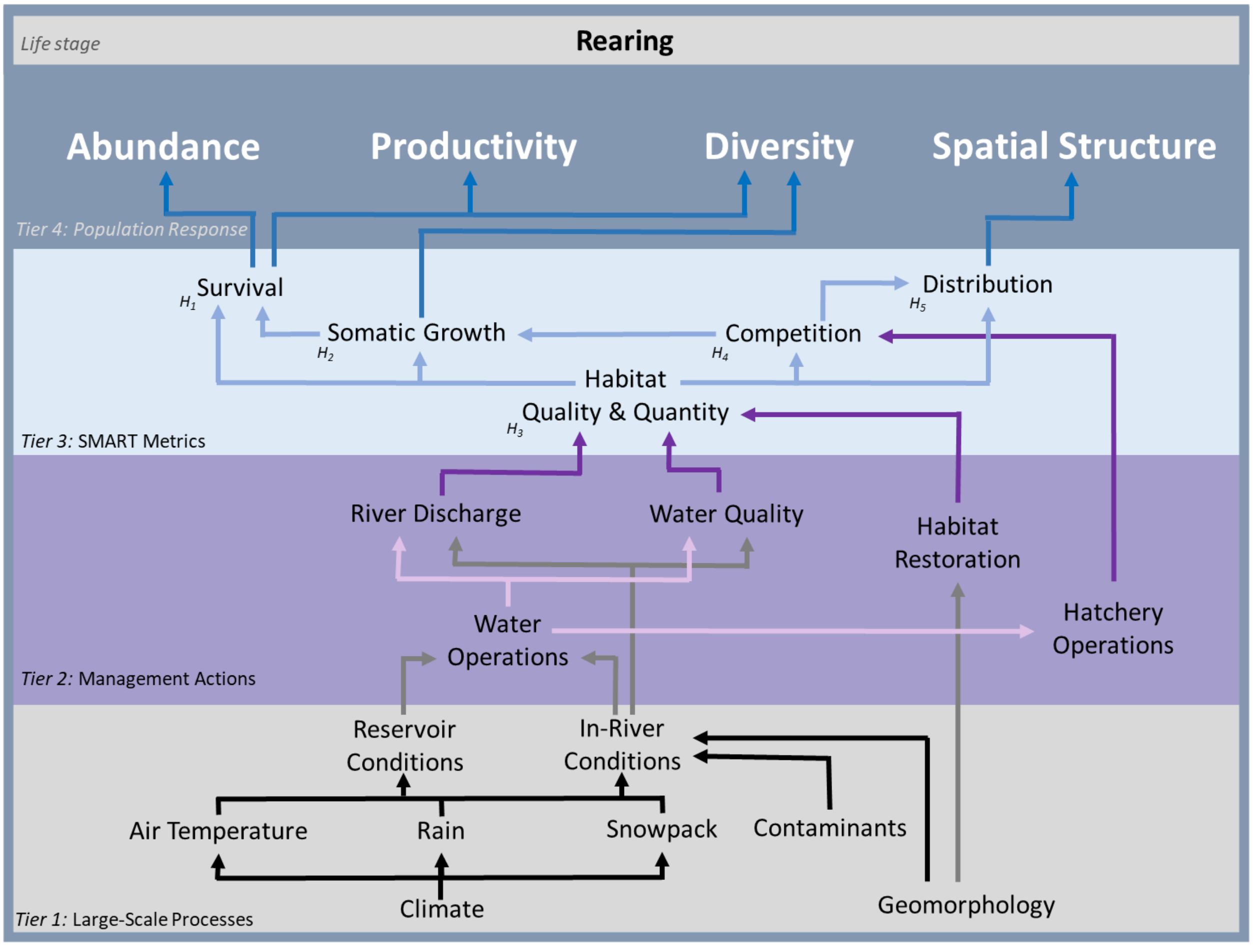

Figure 7: Juvenile rearing conceptual model linking large-scale processes to management actions, SMART metrics, and desired population responses (i.e., VSP criteria).

Monitoring and Special Study Considerations

The primary goal of status and trends monitoring and special studies at this life stage relative to calculating the JPE is estimating fry-to-parr and parr-to-parr abundance and survival rates (Table 1, SFr and SPr, respectively). Survival is difficult to estimate directly and will thus likely require monitoring of seasonal and annual changes in fry and parr abundance. Mean survival rates (i.e., fry, parr, and potentially spawners) can be estimated through studies and analyses that build quantitative relationships between these abundance data.

Variables that directly or indirectly impact survival include somatic growth rates, habitat quality and quantity, and competition (**H_2**, **H_3**, **H_4**; Figure 7). It is likely that competition can be inferred from abundance monitoring if the sample design provides a mechanism for estimating fish density and factors that may mitigate competitive interactions (e.g., food availability, cover, hatchery origin *O. mykiss*). In addition, habitat conditions and water quality (e.g., water temperature, turbidity, etc.) may also impact efficiency of abundance monitoring and thus should be considered in study design and data collection (Figure 7).

It is essential that the JPE can be generalized and/or extrapolated over broad spatial and temporal scales (**H_5**; Figure 7). As such, it will be necessary to implement a spatially and temporally balanced monitoring design (McMillan et al. 2012, Liermann et al. 2015). Doing so will help ensure monitoring and special studies and abundance estimates are not biased due to disproportionate sampling in one particular habitat type, population, or time period.

Status and trend monitoring

O. mykiss can potentially rear in natal tributaries year-round when suitable habitat is available, and changes in abundance through time is likely due to a combination of mortality and outmigration. Here, we describe monitoring methods to evaluate changes in abundance through time as a means to infer survival rates. Outmigration monitoring is discussed in another section. Factors that impact the abundance and survival of rearing *O. mykiss* will likely change throughout the year. As such, it may be necessary to stratify *O. mykiss* monitoring and the data collection of variables that may impact survival and gear efficiency across seasons. Alternative monitoring methods have tradeoffs with respect to feasibility, costs, and the precision and accuracy of detecting the target species (Korman et al. 2010), all of which will likely impact the precision, accuracy, and reliability of abundance estimates generated from the data they provide. Additionally, counts of *O. mykiss* collected at monitoring locations will need to be corrected for sample bias (e.g., detection probably and sample error) and spatially expanded to generate 'true abundance' estimates for a population (e.g., catchability must be estimated with count and effort, otherwise an index rather than an abundance estimate is produced).

There are many approaches to generating river-wide abundance estimates of juvenile salmonids that range from visual observations (e.g., snorkel surveys) to electrofishing (e.g., Hankin and Reeves 1988, Korman et al. 2010) and single-pass index to mark-recapture sampling (e.g., Korman et al. 2016). As noted above, alternative monitoring methods and study design will have feasibility and costs tradeoffs that will impact the precision and accuracy of abundance estimates and the utility of those estimates. It is beyond the scope of this document to provide a comprehensive review of methods for monitoring rearing salmonids and duplicate the work published by Eschenroeder et al. (2022). Rather, we provide a brief description of several methods that commonly appear in published literature.

Visual estimation of rearing salmonids via snorkel surveys is generally considered a cost effective and non-invasive approach for monitoring rearing *O. mykiss* abundance across a range of watershed sizes (Hankin and Reeves 1988, Hagen et al. 2010, Eschenroeder et al. 2022). Larger streams and rivers may require multiple divers to cover the extent of the survey site and multiple passes to estimate detection probability and observation bias (O'neal 2007, Apperson et al. 2015). Time of day or night, environmental conditions (e.g., turbidity and temperature), and fish size can also impact the detection or observation probability of rearing *O. mykiss* (Hillman et al. 1992, Hagen et al. 2010, Korman et al. 2010) and should be considered in the monitoring design and abundance estimation. Snorkel surveys have been conducted in the Stanislaus annually since 2009to monitor juvenile *O. mykiss* abundance (Eschenroeder et al. 2022)

Beach seining and electrofishing are also common methods for monitoring rearing *O. mykiss* (e.g., Thorpe 2020, Eschenroeder et al. 2022). These methods are considered more invasive compared to snorkel surveys and their effective use can be limited by habitat characteristics (e.g., water depth and bank slope; Eschenroeder et al. 2022). However, both approaches allow for the physical capture of juvenile *O. mykiss*, which provides the opportunity to collect biological samples (e.g., scales, DNA) and mark fish for mark-recapture study and monitoring (e.g., Passive Integrated Transponder tags; PIT tags). These methods are currently being deployed in the Stanislaus River as part of efforts to monitor juvenile abundance and demographics (Zeug et al. 2024).

Mark-recapture studies have historically relied on implanting physical tags (e.g., PIT, elastomer, floy, etc.) or physically marking fish by removing tissue (e.g., fin), or batch marking with dye (e.g., Bismarck Brown). Advances in Artificial Intelligence image recognition and genetics have created alternatives for mark-recapture studies. For example, melanophore patterns in the head region of salmon create a natural individual marker much like human fingerprints (Merz et al. 2012), and abundance estimates based on genetic relatedness (i.e., close-kin mark-recapture) have been shown to be closely aligned with estimates based on standard mark-recapture methods (Ruzzante et al. 2019). A close-kin mark recapture effort is currently being implemented on the Stanislaus River in efforts to estimate population size and survival (Zeug et al. 2024).

Mark-recapture is an effective framework for expanding counts or observations of juvenile steelhead to measures of true abundance and density (Boughton et al 2022). Mark-recapture methods can be applied through a variety of fish sampling techniques. In all cases, captured fish are marked in a way that facilitates future identification, released, and potentially recaptured during subsequent sampling events. The true abundance and density of fish within the study reach can then be calculated with several analytical methods based on the proportion of marked fish captured in subsequent sampling events (Seber 1982, Thompson 2012, Boughton et al 2022).

Estimating river-wide population abundance may require extrapolation of data collected at smaller spatial scales. This can be accomplished by linking observed fish abundance and density to mesohabitat types (e.g., pool, riffle), then estimating watershed-scale fish abundance based on the habitat composition of the watershed (e.g., Hankin and Reeves 1988, Roni et al. 2014). Similarly, fish density estimates at a site level can be expanded based on estimates of total wetted area in the target water shed (Boughton et al 2022). Alternatively, advancements in geospatial analyses offer a means to extrapolate fish density surveys to entire watershed networks while incorporating factors (e.g., habitat characteristics) that generate variability in observed fish density (e.g., Isaak et al. 2017).

It will be necessary to monitor habitat characteristics (e.g., mesohabitat type, water depth, velocity, temperature, DO, etc.) in addition to fish abundance through time. Habitat characteristics will impact detection probability during fish sampling events (Korman et al. 2016) and also affects variation in observed fish densities (Myrvold and Kennedy 2015). Accounting for the effect of habitat on observed fish abundance will improve the accuracy of monitoring data by correcting for sample bias, make it possible to extrapolate outside the sampling area and improve our understanding of how habitat characteristics are related the status and trends of rearing *O. mykiss* abundance.

Special studies

All monitoring methods have imperfect detectability and catchability (i.e., efficiency) of fishes including *O. mykiss*. Imperfect detection or catch probabilities can lead to biased abundance estimates. The efficiency of alternative monitoring approaches (e.g., snorkel surveys vs. electrofishing) will likely be impacted by environmental conditions (e.g., water turbidity and conductivity), and *O. mykiss* biology (i.e., fish size). If the monitoring goal is to generate estimates of true abundance rather than indices, then it will be necessary to estimate the efficiency of monitoring methods and estimate how environmental conditions and *O. mykiss* biology individually and interactively impact efficiency.

More specifically, habitat quality and quantity may partly explain variation in rearing *O. mykiss* abundance through time (**H_3**; Figure 7). Estimating changes in habitat quality and quantity over time can be accomplished through hydrodynamic habitat modelling, where suitable rearing habitat is calculated by linking habitat suitability criteria with system hydraulics (i.e., water depth and velocity). Habitat suitability criteria can vary among *O. mykiss* populations and thus will need to be calculated for a target population and watershed. The sum of suitable habitat at a given discharge has been termed weighted usable area or 'WUA', and 'WUA curves' describe changes in WUA across different discharge rates. Having the capacity to estimate changes in WUA over time may prove useful in explaining observed variation in rearing *O. mykiss* abundance while providing a metric that can inform flow and habitat related management actions that are designed in increase rearing *O. mykiss* abundance. For example, a special study could be conducted on a target population of *O. mykiss* where abundance is estimated over multiple years with variable habitat conditions such as high-flow vs low-flow years. Established habitat suitability criteria for that watershed and the resulting weighted usable area over those years, could then, theoretically, have a quantifiable relationship with the population estimates. Thus, in future years with varying system hydraulics, these relationships between WUA and estimated abundance could be used to explain the variation in population estimates.

Another method to account for variation in capture efficiency is the concept of 'double sampling'. Boughton et al. (2022) provide a description of double sampling (Thompson 2012) that can be used to integrate calibration and monitoring methods that vary in approach, cost, and efficiency. The general idea behind double sampling is that it may be more cost effective to generate unbiased abundance estimates by aggregating data generated from more costly and intensive sampling methods (e.g., electrofishing) with data from more cost-effective and less intensive methods (e.g., snorkel survey). However, Boughton et al. (2022) highlight that this approach may not be worthwhile if fish detection among survey sites is highly variable. Thus, a special study may be required to evaluate variability in fish detection between monitoring locations how best to integrate data collected from alternative monitoring approaches.

Life-History Expression

Biology of Life Stage. *Oncorhynchus mykiss* exhibits the most diverse life-history patterns among California's native salmonids (Williams 2006). Unlike Chinook salmon (*Oncorhynchus tshawytscha*), *O. mykiss* can complete their life cycle in freshwater creating two distinct life-history variants including an anadromous form (i.e., steelhead) and freshwater residents (i.e., Rainbow trout). Between the anadromous and resident life-history variants there exists a considerable array of diverse pathways through which *O. mykiss* can complete their life cycle. Based on past research, we assume that survival, growth, and genetics have strong direct effects on if or when a juvenile *O. mykiss* assumes an anadromous or resident life-history pathway.

Hypotheses of factors impacting life-history expression

H_1: Survival
H_2: Somatic growth
H_3: Habitat quality and quantity
H_4: Genetics
H_5: Competition

The patterns of aquatic productivity and the physical challenges associated with migration (e.g., environmental gradient, flow, temperature, predation risk) form an adaptive landscape on which anadromy evolves and environmental conditions provide proximate cues for whether it is expressed. In facultatively anadromous species, like *O. mykiss*, the expression of anadromy is in part influenced by the cost of migration (**H_1**; Figure 8). Specifically, when migration distance, elevation gained, or risk of mortality is high during migration, the anadromous contingent within a species is expected to become less common (Hendry et al., 2004, McMillan et al., 2007). Even where latitude or migratory difficulty are approximately equal, differences in habitat characteristics and growing conditions of adjacent watersheds can generate divergent rates of anadromy (Pavlov et al. 2011, Finstad and Hein 2012, Berejikian et al. 2013, Kendall et al. 2015, **H_2**, **H_3**).

Food availability, water temperature, and stream flow have been associated with patterns of anadromy in *O. mykiss* (**H_3**; Figure 8). Factors that may impact life-history expression on short time scales include many of the same factors that impact the adaptive potential and evolutionary trajectory of *O. mykiss.* Large-scale process and management actions influence habitat conditions (e.g., water temperature and stream flow), somatic growth, and genetics through habitat quality and quantity as well as the impact of hatchery operations on competition and genetics. More specifically, past research provides evidence that juvenile steelhead require water temperatures between 6.5 and 11.3°C (Myrick and Cech 2001) and grow past a size threshold (Satterthwaite et al. 2010, Beakes et al. 2010) to successfully initiate and undergo parr-to-smolt transformation (**H_3**; Figure 8). Further, higher rates of anadromy have been observed in systems with warmer and sometimes stressful temperatures, while residency was more common in cooler systems without stressful temperatures (Sogard et al. 2012). Variability in stream flow has also been associated with differing rates of anadromy across populations (Kendall et al 2015), where higher rates of anadromy were more common in watersheds with variable flow while residency was associated with river sections with more stable flow (Pearsons et al. 2008, **H_3**). For example, low and variable summer stream flows produce warmer temperatures and greater competition for food as suitable habitat contracts. As the conditions become growth-limiting due to density-dependent competition or increasing metabolic demands of the individual, anadromy becomes more common (**H_2**, **H_5**; Figure 8; Pearsons et al., 2008, Courter et al., 2009, Berejikian et al., 2013). By manipulating stream flow, Harvey et al. (2006) found that growth rates of *O. mykiss* were 8.5 times lower in reaches with reduced flow than in control reaches. This line of reasoning has led to the hypothesis that higher summer flows improve opportunities for feeding and development, thereby permitting the expression of larger and older freshwater residents (Figure 8; Cramer et al. 2003; McMillan et al. 2007; Pearsons et al. 1993).

Body size or growth rate is often considered a proxy for growth conditions, but whether anadromy is expressed will depend on the context. Faster growth has been associated with anadromy in field and lab experiments; however, cooler temperatures and lower individual metabolic rates produce higher rates of freshwater maturation for equivalent somatic growth, particularly in females (**H_2**, **H_3**; Figure 8; McMillan et al., 2012, Sloat and Reeves 2014, **H_2**, **H_3**). Size-based thresholds for smolting may occur during 'decision windows' early in the year and well in advance of parr-to-smolt transformation (**H_2**; Figure 8; Beakes et al. 2010). 'Decision windows' are determined by origin, size, date, and growth (Satterthwaite et al. 2010). Altering growth rates or survival over longer timescales can affect the size threshold required for smolting, or number of individuals that reach the threshold (**H_1**, **H_2**; Figure 8; Phillis et al. 2016). For example, if management actions (e.g., habitat restoration) result in accelerated growth then we would hypothesize that the percentage of the population able to reach the threshold required for smolt transformation will increase. However, if survival rates of smolts is positively correlated with fish size and only the larger individuals survive then natural selection will favor larger smolts and the size threshold required to smolt likely increase over time (Phillis et al. 2016). Increased competition and density dependence has been associated with higher rates of anadromy (**H_5**; Figure 8; Bjornn 1978, Kendall et al. 2015), but the mechanism is likely linked to variation in somatic growth.

With all else equal (e.g., environment, sex, and individual condition), the genetic makeup of Omy5 likely impacts the expression of anadromy (**H_4**; Figure 8; Pearse et al. 2014, Kelson et al. 2019). However, it is worth noting that relatively little variation in life-history expression can be explained by genetics alone (Kelson et al. 2019), and that Omy5 has been linked to other factors that likely impact life-history expression such as development rate and growth (Nichols 2008, Miller et al. 2012, Kelson et al. 2020). Density dependence can also influence life history indirectly through selection on traits, such as metabolism, where intense competition for feeding territory favors fish with high standard metabolic rate that are more likely to express anadromy, resulting in a positive feedback loop because those anadromous fish are more fecund than residents producing higher densities of juvenile fish in freshwater that foster intense competition (Morinville and Rasmussen 2003, Sloat and Reeves 2014, Sloat 2013). Similarly, genotyping at Omy5 can inform population-level assessments of anadromy (Abadía-Cardoso et al. 2011, Kelson et al. 2019) but the mechanism driving change at the individual level may be more closely tied to development and growth (Kelson et al. 2019). Collectively, many of these factors affect interannual growth rates, survival, and the maximum size achievable in freshwater, which likely impacts life-history expression and evolution (Satterthwaite et al. 2009, 2010). The indirect genetic control on migration in *O. mykiss* can be described as a reaction norm wherein expression of the migratory tactic is dependent on an individual's status (the integration of the environment experienced) relative to a genetically controlled threshold state (Tomkins and Hazel 2007, Hutchings 2011, Pulido 2011, Dodson et al. 2013). The outcome of these genotype-environment interactions will vary within populations (e.g., males vs. females) and between populations according to the costs and benefits of seaward migration versus freshwater residency for any given system.

Hatchery produced individuals that become resident adults compete with naturally produced resident adults for limited resources (i.e., food, territory, spawning opportunities, $\mathbf{H_5}$; Figure 8). However, hatchery release strategies may inhibit the residualization of hatchery-origin *O. mykiss*. For example, in the Mokelumne River, releasing hatchery individuals at a larger size in the lower watershed (e.g., below Woodbridge Dam) during a pulse event has decreased the proportion of hatchery fish observed moving upstream after release (unpublished data). Hatchery operations have also impacted the genetic structure of *O. mykiss* ($\mathbf{H_4}$). For example, Pearse and Garza (2015) showed that the genetic structure that exists among Central Valley tributaries has been significantly altered in contemporary populations (e.g., *O. mykiss* above and below dams within the same tributary were not found to be each other's closest relatives). In particular, they found evidence of introgression between steelhead in the American River and some neighboring tributaries with coastal steelhead, which is likely the result of imported eggs from coastal steelhead sources, primarily the Eel and Mad rivers (Pears and Garza 2015). However, the expression of life history diversity and its relationship with genetics is complex, as mentioned previously, and the impacts of introgression from stocking and hatchery practices have not been fully evaluated.

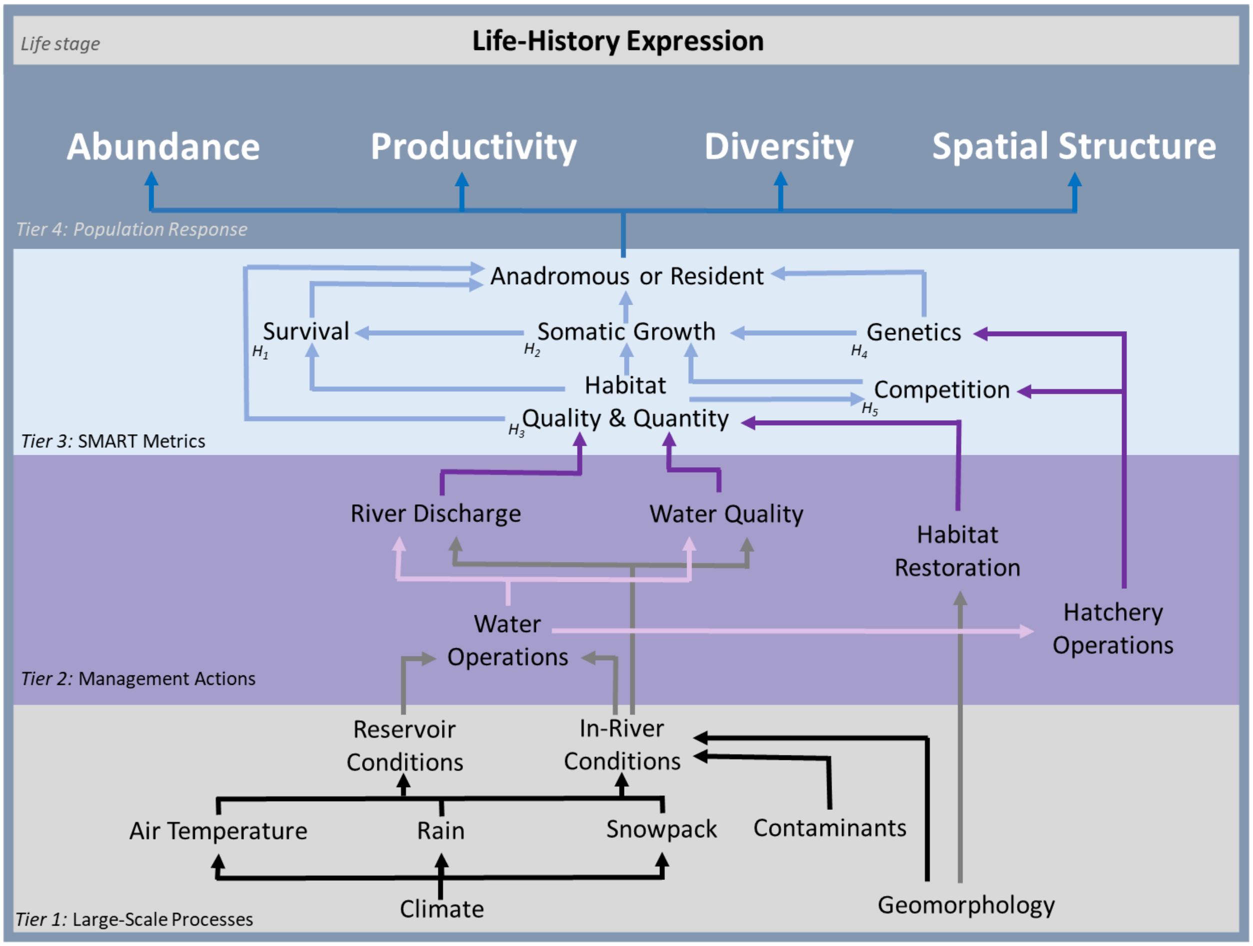

Figure 8: Life-history expression conceptual model linking large-scale processes to management actions, SMART metrics, and desired population responses (i.e., VSP criteria).

Monitoring and Special Study Considerations

The primary goal when monitoring juvenile life-history expression within the context of the JPE is to understand the probability of smoltification (Table 1, PSm_i). There are five underlying hypotheses driving life-history expression during the juvenile life stage (Figure 8). Hypotheses **H_2-H_5** are directly or indirectly related to somatic growth rates (Figure 8). Although survival (**H_1**) has multi-generational implications for life-history expression, for the purposes of estimating a JPE, we focus on monitoring methods that measure within-generation life-history expression. Specifically, this section is centered on strategies for understanding the probability that an individual fish will transition from parr to smolt at age 1-4+ (Figure 2A, B; Table 1, PSm_i).

To estimate the number of smolts produced each year (Figure 2A, B), the size-based threshold (i.e., reaction norms) required for smolting must be identified for Central Valley *O. mykiss* as well as the drivers of variability in size at age (i.e., correlates of growth). Juvenile outmigration size ranges vary by population (coastal vs. Central Valley fish hatchery; Beakes et al. 2010) and are currently a knowledge gap for many populations (Kendall et al. 2014) including those in the

Southern Sierra Nevada Diversity Group. Additionally, variability in outmigration survival can shift the size-based threshold within several decades and appears to be heritable (Phillis et al. 2016).

Further, some evidence suggests that the 'decision' for *O. mykiss* and other iteroparous salmonids to outmigrate (i.e., 'decision window') occurs well in advance of the date at which fish reach these size thresholds and initiate outmigration (Metcalfe et al. 1988, Thorpe 1998, Beakes et al. 2010, Satterthwaite et al. 2009, 2010). Therefore, variation in growth rates will also impact the probability of outmigration (i.e., the size at a given age). Monitoring growth rates (**H_2**) every year in multiple locations is likely infeasible for in-season resource management decision making or restoration evaluation (Simenstad and Cordell 2000). Habitat capacity and opportunity metrics are typically more achievable and can be quantitatively related to variability in growth and habitat use (i.e., **H_3**: habitat quality, such as prey availability and water temperature, and habitat quantity, such as habitat suitability and the effects of density dependence on growth).

Status and trend monitoring

Monitoring should include length frequency data collection of *O. mykiss* juveniles in locations where individuals are expected to transition from parr to smolts at age 1-4+ (i.e., outmigration corridors). This monitoring must be paired with special studies to estimate the size threshold for smolting (i.e., "reaction norms") by location and/or population under varying environmental conditions. Monitoring rearing habitat quantity and quality (**H_3**) will also be important for predicting year-to-year variability in growth (**H_2**) and the likelihood of reaching the size threshold for smolting. However, paired special studies are required to establish an analytical framework between growth and abiotic/food web correlates (see special studies). Monitoring river discharge, water temperature, dissolved oxygen and an index of primary production or prey production in *O. mykiss* rearing locations are recommended (and mirror guidance from the rearing monitoring section above). In addition to fish length and growth rate data, tissue samples should also be collected at juvenile *O. mykiss* monitoring locations. With all else equal (e.g., environment, sex, and individual condition), the genetic makeup of Omy5 likely impacts the expression of anadromy (Pearse et al. 2014, Kelson et al. 2019). As described above, relatively little variation in life-history expression can be explained by genetics alone (Kelson et al. 2019), thus monitoring and genotyping at Omy5 will inform population-level assessments of anadromy (Abadía-Cardoso et al. 2011, Kelson et al. 2019, **H_4**) but the mechanism driving change at the individual level may be more closely tied to development and growth (Kelson et al. 2019). As such, monitoring Omy5 will provide the basis for better understanding the linkages between genetic makeup, individual development, the environment, and life-history expression.

Special studies

Studies focused on understanding population level differences and environmental correlates of the probability of smolting at different ages (Table 1, $PSm_{i,j}$) should be one of the highest priorities for CCV steelhead. There are three potential study designs that can help inform the size threshold for smolting or probability of smolting given the length-at-age of juvenile *O. mykiss*. The first design is a common garden experiment where growth of fish from multiple populations is controlled through time and sea-water challenge tests osmoregulatory capacity at age 1. This approach provides optimal control over genetics and conditions that impact individual growth rates (e.g., temperature, food availability) that may help reveal population-level differences in the size threshold required to smolt. However, realism is lost at the expense of control, and thus the study results may not perfectly mirror field observations.

The second design is based on field observations that compare length frequency of outmigrating juveniles (i.e., presumed smolts) relative to length frequency of parr (i.e., rearing juveniles). Field methods would directly measure behavior at a given time for wild populations and therefore a more accurate representation of the variability in the environment, but medium to large resident fish may bias length frequency estimates of immature parr (this could be partly addressed by checking for mature males during spawning season). Additionally, it may be difficult to standardize monitoring methods. This design also requires monitoring large watersheds and multiple years of field sampling, which is expensive. Further, low population sizes or low sampling efficiency of *O. mykiss* could lead to small sample size of wild fish.

A third design alternative involves the study of otoliths from returning anadromous adults, where length at outmigration is back calculated (paired microstructure and microchemistry analysis). This strategy yields detailed life history information with opportunities to evaluate relationships to short-term and long-term changes in climate/abiotic conditions and habitat (e.g., restoration). Otoliths also provide information on all successful life history variants, which are not always recorded because of size-selective bias in many juvenile sampling techniques or rarity in the juvenile outmigration population (Johnson et al. 2017, Cordoleani et al. 2021). Although otoliths contain important life-history information, the collection of otoliths requires opportunistic sampling of post-spawned carcasses, or lethal take of potentially iteroparous adults. This type of sampling would only measure the subset of the outmigrants that survive (unless otoliths from juveniles are also collected, which would require additional permissions).

To estimate the relative probability of an individual reaching a specific length and a specific age, the drivers of variability in growth for rearing *O. mykiss* must be quantified by measuring both growth and those variables to be monitored as growth surrogates. We recommend a mark-recapture study paired with the monitoring of river discharge, water temperature, dissolved oxygen and an index of primary production or prey production. These data will then be incorporated into an analytical framework for abiotic/food web-rearing habitat relationships, based on a 2D hydrodynamic model, which includes habitat suitability criteria (i.e., water depth, velocity, and cover), and information on territory size needs at different sizes (to infer carrying capacity). This analytical framework may require extensive effort to be initially established but would then be incredibly impactful for making predictions and weighing decisions. Environmental factors (e.g., water temperature, food availability, habitat conditions) are easier to monitoring compared to directly monitoring fish growth. Therefore, once the mechanistic linkages between the environment and a biological outcome of management interest provided by this scheme are formed, the special study would transition to monitoring alone. However, there is the possibility for biased estimates of growth given remaining uncertainties and/or the strength of the resulting correlation, and the relationship between growth and covariates may change over time, which may require follow up studies. This tactic provides a framework for understanding how management actions can directly/indirectly impact growth rates and the associated uncertainty with those predictions.

Outmigration

Biology of Life Stage. Juvenile Central Valley *O. mykiss* typically migrate to the ocean after spending one to three years in freshwater (McEwan 2001). Based on rotary screw trap catches in the Stanislaus River from 1996-2021 (unpublished), the majority (96%) of juveniles leave natal tributaries between January and June, with some exiting as early as October or as late as July. Please note that rotary screw traps operating in tributaries cease operation in late June or early July and we do not know the extent of migration after traps are removed. Juvenile Delta entry, as indexed by Mossdale trawl catch from water year 2000-2020 (IEP 2021), shows the highest passage of unclipped juveniles in April and May (95%), with some passage occurring as early as January or as late as June (Beakes et al. 2021). Delta exit, as indexed by Chipps Island trawl catch from water year 2000-2020, shows highest passage between February and May (90%; IEP 2021), with unclipped juveniles caught nearly year-round (Beakes et al. 2021). It should be noted that passage at Chipps Island includes individuals from the Sacramento River basin and we are unable to assign origin of fish caught at Chipps Island. Further, juveniles may not fully migrate to the ocean, but instead may seasonally rear in estuarine environments (see Hayes et al. 2011; Kendall et al. 2015).

Hypotheses of factors impacting juvenile *O. mykiss* outmigrating from their natal tributary to the ocean.

H_1: Route selection
H_2: Outmigration timing
H_3: Survival
H_4: Habitat quality and quantity
H_5: Somatic growth
H_6: Competition

Upon reaching the Delta, there are many pathways that juvenile *O. mykiss* may take to reach the Pacific Ocean. The Delta is a complex network of waterways, canals, and sloughs that connect the Sacramento and San Joaquin River Basins to the San Francisco Bay. The Delta has been transformed into a major hub of California's agriculture and water supply. There are two pumping facilities in the south Delta that pump water out of the Delta for municipal and agricultural use. As a result, the flows in the Delta are largely driven by water management across the Central Valley via reservoir releases and pumping in the Delta, except during large rain events or significant Sierra Nevada snow melt. The process of pumping water from the Delta influences outmigration route selection by disrupting the natural flow of water from the San Joaquin River to the Ocean. These changes in flows can affect routing for fish entering the Delta and cause more fish to be entrained into the interior Delta (with extremely low survival) and pumping facilities (with low-moderate survival) instead of remaining in the San Joaquin River (with low-moderate survival; see Buchanan et al. 2021; $\mathbf{H_3}$). Thus, changes in the flow regime due to water management can have large impacts on route selection and ultimately survival ($\mathbf{H_3}$).

In addition to modifying the flow of water through the Delta, the management of water modifies the natural hydrographs within natal systems. It is likely that the start of outmigration (i.e., natal exit) is different than would be expected from an undammed system, but the overall impacts of this need to be quantified. Additionally, the duration of the migration, and therefore timing of ocean entry, are also likely impacted by water management in the Central Valley by changing the flow patterns and route selection of outmigrating juveniles. In juvenile Chinook salmon, flow has been linked with travel time in riverine reaches where higher flows are often correlated with faster travel time, but travel time increases once juveniles enter tidally influenced reaches (Michel et al. 2013; Perry et al. 2018; Singer et al. 2020). Assuming impacts are similar for steelhead, water operations in combination with in-river and tidal conditions influence migration speed, route selection and survival **(H_1, H_3**; Figure 9). Further, freshwater flow has been identified as a major factor driving outmigration survival of juvenile salmon in which higher flows are generally associated with higher survival (Kjelson and Brandes 1989; Newman and Rice 2002; Michel 2018; Notch et al. 2020; **H_3**).

There are many interacting sources of mortality for outmigrating juveniles, including predation, temperatures, contaminants (**H_4**; Figure 9), route selection (**H_1**; Figure 9), and timing of migration (**H_2**; Figure 9). For juvenile salmon migrating through the system, it is thought that predation is the major cause of mortality (Grossman et al. 2013), and it is likely similar for juvenile *O. mykiss*. Within the Delta, there has been concern with the impacts of non-native predators (Striped Bass *Morone saxatilis* and black basses *Micropterus* spp.) on survival of migrating salmonids, but it has been extremely difficult to quantify predation rates on juvenile salmonids (see Grossman et al. 2013; Grossman 2016). There have been efforts to actively manipulate predator densities from predator hot spots (i.e., waters surrounding the pumping facilities (DWR 2018; BOR 2021) and below the Woodbridge Irrigation district Dam on the Mokelumne River (Sabal et al. 2016)) and using experimental removals (Cavallo et al. 2012; Michel et al. 2020). Efforts to control predator hotspots have been successful at reducing predation (Sabal et al. 2016) and predator management is a continual effort at the pumping facilities. Outside of these hotspots, the effects of predator removals have been met with mixed results, ranging from higher survival of migrating salmonids to no change in survival, or even increased predator population sizes at the removal sites (Cavallo et al. 2012; Michel et al. 2020). It has also been hypothesized that the establishment and proliferation of non-native aquatic vegetation has influenced the distribution of non-native predators (**H_4**; Figure 9; e.g., Brazilian waterweed *Egeria densa* and subsequent increase in Largemouth Bass *Micropterus salmoides* populations; Conrad et al. 2016). Therefore, controlling and managing the non-native aquatic vegetation could have beneficial effects for outmigrating juvenile salmonids by reducing non-native predator population sizes along the migratory corridor.

Trawl catches of juvenile *O. mykiss* entering the Delta are concentrated between March and May (Beakes et al. 2021). Air temperatures and water temperatures generally increase over the course of the migration season (i.e., late winter through spring). According to the EPA (2003), the recommended temperature thresholds for juvenile steelhead migration is 18°C, but the chronic upper lethal limit is 25°C (Myrick and Cech 2005). Additionally, at temperatures above the 18-20°C threshold, individuals suffer from reduced growth and higher vulnerability to predation (as reviewed in Myrick and Cech 2005). Temperatures in the lower San Joaquin River and south Delta can routinely reach 20°C in April and temperatures can exceed 25°C in May, especially in dry years (based on temperatures at the Mossdale Bridge CDEC station available on the [California Data Exchange Website](). As a result, individuals that migrate earlier should experience more favorable temperatures than those that migrate in May (**H_2**; Figure 9).

We do not know the current extent of *O. mykiss* rearing along the migratory pathways (e.g., mainstem San Joaquin River, Delta, Bays and associated habitats such as floodplain, tidal marshes, etc.). Therefore, it is unclear how much juvenile fish grow during the outmigration and the effects of habitat and water quality (e.g., contaminants) on this life stage. From research on juvenile Chinook salmon, access to floodplain habitat along the migratory route provides important rearing habitat to juvenile Chinook salmon (Sommer et al. 2001; Jeffres et al. 2008; Limm and Marchetti 2009; Bellmore et al. 2013) and these habitats likely provide similar benefits to juvenile *O. mykiss*, but more research on this is needed. Thus, habitat restoration and reconnecting floodplains along the mainstem San Joaquin River and Delta could provide valuable habitat and additional rearing opportunities to juvenile *O. mykiss* outside of the natal habitat. Additional rearing opportunities may also influence migration timing/duration (**H_2**; Figure 9), growth and survival (**H_3**; Figure 9) during this life stage. Additionally, the impacts of contaminants (e.g., selenium, which is elevated in the San Joaquin River; Saiki et al. 1993) within this life stage on survival are not known (**H_3**; Figure 9), but direct effects of contaminants on juveniles may be low because these fish are moving quickly through the system. However, if juveniles are utilizing habitats within the mainstem San Joaquin River, Delta, or bays as rearing habitat, thus spending more time in these habitats, the impacts of contaminants could be greater. Overall, this needs to be quantified to assess the impacts on *O. mykiss* populations.

Competition is a major factor influencing survival and growth in fishes and more research is needed to quantify the effects of competition on survival (**H_3**; Figure 9) and growth (**H_5**; Figure 9) of *O. mykiss* during this stage. However, given the low catches of *O. mykiss* in the Mossdale trawl and DJFMP beach seines in the San Joaquin and south Delta compared to catches along the Sacramento (see Beakes et al. 2021 and data available in IEP 2021) and the low availability of rearing habitat in the San Joaquin mainstem, we expect low competition for resources and space with wild migrating smolts. This may not be the case with hatchery *O. mykiss* because hatcheries have been focusing on releasing smolt-sized fish that can move quickly through the system to the ocean in recent years (Huber et al. 2024). Therefore, competition for resources at this stage may be higher than expected due, in part, to hatchery release practices. Hatcheries often release large numbers of fish at once, which could cause local depletions in limited resources (prey resources and/or space) and increase competition with wild fish in those same areas. Further, these release practices could attract predators along the migration route(s) that may increase predation risk on wild that are using the same migration routes. It should be noted that these hypotheses need to be tested to assess the effects of hatchery release practices on wild *O. mykiss* smolts.

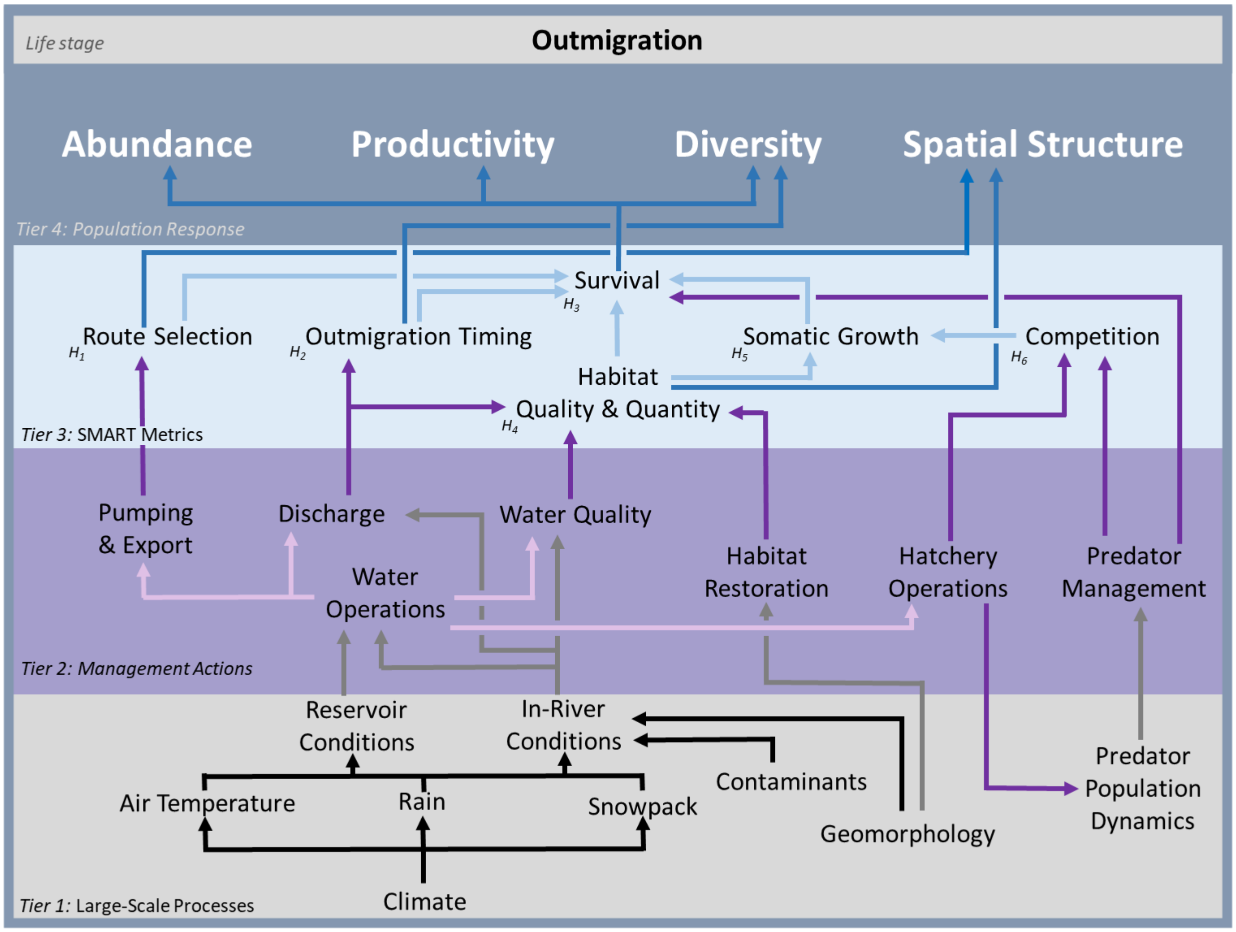

Figure 9: Smolt outmigration conceptual model linking large-scale processes to management actions, SMART metrics, and desired population responses (i.e., VSP criteria).

Monitoring and Special Study Considerations

Calculating a steelhead JPE for entering the Delta, exiting the Delta, or exiting the Golden Gate Bridge will require different datasets, calibration, and assumptions. When considering the calculations of a steelhead JPE, it is important to utilize a method that is feasible to calculate and effectively informs take limits for the facilities. Here we discuss three different locations where a JPE could be calculated to inform take: at natal exit, Delta entry, and Delta exit.

Given the benefits/drawbacks of calculating the JPE at each location, the JPE based on the outmigration monitoring will likely need to rely on a combination of techniques that utilizes information from multiple sampling locations and methodologies. These efforts will likely require a combination of status and trend monitoring with additional special studies directed at understanding the limits of the existing monitoring programs (e.g., efficiency surveys) and identifying ways to improve estimates (e.g., by incorporating mark-recapture techniques). For example, combining estimates of abundance at natal exit with acoustic telemetry or PIT tag arrays to estimate survival to Delta entry (or exit) to inform a Delta entry (or exit) JPE. For a hybrid approach that relies on existing long-term monitoring at natal exit, Delta entry, Delta exit, and mark-recapture methodologies (e.g., PIT tags, acoustic telemetry, etc.), a collaborative effort between multiple agencies and programs will be necessary to ensure data continuity and share resources to maximize the amount of information gleaned from each program. For example, programs that utilize PIT tag technology may be able to leverage sampling outside of their monitoring area to increase the value of their information. Currently, there is a PIT tag antenna array and an *O. mykiss* tagging study on the Stanislaus River and it may be useful for downstream sampling programs (e.g., the Delta Juvenile Fish Monitoring Program) to scan *O. mykiss* catch for PIT tags. Further, studies using acoustic telemetry (i.e., the recent steelhead survival project) have been tagging fish with both acoustic tags and PIT tags. If fish released as part of an acoustic telemetry project pass PIT tag antennas (either shortly after release or upon ocean return), researchers can obtain valuable information on these fish with the PIT tag detections long after the acoustic tag has ceased functioning. Efforts such as this will require a centralized PIT tag database and efforts are underway to develop a centralized database in the Central Valley for this purpose.

Considerable effort has also been directed at understanding the effects of direct and indirect mortality associated with water operations ($\mathbf{H_1}$ and $\mathbf{H_3}$). Direct mortality is usually associated with mortality that can be directly attributed to the pumping facilities, such as physical capture in the fish facility or pre-screen mortality (e.g., predation in Clifton Court Forebay, around the radial gates of the state facility, near the intake of the federal facility, etc.). These sources of mortality are generally associated with defining incidental take levels in the permitting process. Indirect effects are often difficult to quantify and are associated with changes in routing or survival due to changes in hydrology associated with pumping. Based on analyses by Rebecca Buchanan (e.g., Buchanan et al. 2021), survival is often not correlated with water operations (export, inflow:export ratios, etc.) and therefore indirect effects are difficult to identify with methods currently available. Thus, the goals of monitoring outmigration of juvenile *O. mykiss* should also encompass: 1) quantifying the direct and indirect effects of water operations on survival and routing (e.g., effects of exports, mortality in/near the pumping facilities, pulse flows, barriers, etc.), 2) quantifying other effects that influence survival and routing (e.g., temperature, Delta inflow (partially managed), timing of migration, predation, habitat quality/quantity, non-native species, etc.), and 3) identifying areas of poor survival and develop management strategies to address poor survival (e.g., habitat restoration, predation reduction, flow management, barrier operation, etc.).

Status and trend monitoring

Based on a recent study (Beakes et al. 2021), the major tributaries to the San Joaquin River have operated RSTs since the 1990s to early 2000s (Mokelumne, Calaveras, Stanislaus, Tuolumne, Merced) and RSTs or fyke nets have been periodically operated on the San Joaquin River upstream of the Merced confluence. Trawl sampling at the Delta entry (Mossdale) and exit (Chipps Island) has been conducted since the 1970s/80s and year-round since the early 2000s. Additional beach seine sampling has been conducted throughout the lower San Joaquin River and Delta since the 1970s (year-round since the 2000s). These surveys represent a good starting point for the development of a JPE. However, in all surveys mentioned, *O. mykiss* catches have been low and may not reflect true outmigrating abundances (see special studies). In addition to these surveys, additional sampling is common on many San Joaquin River tributaries and includes beach seine, electrofishing, fyke net surveys, and may include the use of PIT tags for mark-recapture efforts (e.g., Mokelumne [in the 2010s] and Stanislaus Rivers [ongoing]). Finally, past and ongoing survival studies (2011-2016 and 2021-present) provide a valuable dataset for understanding through-Delta survival of *O. mykiss* migrating through the South Delta.

Calculating tributary-level JPEs (i.e., at natal exit) would be relatively straight forward using the existing monitoring programs in each of the San Joaquin River tributaries. Each tributary has a long-term rotary screw trap (RST) or fyke net (on mainstem) program that could be leveraged to develop the JPE. Assuming *O. mykiss* catch (or catch per unit effort [CPUE]) is proportional to abundance (see special studies) and all age classes of outmigrants are represented in the catch operators could develop efficiency surveys to scale catch to abundance for estimating the total numbers outmigrating each year. However, RST programs targeting juvenile Chinook salmon do not operate during the summer months (see Goertler et al. 2021), likely miss a proportion of the outmigration window (**H_2**) and are considered relatively inefficient at catching lager fish like outmigrating steelhead. If developed for each tributary, it would be possible to manage water operations for tributary specific JPE goals. Issues with this method include variable mortality during outmigration, which will lead to uncertainty in understanding the population-level consequences of take limits. Also, the origins of individuals encountered at the pumping facilities would need determined (e.g., genetic identification) to inform tributary-specific incidental take levels.

Calculating JPE at Delta entry (i.e., near the Mossdale Crossing Regional Park) would provide the best estimate for the numbers of juveniles that will have an opportunity to interact with the pumping facilities. Except for the Mokelumne and Calaveras Rivers, a JPE at Delta entry will provide the best metric for San Joaquin River populations because we currently do not differentiate San Joaquin River from Sacramento River *O. mykiss* caught at Chipps Island (Delta exit). This JPE will likely rely on trawl catch at Mossdale, however efficiency surveys are needed to determine if trawl catch (or CPUE) is proportional to abundance (similar to efforts required to estimate efficiency of RSTs or fyke nets mentioned above and in special studies).

While trawls monitoring Delta entry operate year-round, low flows in recent years have prevented trawl surveys during parts of the year, including during the *O. mykiss* outmigration window. Further, this method does not account for variable (and possibly extremely low) through-Delta survival (**H_3**). Therefore, take generated from JPE at Delta entry may exacerbate low through-Delta survival in years in which few fish make it to Chipps Island.

An *O. mykiss* JPE calculated at Delta exit would provide an estimate for the number of individuals that made it through the Delta and past the direct and indirect effects of pumping. This JPE will likely rely on Chipps Island trawl catch indices, which will require efficiency estimates to determine if catch is proportional to abundance (see special studies). Nobriga and Cadrett (2001) used the proportion of hatchery fish collected at Chipps Island to derive a population estimate of wild steelhead smolts; however, they assumed zero mortality from release location to Chipps Island and that gear efficiency is constant across space and time. Moreover, *O. mykiss* catch at Chipps Island is a mixture of San Joaquin River and Sacramento River origin fish and we currently do not differentiate or estimates *O. mykiss* origin. Therefore, a

Delta exit JPE will require additional sampling to assign origin to *O. mykiss* (e.g., genetics or hard-part sampling plan; see special studies).

Juvenile *O. mykiss* outmigration routing (**H_1**) and survival (**H_3**) through the South Delta to Chipps Island has been monitored with acoustic telemetry for several years (2011-2016; see Buchanan et al. 2021) and as part of ongoing efforts (2021-present; Matthias personal communication). Results from the 6-year steelhead survival project conducted from 2011-2016 showed variable survival from Delta entry at Mossdale to Chipps Island ranging from 6-69% (Buchanan et al. 2021) and preliminary results from 2021 and 2022 suggest low survival from release upstream of Mossdale to Chipps Island (likely <10%; see the Ocean View website index). It should be noted that these survival studies have mainly focused on through-Delta survival. Additional efforts will be needed to quantify outmigration survival from natal exit to Delta entry. Agencies and universities working the Central Valley have developed an expansive telemetry array that covers accessible anadromous waters along the mainstem Sacramento River and some tributaries, including an extensive telemetry array in the San Joaquin River (see 2023 locations in Cordoleani et al. 2024). However, some of these receivers have been connected to special studies and are not consistently operational, and many of the receivers, especially those in the mainstem San Joaquin river upstream of the Delta, are not currently connected to the real-time receiver array that delivers frequent data uploads to CalFishTrack for real-time monitoring. Utilizing acoustic telemetry technologies in the Central Valley has provided valuable information for water operations and monitoring outmigration survival, and prioritization efforts have been coordinated in the Delta and Upper Sacramento recently, but efforts in the San Joaquin River basin need to be enhanced with real-time data uploads to support real-time water operations, similar to what has been done in the Sacramento River basin, when frequent time sensitive decisions need to be made by managers.

Special studies

Given the uncertainty in catch trends from existing monitoring, a concerted effort is required to understand the capture efficiency of the existing monitoring surveys (e.g., quantifying the impacts of flow, turbidity, size/length, etc. on the ability of a given gear/survey of capturing fish). Without efficiency surveys there remains high uncertainty in relating the observed catch (or CPUE) trends to true abundance, which will be necessary to develop JPE estimates. Additional efforts will likely be needed to estimate outmigration survival from natal exit to Delta entry, including quantifying the effects of outmigration timing, flow, and temperature on survival along the mainstem San Joaquin River. Existing efforts to estimate outmigration survival and routing have used hatchery fish as surrogates for wild. While these hatchery fish (spring yearlings) may reflect the size distribution of outmigrating juveniles, they do not reflect the age distribution and, combined with differences in wild versus hatchery behavior, may violate the assumption that hatchery fish can be used as surrogates for wild fish. Additional efforts need to focus on understanding the effects of partial migration on estimates of outmigration survival. Current methods to estimate outmigration survival do not differentiate between mortality and partial migration (i.e., any fish that does not make it to Chipps Island is considered a mortality, except for fish that migrate upstream immediately after release). Assessing the impacts of individuals remaining in freshwater (e.g., migrating upstream into San Joaquin River tributaries or upstream into the Sacramento River basin) will bias the reach-specific survival estimates. This is particularly troublesome in areas where tributaries connect with the San Joaquin River in the

Delta (i.e., Mokelumne and Calaveras Rivers) and fish that migrate up these rivers will introduce downward bias in survival for these reaches (i.e., true survival will be higher than estimated). While traditional estimation procedures (i.e., assuming these fish are mortalities) may be appropriate for estimating the fraction of hatchery releases that make it past Chipps Island, this may complicate attempts to estimate the effects of water operations on reach-specific survival and when using hatchery fish as surrogates for wild fish.

Given the low survival of outmigrating *O. mykiss* and Chinook salmon (see Buchanan et al. 2018, 2021; Buchanan and Skalski 2020; Buchanan and Whitlock 2022), it may also be beneficial to monitor predator populations and habitat along the various routes along the migration pathway. As described in the outmigration CM, predation is likely a major driver of mortality in outmigrating juveniles (**H_3**). Understanding how population dynamics (e.g., spatial and/or temporal distribution trends) of Striped Bass and the black basses may provide insight into regions of low survival. Further, given the relationship between non-native aquatic vegetation and predatory Largemouth Bass (**H_4**; Conrad et al. 2016), it may also be beneficial to monitor spatial/temporal trends in habitat availability along the migration corridors. Finally, understanding the impacts of other piscivores (e.g., mammalian and avian) may be beneficial and provide relative impacts of the various predator types.

Ocean Residence

Biology of Life Stage. Steelhead in the western United States range widely from California to Alaska and are phenotypically variable and iteroparous (Quinn 2005). Steelhead are facultatively anadromous, and the anadromous form can emigrate to the ocean at a wide range of ages (Satterthwaite et al. 2010). Steelhead spend little time in estuaries, migrate long distances from their natal streams, and typically spend 1–3 years in the ocean before returning to freshwater (Burgner et al. 1992). Based on the high seas distribution and origins of steelhead from vessel catch data and results of tagging studies, Burgner et al. (1992) conclude that soon after steelhead smolts enter the ocean they initiate a directed movement offshore. California Central Valley Chinook salmon enter the ocean in the Gulf of the Farallones and spread north and south along the continental shelf, mainly between Point Conception to the south and the coast of Washington to the north, although a few go farther north (Williams 2006). While the same may be true of CCV steelhead, observations of ocean residency for these fish are limited and uncertain due to a lack of commercial harvest in coastal U.S. fisheries. Brodeur et al. (2004) collected allozyme data from 58 steelhead collected in nearshore habitats south of Cape Blanco, Oregon. Of these, 14% were estimated to have originated from the Sacramento and San Joaquin rivers. Burgner et al. (1992) note that steelhead from coastal Oregon and California rivers may have a more restricted westward migration in the ocean compared to more northern stocks. A general pattern for Central Valley steelhead stocks seems to be that the American River winter run steelhead (Eel River stock) has an oceanic/offshore migration pattern more typical of other coastal California stocks, compared to interior populations that display a more coastal/inshore pattern (Nate Mantua, SWFSC, personal communication, August 23, 2021). In general, the distribution of CCV steelhead stocks in the ocean is poorly understood. Steelhead are iteroparous and Burgner et al. (1992) reported that of 251 kelts subsampled from a sample population of 709 kelts, 71%, 21%, and 8% had spawned once, twice, or three times, respectively (and interestingly, one fish had spawned 4 times).

Ocean conditions are a major driver of salmonid abundance (Crozier et al. 2019). The ocean is where steelhead, including CCV steelhead, put on most of their growth and weight. Quinn (2005) reports that 98% of the final weight of steelhead sampled was achieved at sea. Growth curves suggest rapid growth during ocean residency, especially in the first and second years in marine environments (Burgner et al. 1992). Daly et al. (2014) compared the distribution, diet, and growth of juvenile steelhead collected during surveys of the Columbia River estuary and coastal waters in May, June, and September from 1998 to 2011. Most ocean catch occurred during May (96%) and at the westernmost stations (>55 km from shore), indicating an offshore distribution and that steelhead appeared to migrate westward rapidly. Fork length, condition, stomach fullness, and IGF-1 (insulin-like growth factor-1) in steelhead increased with distance offshore, indicating a pattern of increased feeding and growth in these waters.

Unfortunately, information on steelhead diet during ocean residency is limited compared to salmon stocks due to limited time spent in coastal environments. A great deal of information has been collected on salmon stocks in coastal water off the Pacific Northwest (e.g., Brodeur et al. 2004; Litz et al. 2017) and on trophic relationships for salmon in nearshore coastal habitats in California (e.g., Wells et al. 2016). We can expect that steelhead in the ocean will differ from salmon due to steelhead emigrating as older age classes and thus sizes compared to Chinook salmon and coho salmon. Nonetheless, Daly et al. (2014) did monitor diet composition and reported it to be quite diverse. Prey from juvenile steelhead caught in the ocean were grouped into a total of 13 categories that contributed at least 5% of the diet by weight in any year (euphausiids, decapods (crabs), amphipods, copepods, pteropods, insects, rockfishes *Sebastes* spp., hexagrammids (greenlings), cottids (sculpins), Sablefish (*Anoplopoma fimbria*), Pacific Sand Lances (*Ammodytes hexapterus*), other teleosts, and other invertebrates). Daly et al. (2014) also measured the proportion of steelhead with empty stomachs. Consistent with the benefits of ocean residency discussed above, roughly half of the fish sampled in the Columbia River estuary had empty stomachs compared to most of the ocean-caught steelhead (87.9% of hatchery fish; 92.3% of unmarked fish) having food in their stomachs.

After maturing for one to several years in the ocean, steelhead migrate from distant feeding grounds and return to their natal streams to spawn (Burgner et al. 1992). Steelhead home back to their natal river and have been shown to return to reaches within rivers where they were released as smolts (Wagner 1969 as reported in Quinn 2005).

Hypotheses of factors impacting *O. mykiss* from ocean entry to ocean exit.

H_1: Fishing mortality
H_2: Habitat quality and quantity
H_3: Survival
H_4: Somatic growth

Ocean harvest allocation and fishing mortality can have a direct effect on steelhead survival in the ocean, and in turn, steelhead population metrics (**H_1**; Figure 10). Harvest in coastal waters is managed by the Pacific Fishery Management Council (Council). The pre-season forecast for salmon in 2022 indicates that commercial harvest on steelhead stocks in coastal waters is limited to non-existent (PFMC 2022). The forecast points out that 11 steelhead ESUs listed under ESA from Southern California to Puget Sound are found within the Council's management area, but none are substantively impacted by fisheries managed by the Council because steelhead are rarely encountered in ocean salmon fisheries. The Council maintains no specific management plan for steelhead harvest, as its harvest allocations focus on Chinook, coho, and pink salmon. Harvest in high-seas is regulated according to the International Convention for the High Seas Fisheries of the North Pacific Ocean that was signed by the United States, Canada, and Japan. High-seas fisheries are managed through the North Pacific Anadromous Fish Commission (NPAFC). The most recent data available in NPAFC annual reports covers 2020. The data indicate that steelhead harvest represents a low portion of total catch. For 2020, the overall commercial catch of Pacific salmon (322,522 fish or 606,682 metric ton, mt) was the lowest recorded since 1982. Russia caught the largest proportion of the total catch (292,674 mt, 48.2% of total weight) followed by the United States (245,682 mt, 40.5% of total weight. Pink and chum salmon made up most of the total catch (46.0% and 27.3% by weight, respectively), followed by sockeye salmon (22.6%), coho salmon (3.0%), while Chinook salmon (0.8%), cherry salmon (0.2%), and steelhead trout (< 0.1%) were less than 1% of the catch by weight (NPAFC 2020). Given this information, we assume that the impact of commercial ocean fisheries on steelhead is quite limited and does not have a large impact on the survival of steelhead from the San Joaquin River basin.

Juvenile, sub-adult and adult steelhead during their ocean phase of the life cycle depend on habitat quality and quantity, similar to all other life stages. NOAA maintains long-term monitoring data ocean conditions, and their effect on juvenile Pacific salmon survival off Oregon and Washington. Decades of sampling and analyses have improved the understanding of how trends in salmon survival track regime shifts in the North Pacific Ocean, and these shifts are transmitted up the trophic ladder in a bottom–up fashion:

upwelling → nutrients → plankton → forage fish → salmon

The same regime shifts that affect Pacific salmon also affect the migration of Pacific hake and the abundance of sea birds, both of which prey on migrating juvenile salmon. Therefore, climate variability can also have "top down" impacts on salmon through predation by hake and sea birds (terns and cormorants). Thus, both "bottom up" and "top down" linkages exist between salmonids in the ocean and the ocean environment (Peterson et al. 2013) and habitat quality and quantity (**H_2**; Figure 10) and food resources available to steelhead in the ocean directly and indirectly affect survival (**H_3**; Figure 10). The ecological processes involved are complex and are influenced by numerous dynamic environmental and biological factors, resulting in variability in the survival of different age groups and thus, the abundance of steelhead returning to freshwater each year to spawn. As discussed above, most of the weight gain, or somatic growth, of steelhead across their life span is achieved at sea, and growth rates during ocean residency are rapid. Stochastic processes in the ocean directly affect the overall productivity of steelhead populations through effects on individual growth, size at maturity, and fecundity. Overall, survival is affected both by bottom-up processes (somatic growth of individuals (**H_4**; Figure 10), which is a result of habitat quality based on trophic conditions and location) and top-down processes that reflect predator pressures and population dynamics (Figure 10). Taken together, all of these factors and processes act on steelhead in the ocean and influence abundance, productivity, diversity and spatial structure (Figure 10).

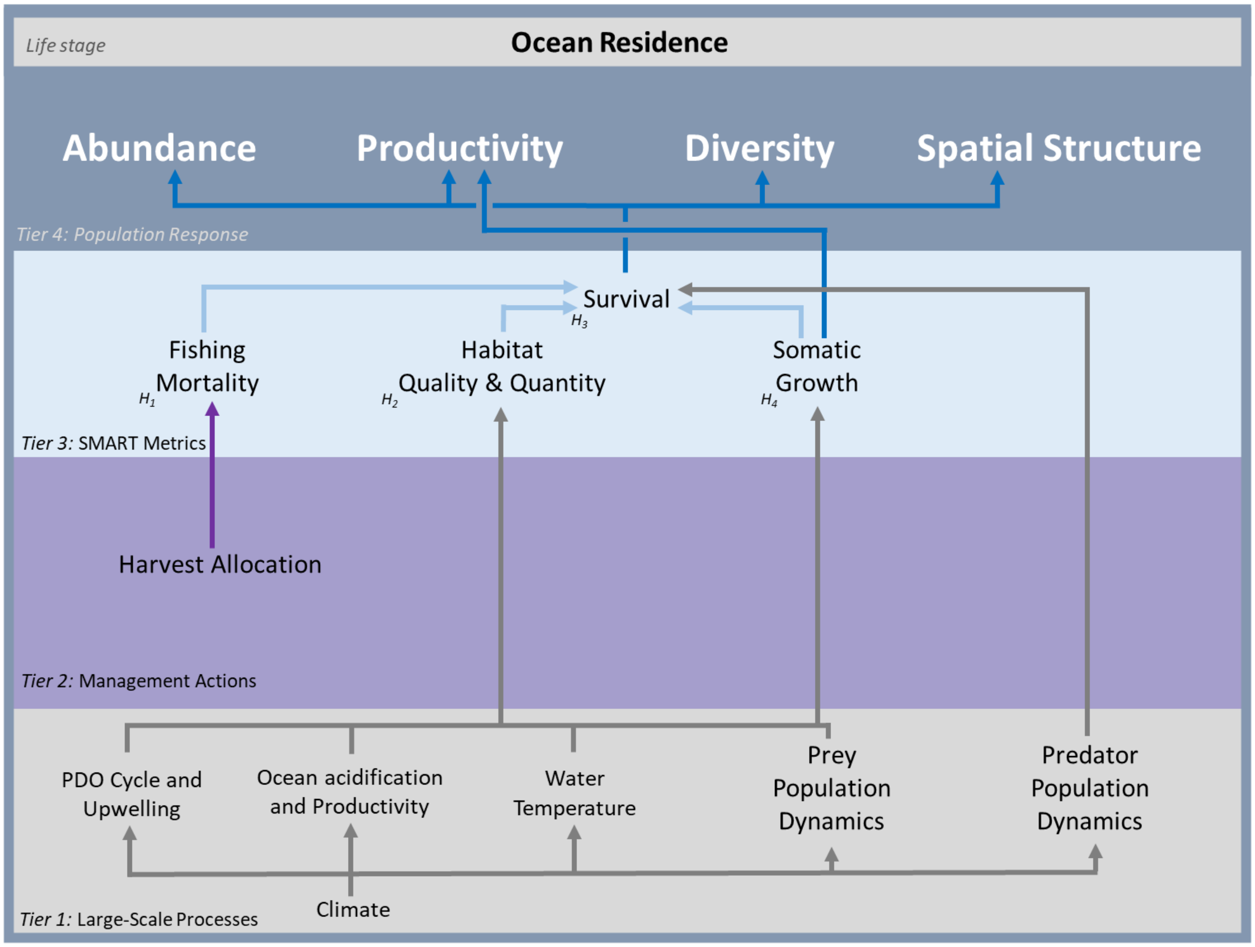

Figure 10: Ocean residence conceptual model describing the time prior to migration back to natal spawning grounds.

Monitoring and Special Study Considerations

The ocean residence component of the steelhead lifecycle is not a specific element of the conceptual framework of life-stage transitions and estimation of cohort parr and smolt abundance (Figure 2A, B). However, ocean conditions and productivity impact the quality and quantity of habitat available to steelhead when in marine environments (**H_2**), survival (**H_3**), and size and weight (**H_4**) of adult fish that return to the Delta and migrate to their spawning grounds each year. Fishing mortality also impacts survival (**H_1**) but is not expected to be a significant source of mortality in steelhead due to a lack of commercial and recreation fisheries in the ocean. The number of spawning females directly relates to the number of redds, which is the initial element of the juvenile production estimation framework (Figure 2A, B). Therefore, understanding ocean conditions and how those conditions influence the number of adult steelhead returning to the Delta each year will help managers understand and interpret the JPE, and could also inform water management decisions.

Status and trend monitoring

Ideally, an annual census would be conducted to determine the number of fish that survive ocean residence and return to the estuary to begin the upstream migration through the Delta and to the spawning grounds. This would allow managers to evaluate if survival between the Golden Gate Bridge and natal tributaries is being impacted and identify where to focus management efforts. However, there is no known method to efficiently obtain this information. Therefore, it is necessary to evaluate how ocean conditions impact the number and condition of fish that return to the spawning grounds through the collection of ocean indictor data.

Existing status and trend monitoring of ocean conditions is conducted through the U.S. Integrated Ocean Observing System (U.S. IOOS). This program consists of regional systems, including the following three that span the West Coast: 1) Southern California Coastal Ocean Observing System, 2) Central and Northern California Ocean Observing System, and 3) Northwest Association of Networked Ocean Observing Systems.

Each regional system provides information and data to meet place-based needs through collaborations with academic institutions, state, tribal, and federal agencies, private industry, and non-profit organizations (Patterson et. al. 2012). The three West Coast regional systems also share responsibility for observing larger scale ocean processes that occur within the California Current Large Marine Ecosystem, which extends from Canada to Baja California. The West Coast regional systems collect physical, chemical, biological, and geological measurements that support the operation of small- and large-scale numerical ocean models to fill in measurement gaps and provide forecasts of future conditions. This information would support evaluations of steelhead stocks that are more oriented to the coastal areas. Some stocks transit across the North Pacific Ocean in addition to stocks that occupy coastal waters. Ideally, ocean indicator data from the western Pacific Ocean is also being collected and could be accessed to determine the influence on recruitment for the steelhead that move further offshore.

In addition to U.S. IOOS Program, NOAA Fisheries also collects data on ocean conditions and juvenile abundance through its Northwest and Southwest Fisheries Science Centers. Since 1996, the Northwest Fisheries Science Center has monitored the ocean environment off the Washington and Oregon coasts, its interaction with the California Current, and how ocean conditions affect fisheries, focusing on juvenile salmonids. Each year conditions are synthesized and used to forecast Chinook and coho salmon returns, which are shared on the NOAA Fisheries website. The Southwest Fisheries Science Center also conducts surveys and publishes results of specific analyses (e.g., Wells et al. 2016).

Although the coastal ocean data is collected on a regular basis, little has been done to analyze and correlate the data with adult steelhead returns in general and specifically for fish from the San Joaquin River Basin. As such, no additional status and trend monitoring activities beyond what is currently being conducted on ocean conditions are recommended for the coastal areas. However, special studies are needed to synthesize and evaluate the data that is being collected in coastal areas and that is recommended for collection (or accessing) in offshore areas, as described in the next section.

Special studies

Special studies are needed to evaluate how ocean conditions relate to steelhead recruitment success such that ocean conditions could be used to predict recruitment success from year to year. To do this, it will first be necessary to determine where steelhead go after they migrate to the ocean. The distribution of steelhead stocks in the ocean is poorly understood and the available information, while limited, appears to indicate that interior stocks move farther offshore than coastal stocks and that both offshore areas and continental shelf areas are used by steelhead. To resolve how to relate ocean conditions to recruitment success and escapement, a special study focused on steelhead ocean migration patterns is needed to for San Joaquin River fish.

Once ocean migration patterns are more fully understood, synthesis and analysis of existing ocean conditions data would need to be conducted. This would include analysis of West Coast regional IOOS system data or data collected by NOAA Fisheries for steelhead residing in coastal waters, and similar data from the western Pacific Ocean for fish residing offshore. Ocean conditions that are important to monitor are similar to those being analyzed for Chinook and coho salmon off Washington and Oregon. These include climate and atmospheric indicators, local physical indicators, and local biological indicators, listed on NOAA Fisheries website. The synthesis and analysis would relate ocean conditions to recruitment success and ultimately to the number of spawning females returning to tributaries each year, which is the initial parameter proposed to estimate steelhead JPE. This will also help inform managers as to conditions that could be contributing to recruitment success and if water management decisions could help improve recruitment success and the overall JPE.

Returning Adults

Biology of Life Stage. Steelhead appear to use the earth's magnetic field to some extent to orient themselves in the open ocean (Walker et al. 1997). This compass-like orientation appears to shift towards more olfaction-based migration in rivers, though it remains unclear how and when the transition happens (Quinn 2005). Salmon and steelhead learn odors (e.g., chemical signatures) from their natal river prior to and/or during their juvenile outmigration into the ocean. This imprinting of natal site odors is what allows most adult salmonids to return to their home river/stream to spawn. The return of adults to their natal site, referred to as homing behavior, is a characteristic pattern observed in all salmonids. Despite the importance of homing behavior, straying (the failure to return to natal site or decision to spawn elsewhere) has also played a key role in the resilience of salmonids (Quinn 2005). Although straying is a natural component of salmonid life history, multiple studies on steelhead straying rates indicated that hatchery practices can lead to a higher straying rate (Schroeder et al. 2001, Clarke et al. 2014), likely due to reduced olfactory imprinting in juveniles. CCV steelhead typically begin to enter freshwater in August, with a peak around late September and October (Moyle 2002). It is believed that most steelhead would hold in deeper pools until flows are high enough in tributaries to enter for spawning, which generally occurs around December to March (McEwan 2001, Moyle 2002).

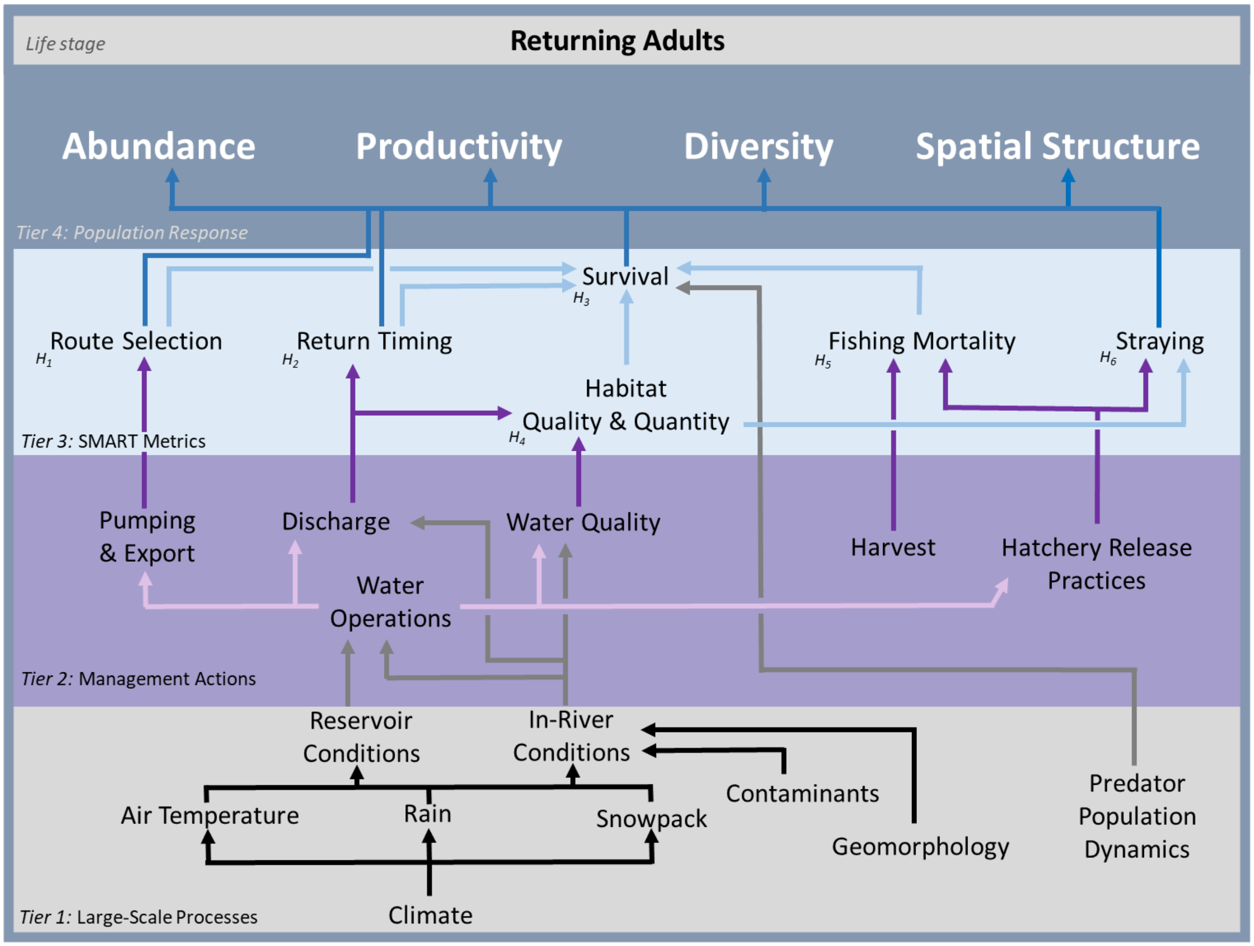

Figure 11: Returning adults conceptual model describing adult migration back to the spawning grounds of natal tributaries.

Monitoring and Special Study Considerations

The returning adults life history stage focuses on the time between freshwater entry and migration to their natal tributaries before spawning occurs. Similar to the ocean residence component of the steelhead lifecycle, returning adults is not a specific element of the conceptual framework of life-stage transitions and estimation of cohort parr and smolt abundance (Figure 2A, B). However, returning adults relates directly to the number, size, and condition of adult fish that return to their spawning grounds each year via the environmental conditions the fish encounter on their journey from the Golden Gate Bridge to their spawning tributaries. The number of spawning females directly relates to the number of redds, which is the initial element of the juvenile production estimation framework (Figure 2A, B). Therefore, understanding the environmental conditions encountered by returning adults and how those conditions impact survival and their ability to spawn directly relates to the JPE. Metrics selected to evaluate population response include route selection through the Delta (**H_1**), return timing (**H_2**), survival (**H_3**) of returning adults, habitat quality and quantity (**H_4**), and fishing mortality (**H_5**). Although hatchery fish are not the focus of the monitoring or special studies listed below, it is recognized that hatchery release practices can influence straying (**H_6**; Figure 11), which can affect the diversity of the adult population returning to spawn. It is also recognized that hatchery release numbers directly impact in-river harvest (**H_5**; Figure 11) allocations, which, in turn, have a direct effect on the overall abundance and productivity of returning adult spawners.

Status and trend monitoring

Status and trend monitoring for returning adults should focus on determining the number of adults that return to the spawning grounds. The number of adult steelhead returning to the spawning tributary before spawning is often determined using a counting survey at a barrier. In California, weirs that span the width of a river and funnel adult fish into a counting device (i.e., counting weirs), are in place at certain tributaries (Eilers et al. 2010). In other places, such as Hood River, Oregon, the Powerdale Dam itself allows for complete sampling of all returning adult steelhead (Christie et al. 2011). This type of method can provide fairly accurate numbers of returning steelhead into a tributary and can be effectively linked to other studies. The counting process can be automated or operated remotely (e.g., VAKI Riverwatcher fish counter or Dual-frequency Identification Sonar [DIDSON], which has been updated to ARIS), and when counting manually, sampling of tissue for other data collection needs may be done. For example, scales can be collected for age structure information and fin clips or mucus swabs can be acquired for genetic information. With genetic data, one can potentially evaluate the propensity of the tributary to produce steelhead (Pearse et al. 2014), the fitness of hatchery vs. wild fish (Araki et al. 2007, Christie et al. 2012), the fitness of resident vs. anadromous fish (Christie et al. 2011), and other information useful for understanding the structure, diversity and productivity of the Southern Sierra Nevada Diversity Group. However, despite these advantages, counting weirs are only feasible in smaller tributaries because they often cannot be operated during high flow periods and ignore resident spawners in the system (Eschenroeder et al. 2022). For larger tributaries, fyke traps can be used instead to sample returning steelhead. This method has similar advantages to the counting weirs in that tissue samples can also be collected for additional information. However, the efficiency of fyke traps can often be low and operating the necessary number of traps to gain the proper statistical power may be costly (Eschenroeder et al. 2022). Another method for large rivers where weirs cannot be installed is to use nets or pickets to guide adult fish into an area where they can be counted with an ARIS. Fish would not be handled, so no other data could be obtained. ARIS systems can count fish to a distance of 15 m or 35 m, depending on the model.

This status and trends monitoring should be done on an annual basis and should focus on the time of the year when most fish return to the spawning grounds (i.e., September through June). Data on the estimated number of fish arriving each at tributaries where steelhead are likely to spawn can be combined with information from the Delta to inform survival through the Lower San Joaquin River and redd counts to inform holding conditions and pre-spawn mortality rates. Together this information can be used to identify issues that may need to be addressed to improve survival conditions.

As described in the 2010 Central Valley Steelhead Monitoring Plan (Eilers et al. 2010), the following tributary counting systems are likely suitable for monitoring the Southern Sierra Nevada Diversity Group of steelhead. These tributaries were selected based on their potential to support a viable population of steelhead (Eilers et al. 2010):

- Mokelumne River—East Bay Municipal Utility District monitors fish passage using video monitoring in the fish ladder at the Woodbridge Irrigation District Dam. However, the video monitoring is limited based on the dam gate operations and does not operate throughout the steelhead spawning migration period. There is a need to install a weir with a fish counter device above or below the dam to monitor steelhead from September to June each year. The number of returning hatchery fish and naturally produced fish should also be determined given the operation of the Mokelumne Hatchery adjacent to Camanche Dam.
- Calaveras River—There are no existing counting systems in place, but it is recommended that one be installed using a resistance board weir and VAKI Riverwatcher fish counter system, or horizontal-bar weir with a video camera and DIDSON.
- Stanislaus River—Currently there is a resistance board weir and VAKI Riverwatcher fish counter system (or similar) in place that is used for monitoring Chinook salmon. It is recommended that this system operate through June and be used to count returning steelhead adults since the current monitoring only goes until December.
- Tuolumne River— Currently there is a resistance board weir and VAKI Riverwatcher fish counter system (or similar) in place that is used for monitoring Chinook salmon. It is recommended that this monitoring be expanded to include steelhead between September and June.
- Merced River—There are no existing counting systems in place, but it is recommended that a resistance board weir and VAKI Riverwatcher fish counter system (or similar) installed to monitor for steelhead between September and June.

Special studies

Little is known about how adult steelhead navigate through the Delta and how water operations and management actions influence navigational cues. To address this data gap, a telemetry study of adult steelhead is needed to determine how the Delta water operations and management actions influence navigational cues and migration rates for returning adults as measured by route selection, migration delays, and stray rates and how those conditions impact survival and fish condition/health when they arrive at the spawning grounds. The amount of energy and quality of health of returning adults at spawning is greatly impacted by not only the length of time it takes a fish to move through the Delta but also the conditions the fish encounters along the way. Autonomous acoustic telemetry receivers could be placed throughout the Delta at key junctions and routes to detect fish that were collected in tributary counting systems, tagged, and released downstream to reascend through Delta routes.

Little is known about adult survival through the lower San Joaquin River and survival and holding behavior prior to spawning in tributaries. To address this data gap, additional acoustic receivers could be deployed to track fish tagged and released in the lower Delta (described above) while migrating through the lower San Joaquin River, entering tributaries, and holding. Target rivers should include tributaries with the most potential to support steelhead, including the Mokelumne, Calaveras, Stanislaus, Tuolumne, and Merced (Eilers et. al. 2010). The study should answer the following questions: 1) What is survival through various river reaches given flow, water quality, and amount of Submerged Aquatic Vegetation, 2) where are fish holding in tributaries and for how long, 3) is the habitat quality and quantity sufficient to support adult holding (e.g., are there sufficient pools and is the water temperature and dissolved oxygen in the range needed to support adult steelhead), and 4) are fish affected by or redistribute in the tributary due to freshets and flow conditions below dams in each target river such that spawn timing to success is affected? A study to evaluate the accuracy and variability of the method selected to count adult fish should also be done to support the annual abundance status and trend monitoring. Potential methods include comparing device counts to paired visual counts, use artificial known targets to determine count error rates for various conditions; or compare counts using two different methods (Eilers et. al. 2010).

Data Guidance

Data are a fundamental product of monitoring and form the basis in which abundance estimates, life cycle model, and decision support tool are constructed. Ultimately, these monitoring data provide the means to inform ourselves on the environmental impacts that drive steelhead population dynamics (e.g., water project operations, habitat restoration, hatcheries, and harvest). The goal of this data guidance section is to increase, manage, and protect the value of data needed and generated by the existing and future steelhead surveys in the San Joaquin basin. We acknowledge that data management requires a substantial amount of effort. For many monitoring projects, this will likely require staff members dedicated to data management, which should be considered at the initiation of any monitoring project.

Data Management Plan

Monitoring projects or surveys should state how they address the monitoring goals listed in this document. Subsequently, monitoring projects should specify the purpose of the monitoring, the management question the monitoring is designed to answer, the types of data to be collected, the location to be monitored, and the interval at which data will be collected and published. This includes establishing detailed description on data generation, organization, and how it will be preserved (an especially important step prior to initiating a new monitoring project). Data should be managed so that anyone (including data collectors) can discover, use and interpret the data after a period of time has passed (DataONE 2021). Quality assurance and control should also be a part of any monitoring project's data management plan. Effective decision making ultimately would require data that are largely error free and of the appropriate type and quality. A proper quality assurance and control protocol should allow for early detection of errors at various stages of the data collection process (e.g., field sampling, data entry, data summary, model estimation, etc.).

Metadata Standards

The goal of monitoring projects should be to produce self-describing datasets through a proper metadata. Metadata is information about data that describes the 'who, what, where, when, why, and how' of data sets. Metadata is a critical component of a data set because it ensures the correct use and interpretation of the data by its owners and users. Although metadata varies in format and content, there are several basic elements common across multiple metadata standards. Monitoring projects can use established metadata standards or formats (e.g., Ecological Metadata Language, Federal Geographic Data Committee schema, etc.) to increase the utility of their data.

Data Accessibility

Data (new and historical) should be open and when possible, centralized. Open data means that the full dataset (i.e., not data summary) is available and easily accessible without requiring a request or permission of some sort. Having open data ensures a smooth dataset integration across steelhead monitoring projects for abundance estimation or other analyses central to answering key management questions. Open data also allows others verify findings and correct any errors that the data collectors may have missed. When posting datasets, we recommended the use of machine-readable, stable, non-proprietary, and standardized data formats (e.g., .csv).

Centralization of data is key for efficient data integration and analyses. We recommend the posting of data from monitoring projects to widely used data repository websites with metadata standards. The Environmental Data Initiative (EDI) is one example of such data repository that is gaining interest in the system. EDI is a National Science Foundation funded project that actively promotes and enables curation and re-use of environmental data. EDI supports high-level analysis and synthesis of complex ecosystem data across the science-policy-management continuum and host to the Long-Term Ecological Research network. Other data repository options include the Bureau of Reclamation Information Sharing Environment and the California Natural Resource Agency data portal.

A component to consider when selecting data repository is whether it offers a Digital Object Identifier (DOI) for data sets and allows for easy versioning (to allow access to previous versions of the data set). DOI is a universally recognized alphanumeric sequence assigned by a registration agency (e.g., DataCite or Crossref) to provide a persistent link to the data package's online location. Having a DOI assigned to a data package facilitates data discovery, usage tracking, documentation of data set versions, and retention of the relationship between a data set and its metadata. Publication of dataset with a DOI also allows the data collectors to receive proper credit through citation and increase opportunities for collaboration.

Acknowledgments

We thank Lenny Grimaldo, Jeffrey McLain, and Tony Yang for providing review to this document. Karissa Bridges provided information for Table 2. The statements, findings, conclusions, and recommendations are those of the authors and do not necessarily reflect the views of the Bureau of Reclamation, USFWS, or NMFS.

This page intentionally left blank.

Literature Cited

Abadía-Cardoso, Alicia, Clemento, A.J. and Garza, J.C., 2011. Discovery and characterization of single-nucleotide polymorphisms in steelhead/rainbow trout, Oncorhynchus mykiss. Molecular Ecology Resources, 11, pp.31-49.

Apperson, K.A., Copeland, T., Flinders, J.M., Kennedy, P.A. and Roberts, R.V., 2015. Field protocols for stream snorkel surveys and efficiency evaluations for anadromous parr monitoring. Idaho Department of Fish and Game.

Araki, H., Berejikian, B.A., Ford, M.J., and Blouin, M.S. 2008. Fitness of hatchery-reared salmonids in the wild. Evolutionary Applications 1:342-355.

Araki, H., Cooper, B., & Blouin, M. S. (2007). Genetic Effects of Captive Breeding Cause a Rapid, Cumulative Fitness Decline in the Wild. Science, 318, 100–103. https://doi.org/10.1126/science.1145621

Armstrong, J.B., Schindler, D.E. Going with the Flow: Spatial Distributions of Juvenile Coho Salmon Track an Annually Shifting Mosaic of Water Temperature. Ecosystems 16, 1429–1441 (2013). https://doi.org/10.1007/s10021-013-9693-9

Baxter, J.S. 1997. Kispiox River Steelhead: Summary of Current Data and Status Review, 1997. British Columbia Ministry of Environment, Lands, and Parks. Skeena Fisheries Report SK-100, 83 pages.

Baxter, R., Brown, L.R., Castillo, G., Conrad, L., Culberson, S.D., Dekar, M.P., Dekar, M., Feyrer, F., Hunt, T., Jones, K. and Kirsch, J. 2015. An updated conceptual model of Delta Smelt biology: our evolving understanding of an estuarine fish (No. 90). Interagency Ecological Program, California Department of Water Resources.

Beakes, M.P., Satterthwaite, W.H., Collins, E.M., Swank, D.R., Merz, J.E., Titus, R.G., Sogard, S.M. and Mangel, M. 2010. Smolt transformation in two California steelhead populations: effects of temporal variability in growth. Transactions of the American Fisheries Society 139:1263-1275.

Beakes, M.P., Moore, J.W., Hayes, S.A. and Sogard, S.M. 2014. Wildfire and the effects of shifting stream temperature on salmonids. Ecosphere 5:1-14.

Beakes, M., Bilski, R., Matthias, B., Byrne, B., Vick, P. and Goertler, P. 2021 *Oncorhynchus mykiss* Monitoring and Research Gap Analysis. In Monitoring Steelhead Populations in the San Joaquin Basin. Edited by Delta Science Program - Delta Stewardship Council, Joint Delta Science Program – U.S. Bureau of Reclamation Workshop, Sacramento, CA. DOI: 10.13140/RG.2.2.29383.21927 (https://deltacouncil.ca.gov/pdf/science-program/fact-sheets/2021-02-03-monitoring-steelhead-populations-monitoring-and-research-gap-analysis.pdf)

Becker, C.D., Neitzel, D.A., and Fickeisen, D.H. 1982. Effects of dewatering on Chinook Salmon redds: tolerance of four developmental phases to daily dewaterings. Transactions of the American Fisheries Society 111:624–637. doi:10.1577/1548-8659(1982) 1112.0.CO;2.

Bellmore, J.R., Baxter, C.V., Martens, K., Connolly, P.J. 2013. The floodplain food web mosaic: a study of its importance to salmon and steelhead with implications for their recovery. Ecological Applications 23: 189–207. https://doi.org/10.1890/12-0806.1

Benjamin, J.R., Connolly, P.J., Romine, J.G. and Perry, R.W. 2013. Potential effects of changes in temperature and food resources on life history trajectories of juvenile Oncorhynchus mykiss. Transactions of the American Fisheries Society 142:208-220.

Bennett, D.H., Connor, W.P., and Eaton, C.A. 2003. Substrate composition and emergence success of fall Chinook salmon in the Snake River. Northwest Science 77:93–99.

Berdahl, A., Westley, P.A.H., Levin, S.A., Couzin, I.D., and Quinn, T.P. 2014. A collective navigation hypothesis for homeward migration in anadromous salmonids. Fish and Fisheries 17:525-542. DOI:10.1111/faf.12084

Berejikian, B.A., Campbell, L.A. and Moore, M.E. 2013. Large-scale freshwater habitat features influence the degree of anadromy in eight Hood Canal Oncorhynchus mykiss populations. Canadian Journal of Fisheries and Aquatic Sciences 70:756-765.

Beschta, R. L., and Jackson, W. L. 1979. The intrusion of fine sediments into a stable gravel bed. Journal of the Fisheries Research Board Canada 36. p.204–210.

Bjornn, T.C. 1978. Survival, production, and yield of trout and chinook salmon in the Lemhi River, Idaho A Final Report for Federal Aid to Fish Restoration, Project F-49-R, Salmon and Steelhead Investigations. Idaho Cooperative Fishery Research Unit, College of Forestry, Wildlife and Range Sciences, University of Idaho.

Bond, M.H., Hayes, S.A., Hanson, C.V. and MacFarlane, R.B., 2008. Marine survival of steelhead (Oncorhynchus mykiss) enhanced by a seasonally closed estuary. Canadian Journal of Fisheries and Aquatic Sciences, 65(10), pp.2242-2252.

Booth, M.T., 2020. Patterns and Potential Drivers of Steelhead Smolt Migration in Southern California. North American Journal of Fisheries Management, 40:4, pp.1032-1050.

Boughton, B., Nelson, J., and Lacy, M.K. 2022. Integration of Steelhead Viability Monitoring, Recovery Plans and Fisheries Management in the Southern Coastal Area. State of California The Natural Resources Agency Department of Fish and Wildlife. Fish Bulletin 182. pp. 1-116.

Box, G.E., Hunter, J.S. and Hunter, W.G., 2005. Statistics for experimenters. In Wiley series in probability and statistics. Hoboken, NJ: Wiley.

Bratovich, P., Link, G.W., Ellrott, B.J., and Pinero, J.A. 2005. Impacts on Lower American River Salmonids and Recommendations Associated with Folsom Reservoir Operations to Meet Delta Water Quality Objectives and Demands (Draft Report). Surface Water Resources Inc., Sacramento, California.

Brewitt, K.S. and Danner, E.M., 2014. Spatio-temporal temperature variation influences juvenile steelhead (*Oncorhynchus mykiss*) use of thermal refuges. Ecosphere, 5(7), pp.1-26.

Brodeur, R.D., Fisher, J.P., Teel, D.J., Emmett, R.L., Casillas, E. and Miller, T.W. 2004. Juvenile Salmonid distribution, growth, condition, origin, and environmental and species associations in the Northern California Current. Fishery Bulletin 102:25–46.

Brown, R.A., and Pasternack, G.B. 2008. Engineered channel controls limiting spawning habitat rehabilitation success on regulated gravel-bed rivers. Geomorphology 97:3-4. doi: 10.1016/j.geomorph.2007.09.012.

Buchanan, R.A., Brandes, P.L., and Skalski, J.R. 2018. Survival of juvenile fall-run Chinook salmon through the San Joaquin River Delta, California, 2010-2015. North American Journal of Fisheries Management 38:663-679. https://doi.org/10.1002/nafm.10063

Buchanan, R.A., Buttermore, E., and Israel, J. 2021. Outmigration survival of a threatened steelhead population through a tidal estuary. Canadian Journal of Fisheries and Aquatic Sciences 78:1869-1886.

Buchanan, R.A. and Skalski, J.R. 2020. Relating survival of fall-run Chinook salmon through the San Joaquin Delta to river flow. Environmental Biology of Fishes 103:389-410. https://doi.org/10.1007/s10641-019-00918-y

Buchanan, R.A. and Whitlock, S.L. 2022. Understanding salmon migration dynamics in a data-limited environment. North American Journal of Fisheries Management. https://doi.org/10.1002/nafm.10799

Burgner, R.L., Light, J.T., Margolis, L., Okazaki, T., Tautz, A., and Ito, S. 1992. Distribution and origins of steelhead trout (Oncorhynchus mykiss) in offshore waters of the North Pacific Ocean. International North Pacific Fisheries Commission, Bulletin 51, 101 p.

Busby, P.J., Wainwright, T.C., Bryant, G.J., Lierheimer, L.J., Waples, R.S., Waknitz, F.W., and Lagomarsino, F.W. 1996. Status Review of West Coast Steelhead from Washington, Idaho, Oregon, and California. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-NWFSC-27.

California Data Exchange Center [CDEC]. 2022. Sacramento (CA): Department of Water Resources; [cited 2022 Jun 22]. Available from: http://cdec.water.ca.gov/

California Department of Fish and Game (CDFG). 1996. Steelhead Restoration and Management Plan for California. California Department of Fish and Game. February 1996. Sacramento, CA 234pp.

California Department of Fish and Wildlife (CDFW). 2021a. Steelhead report and restoration card program report to the legislature 2015-2019, 24 p.

California Department of Fish and Wildlife (CDFW). 2021b. 2018-2019 Mokelumne River Hatchery California Central Valley steelhead trout spawning and release protocol. Draft procedures and protocols for 2018-2019 steelhead trout spawning operations at Mokelumne River Hatchery –subject to revisions-, January 15, 2019, 17 p.

California Department of Water Resources (DWR). 2018. Clifton Court Forebay predatory fish relocation study. Biological assessment 140883.12 https://www.noaa.gov/sites/default/files/legacy/document/2020/Oct/0.7.115.9071-000006.pdf

Canessa, S., Guillera-Arroita, G., Lahoz-Monfort, J.J., Southwell, D.M., Armstrong, D.P., Chadès, I., Lacy, R.C. and Converse, S.J. 2015. When do we need more data? A primer on calculating the value of information for applied ecologists. Methods Ecol Evol, 6: 1219-1228. https://doi.org/10.1111/2041-210X.12423

Carlson, S.M. and Seamons, T.R. 2008. A review of quantitative genetic components of fitness in salmonids: implications for adaptation to future change. Evolutionary Applications 1:222-238.

Carter, K. 2005. The effects of dissolved oxygen on steelhead trout, Coho salmon, and Chinook salmon biology and function by life stage. California Regional Water Quality Control Board North Coast Region, Santa Rosa, California, USA.

Castle, C., and Jackson, Z. 2014. Egg survival and emergence reaches 1A and 1B in the San Joaquin River restoration area. 2014 mid-year teachnical report for the SJRRP. U.S. Fish and Wildlife Service. Lodi, CA.

Cavallo, B., Merz, J., Setka, J. 2012. Effects of predator and flow manipulation on Chinook fish (Oncorhynchus tshawytscha) survival in an imperiled estuary. Environmental Biology of Fishes 96: 393-403. doi: http://dx.doi.org/10.1007/s10641-012-9993-5

Chapman, D.W. 1988. Critical review of variables used to define effects of fines in redds of large salmonids. Transactions of the American Fisheries Society 117:1–21.

Chelberg, J. 2023. Redd Dewatering and Juvenile Stranding in the Upper Sacramento River Year 2022-2023. California Department of Fish and Wildlife. RBFO Technical Report. (No. 01-2023), 37 pages.

Christie, M. R., Marine, M. L., & Blouin, M. S. (2011). Who are the missing parents? Grandparentage analysis identifies multiple sources of gene flow into a wild population. Molecular Ecology, 20(6), 1263–1276. https://doi.org/10.1111/j.1365-294X.2010.04994.x

Christie, M. R., Marine, M. L., French, R. A., Waples, R. S., & Blouin, M. S. (2012). Effective size of a wild salmonid population is greatly reduced by hatchery supplementation. Heredity, 109(4), 254–260. https://doi.org/10.1038/hdy.2012.39

Clarke, L. R., Flesher, M. W., & Carmichael, R. W. (2014). Hatchery Steelhead Smolt Release Size Effects on Adult Production and Straying. North American Journal of Aquaculture, 76(1), 39–44. https://doi.org/10.1080/15222055.2013.837127

Conner, M.M., Bennett, S.N., Saunders, W.C. and Bouwes, N., 2015. Comparison of tributary survival estimates of steelhead using Cormack–Jolly–Seber and Barker models: implications for sampling efforts and designs. Transactions of the american fisheries society, 144:1, pp.34-47.

Conner, M.M., Budy, P.E., Wilkison, R.A., Mills, M., Speas, D., Mackinnon, P.D. and Mckinstry, M.C., 2020. Estimating population abundance with a mixture of physical capture and PIT tag antenna detection data. Canadian Journal of Fisheries and Aquatic Sciences, 77(7), pp.1163-1171.

Conrad, J.L., Bibian, A.J., Weinersmith, K.L., De Carion, D., Young, M.J., Crain, P., Hestir, E.L., Santos, M.J., and Sih, A. 2016. Novel species interaction in a highly modified estuary: association of largemouth bass with Brazilian waterweed Egeria densa. Transactions of the Americal Fisheries Society 145:249–263. doi:10.1080/00028487.2015.1114521.

Cordoleani, F., Phillis, C.C., Sturrock, A.M., FitzGerald, A.M., Malkassian, A., Whitman, G.E., Weber, P.K. and Johnson, R.C., 2021. Threatened salmon rely on a rare life history strategy in a warming landscape. Nature Climate Change, 11:11, pp.982-988.

Cordoleani, F., Ammann, A., Johnson, R., Kelly, J., Notch, J., Michel, C., Tracy, E. 2024. Summary of Interagency Telemetry Advisory Group Activities -Water Year 2023. doi:10.13140/RG.2.2.11441.76642.

Courter, I., Justice, C., and Cramer, S. 2009. Flow and temperature effects on life history diversity of Oncorhynchus mykiss in the Yakima River basin. Cramer Fish Sciences, Gresham, Ore.

Cramer, S.P., and Beamesderfer, R.C.P. 2006. Population Dynamics, Habitat Capacity, and a Life History Simulation Model for Steelhead in the Deschutes River, Oregon. Prepared for Portland General Electric, Portland, OR.

Crozier, L.G., McClure, M.M., Beechie, T., Bograd, S.J., Boughton, D.A., Carr, M., et al. 2019. Climate vulnerability assessment for Pacific salmon and steelhead in the California Current Large Marine Ecosystem. PLoS ONE 14: e0217711. https://doi.org/10.1371/journal.pone.0217711

Cunjak, R.A. and J. Therrien. 1998. Inter-stage survival of wild juvenile Atlantic salmon, Salmo salar L. Fisheries Management and Ecology 5:209-223.

Daly, E.A., Brodeur, R.D., Fisher, J.P., Weitkamp, L.A., Teel, D.J., and Beckman, B.R. 2012. Spatial and trophic overlap of marked and unmarked Columbia River Basin spring Chinook salmon during early marine residence with implications for competition between hatchery and naturally produced fish. Environmental Biology of Fishes 94:117-134.

Daly, E.A., Scheurer, J.A., Brodeur, R.D., Weitkamp, L.A., Beckman, B.R., and Miller, J.A. 2014. Juvenile steelhead distribution, migration, growth, and feeding in the Columbia River estuary, plume, and coastal waters. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science [online serial] 6:62–80.

Dodson, J.J., Aubin-Horth, N., Thériault, V. and Páez, D.J. 2013. The evolutionary ecology of alternative migratory tactics in salmonid fishes. Biological Reviews 88:602-625.

Department of Fish and Wildlife (California) and United States Fish and Wildlife Service. 2010. Final Hatchery and Stocking Program Environmental Impact Report/ Environmental Impact Statement, Appendix A, Hatchery Operations 56 pp.

Devries, P. 1997. Riverine salmonid egg burial depths: review of published data and implications for scour studies. Canadian Journal of Fisheries and Aquatic Sciences 54:1685-1698.

Ebersole, J.L., Liss, W.J., and Frissell, C.A. 2001. Relationship between stream temperature, thermal refugia and rainbow trout Oncorhynchus mykiss abundance in arid-land streams in the northwestern United States. Ecology of Freshwater Fish 10:1–10.

Eilers, C.D. 2010. Review of present steelhead monitoring programs in the California Central Valley May 2008. Fisheries Branch Administrative Report Number: 2010-1

Ellrott, B., Johnson, R., and Brown, H. 2021. California Central Valley Steelhead Distinct Population Segment Factsheet Author List California Central Valley Steelhead Distinct Population Segment (DPS) Definition. DOI: 10.13140/RG.2.2.30997.04329

Emmett, R.L. and Krutzikowsky, G.K. 2008. Nocturnal feeding of Pacific hake and jack mackerel off the mouth of the Columbia River, 1998-2008: implications for juvenile salmon predation. Transactions of the American Fisheries Society 137:657-676.

Eschenroeder, J., Peterson, M., Hellmair, M., Pilger, T. J., Demko, D., & Fuller, A. (2022). Counting the Parts to Understand the Whole: Rethinking Monitoring of Steelhead in California's Central Valley. San Francisco Estuary and Watershed Science, 20(1). https://doi.org/10.15447/sfews.2022v20iss1art2

Finstad, A.G. and Hein, C.L. 2012. Migrate or stay: terrestrial primary productivity and climate drive anadromy in Arctic char. Global Change Biology 18:2487-2497.

Fisk, J.M., III, Kwak, T.J., Heise, R.J., and Sessions, F.W. 2013. Redd dewatering effects on hatching and larval survival of the robust redhorse. River Research Applications 29:574–581. doi:10.1002/rra.2561.

Fortier, R., Nelson, J., Bellmer, R., and Nielson, R. 2014. Implementation Plan for the Central Valley Steelhead Monitoring Program. California Department of Fish and Wildlife, Fisheries Branch. July 2014.

Gard, M. 2009. Comparison of spawning habitat predictions of PHABSIM and River2D models. International Journal of River Basin Management 7(1): 55-71. doi: 10.1080/15715124.2009.9635370.

Goertler, P., Mahardja, B., and Sommer, T. 2021. Striped bass (*Morone saxatilis*) migration timing driven by estuary outflow and sea surface temperature in the San Francisco Bay-Delta, California. Scientific Reports 1510:1-11. https://doi.org/10.1038/s41598-020-80517-5

Goetz, L.C., Nuetzel, H., Vendrami, D.L., Beulke, A.K., Anderson, E.C., Garza, J.C. and Pearse, D.E., 2024. Genetic parentage reveals the (un) natural history of Central Valley hatchery steelhead. Evolutionary Applications, 17(3), p.e13681.

Good, T. P., R. S. Waples, and P. Adams. 2005. Updated Status of Federally Listed ESUs of West Coast Salmon and Steelhead. Pages 1-598 in National Marine Fisheries Service, editor.

Goodman, D.H., Som, N.A., and Hetrick, N.J. 2018. Increasing the availability and spatial variation of spawning habitats through ascending baseflows. River Research Applications 34:844-853. doi: 10.1002/rra.3302.

Grantham, T.E., Newburn, D.A., McCarthy, M.A. and Merenlender, A.M., 2012. The role of streamflow and land use in limiting oversummer survival of juvenile steelhead in California streams. Transactions of the American Fisheries Society, 141(3), pp.585-598.

Greig, S.M., Sear, D.A., and Carling, P.A. 2007. A review of factors influencing the availability of dissolved oxygen to incubating salmonid embryos. Hydrological Processes 21: 323-334.

Grossman, G.D. 2016. Predation on fishes in the Sacramento–San Joaquin Delta: current knowledge and future directions. San Francisco Estuary and Watershed Science 14:1-23. http://dx.doi.org/10.15447/sfews.2016v14iss2art8

Grossman, G.D., Essington, T., Johnson, B., Miller, J.A., Monsen, N.E., and Pearsons, T.N. 2013. Effects of fish predation on salmonids in the Sacramento River–San Joaquin Delta and associated ecosystems. Panel final report: 71 p. Sacramento (CA): California Department Fish Wildlife, Delta Stewardship Council, and National Marine Fisheries Service. https://nrm.dfg.ca.gov/FileHandler.ashx?DocumentID=73874

Hagen, J., Decker, S., Korman, J. and Bison, R.G., 2010. Effectiveness of night snorkeling for estimating steelhead parr abundance in a large river basin. North American Journal of Fisheries Management, 30:5, pp.1303-1314.

Hallock, R.J., W.F. Van Woert, and L. Shapolov. 1961. An Evaluation of Stocking Hatcheryreared Steelhead Rainbow Trout (*Salmo gairdnerii gairdnerii*) in the Sacramento River System. California Department of Fish and Game. Fish Bulletin 114. 74 p.

Hallock, R. J. 1989. Upper Sacramento River steelhead (*Oncorhynchus mykiss*), 1952–1988. Report to the Fish and Wildlife Service, Sacramento, California.

Hankin, D.G. and Reeves, G.H., 1988. Estimating total fish abundance and total habitat area in small streams based on visual estimation methods. Canadian journal of fisheries and aquatic sciences, 45:5, pp.834-844.

Harnish, R.A., Green, E.D., Vernon, C.R. and Mcmichael, G.A., 2014. Ecological interactions between hatchery summer steelhead and wild Oncorhynchus mykiss in the Willamette River basin, 2014 (No. PNNL-23891). Pacific Northwest National Lab.(PNNL), Richland, WA (United States).

Harvey, B., Sommer, T., Nelson, P., Baerwald, M., Gille, D., Kindopp, J., et al. 2020. Incidental take permit spring-run Chinook Salmon juvenile production estimate science plan 2020-2024 California Department of Water Resources and others. December 2020.

Hasler, A.D. and W.J. Wisby. 1951. Discrimination of stream odors by fishes and its relation to parent stream behavior. The American Naturalist 823:223-238.

Hausch, S.J. and Melnychuk, M.C., 2012. Residualization of hatchery steelhead: a meta-analysis of hatchery practices. North American Journal of Fisheries Management, 32(5), pp.905-921.

Hayes, S.A., Bond, M.H., Hanson, C.V., Freund, E.V., Smith, J.J., Anderson, E.C., Ammann, A.J. and MacFarlane, R.B., 2008. Steelhead growth in a small central California watershed:

upstream and estuarine rearing patterns. Transactions of the American Fisheries Society, 137(1), pp.114-128.

Hayes, S.A., Bond, M.H., Hanson, C.V., Jones, A.W., Ammann, A.J., Harding, J.A., Collins, A.L., Perez, J. and MacFarlane, R.B. 2011. Down, up, down and "smolting" twice? Seasonal movement patterns by juvenile steelhead (*Oncorhynchus mykiss*) in a coastal watershed with a bar closing estuary. Canadian Journal of Fisheries and Aquatic Sciences 68:1341-1350.

Hazel, W.N., Smock, R., and Johnson, M.D. 1990. A polygenic model for the evolution and maintenance of conditional strategies. Proceedings of the Royal Society: B Biological Sciences 242:181–187. doi:10.1098/rspb.1990.0122.

Healey, M.C. 1991. Life history of Chinook salmon (Oncorhynchus tshawytscha). In: Groot, C, Margolis, L, editors. Pacific salmon life histories. P. 311-394.

Hendrix, N., Osterback, A.M.K., Jennings, E., Danner, E. Sridharan, V., Greene, C.M., and Lindley, S.T. 2017. Model description for the Sacramento River winter-run Chinook Salmon life cycle model. Appendix H of California WaterFix Biological Opinion prepared by NOAA Fisheries, 45 p.

Hendry, A.P., Bohlin, T., Jonsson, B., and Berg, O.K. 2004. To sea or not to sea? Anadromy versus non-anadromy in salmonids. In Evolution illuminated: salmon and their relatives. Edited by A.P. Hendry and S.C. Stearns. Oxford University Press, Oxford. pp. 92–125.

Hillman, T.W., Mullan, J.W. and Griffith, J.S., 1992. Accuracy of underwater counts of juvenile chinook salmon, coho salmon, and steelhead. North American Journal of Fisheries Management, 12:3, pp.598-603.

Hodge, B.W., Wilzbach, M.A., Duffy, W.G., Quiñones, R.M. and Hobbs, J.A. 2016. Life history diversity in Klamath River steelhead. Transactions of the American Fisheries Society 145:227-238.

Holmes, R.W., Allen, M.A. and Bros-Seeman, S. 2014. Seasonal microhabitat selectivity by juvenile steelhead in a central California coastal river. California Fish and Game 100:590-615.

Huber, E.R., Ryan, R., Johnson, R.C., Sturrock, A.M., Lusardi, R.A., and Carlson, S.M. 2024. Seventy years of diminishing biocomplexity of California Central Valley steelhead, *Oncorhynchus mykiss.* Canadian Journal of Fisheries and Aquatic Sciences 81: 355-367. https://doi.org/10.1139/cjfas-2023-0077 Hutchings, J.A. 2011. Old wine in new bottles: reaction norms in salmonid fishes. Heredity 106:421-437.

Imre, I., Grant, J.W.A. and Keeley, E.R., 2004. The effect of food abundance on territory size and population density of juvenile steelhead trout (*Oncorhynchus mykiss*). Oecologia, 138(3), pp.371-378.

Interagency Ecological Program Management Analysis and Synthesis Team (IEP MAST). 2015. An updated conceptual model of Delta Smelt biology: our evolving understanding of an estuarine fish. Technical Report 90; January 2015. 206pp.

Interagency Ecological Program (IEP), McKenzie, R., Speegle, J., Nanninga, A., Cook, J.R., and Hagen, J. 2021. Interagency Ecological Program: Over four decades of juvenile fish monitoring data from the San Francisco Estuary, collected by the Delta Juvenile Fish Monitoring Program, 1976-2021 ver 8. Environmental Data Initiative. https://doi.org/10.6073/pasta/8dfe5eac4ecf157b7b91ced772aa214a (Accessed 2022-04-04).

Isaak, D.J., Ver Hoef, J.M., Peterson, E.E., Horan, D.L. and Nagel, D.E., 2017. Scalable population estimates using spatial-stream-network models, fish density surveys, and national geospatial database frameworks for streams. Canadian Journal of Fisheries and Aquatic Sciences, 74:2, pp.147-156.

Jeffres, C.A., Opperman, J.J. & Moyle, P.B. Ephemeral floodplain habitats provide best growth conditions for juvenile Chinook salmon in a California river. Environ Biol Fish 83, 449–458 (2008). https://doi.org/10.1007/s10641-008-9367-1

Jensen, D.W., Steel, E.A., Fullerton, A.H., and Pess, G.R. 2009. Impacts of fine sediment on egg-to-fry survival of pacific salmon: A meta-analysis of published studies. Reviews in Fisheries Science 17: 348-359. doi: 10.1080/10641260902716954.

Johnson, R.C., P.K. Weber, J.D. Wikert, M.L. Workman, R.B. MacFarlane, M.J. Grove, and A.K. Schmitt. 2012. Managed metapopulations: Do salmon hatchery “sources” lead to in-river “sinks” in conservation? PLoS ONE 7(2).

Johnson, R.C., Garza, J.C., MacFarlane, R.B., Phillis, C.C., Koch, P.L., Weber, P.K., and Carr M.H. 2016. Isotopes and genes reveal freshwater origins of Chinook salmon (Oncorhynchus tshawytscha) aggregations in California’s coastal ocean. Marine Ecology Progress Series 548:181–196. doi:10.3354/MEPS11623.

Johnson, R. C., Windell, S., Brandes, P. L., Conrad, J. L., Ferguson, J., Goertler, P. A. L., Harvey, B. N., Heublein, J., Israel, J. A., Kratville, D. W., Kirsch, J. E., Perry, R. W., Pisciooto, J., Poytress, W. R., Reece, K., & Swart, B. G. (2017). Science Advancements Key to Increasing Management Value of Life Stage Monitoring Networks for Endangered Sacramento River Winter-Run Chinook Salmon in California. San Francisco Estuary and Watershed Science, 15(3). https://doi.org/10.15447/sfews.2017v15iss3art1 A

Keefer, M.L., Peery, C.A., and Caudill, C.C. 2008. Migration Timing of Columbia River Spring Chinook Salmon: Effects of Temperature, River Discharge, and Ocean Environment. Transactions of the American Fisheries Society 137:1120–1133.

Keefer, M.L. and Caudill, C.C. 2013. Homing and straying by anadromous salmonids: a review of mechanisms and rates. Reviews in Fish Biology and Fisheries 24:333. doi: https://doi.org/10.1007/s11160-013-9334-6

Keeley, E.R. 2001. Demographic responses to food and space competition. Ecology 82:1247–1259.

Kelson, S.J., Miller, M.R., Thompson, T.Q., O’Rourke, S.M. and Carlson, S.M. 2019. Do genomics and sex predict migration in a partially migratory salmonid fish, Oncorhynchus mykiss? Canadian Journal of Fisheries and Aquatic Sciences 76:2080-2088.

Kelson, S.J., Carlson, S.M. and Miller, M.R. 2020. Indirect genetic control of migration in a salmonid fish. Biology Letters 16:20200299. https://doi.org/10.1098/rsbl.2020.0299

Kendall, N.W., McMillan, J.R., Sloat, M.R., Buehrens, T.W., Quinn, T.P., Pess, G.R., Kuzishchin, K.V., McClure, M.M. and Zabel, R.W. 2015. Anadromy and residency in steelhead and rainbow trout (Oncorhynchus mykiss): a review of the processes and patterns. Canadian Journal of Fisheries and Aquatic Sciences 72:319-342.

Kjelson, M. A., and P. L. Brandes. 1989. The use of smolt survival estimates to quantify the effects of habitat changes on salmonid stocks in the Sacramento-San Joaquin rivers, California. Pages 100–115 in C. D. Levings, L. B. Holtby, and M. A. Henderson, editors. Proceedings of the national workshop on effects of habitat alteration on salmonid stocks. Canadian Special Publication of Fisheries and Aquatic Sciences 105.

Kondolf, G.M. 1997. Hungry water: effects of dams and gravel mining on river channels. Environmental Management 21:533–551.

Kondolf, G.M. 2000. Assessing salmonid spawning gravel quality. Transactions of the American Fisheries Society 129:262-281.

Kondolf, G.M., Williams, J.G., Horner, T.C., and Milan, D. 2008. Assessing physical quality of spawning habitat. American Fisheries Society Symposium 65:00-00.

Korman, J., Decker, A.S., Mossop, B. and Hagen, J., 2010. Comparison of electrofishing and snorkeling mark–recapture estimation of detection probability and abundance of juvenile steelhead in a medium-sized river. North American Journal of Fisheries Management, 30:5, pp.1280-1302.

Korman, J., Schick, J. and Mossop, B., 2016. Estimating riverwide abundance of juvenile fish populations: how much sampling is enough? North American Journal of Fisheries Management, 36(2), pp.213-229.

LaCroix, J.J., Wertheimer, A.C., Orsi, J.A., Sturdevant, M.V., Fergusson, E.A., and Bond, N.A. 2009. A top-down survival mechanism during early marine residency explains coho salmon year-class strength in southeast Alaska. Deep-Sea Research Part II 56:2560-2569.

Le Gall, R., Barthelemy, N., Clemento, A.J., Columbus, C.D., Campbell, E., Correa, E.C.A., Rodzen, J.A., Garza, J.C., and Pearse, D.E. 2023. Development of a novel microhaplotype panel for steelhead/rainbow trout (Oncorhynchus mykiss) and application for phylogenetic analysis in California. Preprint. https://doi.org/10.21203/rs.3.rs-2949400/v1

Levin, P.S., Zabel, R.W., and Williams, J.G. 2001. The road to extinction is paved with good intentions: negative association of fish hatcheries with threatened salmon. Proceedings of the Royal Society of London, Series B 268B:1153-1158.

Liermann, M.C., Rawding, D., Pess, G.R. and Glaser, B., 2015. The spatial distribution of salmon and steelhead redds and optimal sampling design. Canadian Journal of Fisheries and Aquatic Sciences, 72(3), pp.434-446.

Limm, M.P. and Marchetti, M.P. 2009. Juvenile Chinook salmon (Oncorhynchus tshawytscha) growth in off-channel and main-channel habitats on the Sacramento River, CA using otolith increment widths. Environmental Biology of Fishes 85:141–151. https://doi.org/10.1007/s10641-009-9473-8

Lindley, S. T., Schick, R.S., Agrawal, A., Goslin, M., Pearson, T.E., Mora, E., Anderson, J.J., May, B., Greene, S., Hanson, C., Low, A., McEwan, D., MacFarlane, R.B., Swanson, C., and Williams, J. G. 2006. Historical Population Structure of Central Valley Steelhead and its Alteration by Dams. San Francisco Estuary and Watershed Science 4(1).

Lindley, S. T; Schick, R. S; Mora, E.; Adams, P. B; Anderson, J. J; Greene, S., et al. (2007). Framework for Assessing Viability of Threatened and Endangered Chinook Salmon and Steelhead in the Sacramento–San Joaquin Basin. San Francisco Estuary and Watershed Science, 5(1). http://dx.doi.org/10.15447/sfews.2007v5iss1art4

Litz, M., Miller, J., Copeman, L., Teel, D., Weitkamp, L., Daly, E. and Claiborne, A. 2017. Ontogenetic shifts in the diets of juvenile Chinook Salmon: new insight from stable isotopes and fatty acids. Environmental Biology of Fishes 100:337–360.

Malcolm, I.A., Youngson, A.F., and Soulsby, C. 2003. Survival of salmonid eggs in a degraded gravel-bed stream: Effects of groundwater-surface water interactions. River Research and Application 19: 303-316.

Malcolm, I.A., Gibbins, C.N., Soulsby, C., Tetzlaff, D., and Moir, H.J. 2012. The influence of hydrology and hydraulics on salmonids between spawning and emergence: implications for the management of flows in regulated rivers. Fisheries Management and Ecology 19:464-474. doi: 10.1111/j.1365-2400.2011.00836.x.

Mangel, M. and Satterthwaite, W.H. 2008. Combining proximate and ultimate approaches to understand life history variation in salmonids with application to fisheries, conservation, and aquaculture. Bulletin of Marine Science 83:107-130.

Manhard, C.V., Som, N.A., Perry, R.W. and Plumb, J.M. 2018. A laboratory-calibrated model of coho salmon growth with utility for ecological analyses. Canadian Journal of Fisheries and Aquatic Sciences, 75:682-690.

Mayer, K., Schuck, M. and Hathaway, D. 2008. Assess salmonids in the Asotin Creek watershed, 2007 Annual Report, Project No. 200205300, Report for Bonneville Power Administration, P.O. Box 3621, Portland, OR 97208.

McElhany, P., Ruckelshaus, M.H., Ford, M.J., Wainwright, T.C., and Bjorkstedt, E.P. 2000. Viable salmonid populations and the recovery of evolutionarily significant units. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-NWFSC-42.

McEwan, D. 2001. Contributions to the Biology of Central Valley Salmonids. Fish Bulletin 179:44.

McKenzie, R. 2019. 2019 Delta Juvenile Fish Monitoring Program- Salmonid Annual Report. Annual Report for the Delta Juvenile Fish Monitoring Program. Lodi, CA: United States Fish and Wildlife Service. 14 p.

McLean, J.E., Bentzen, P., and Quinn, T.P. 2005. Nonrandom, size- and timing-biased breeding in a hatchery population of steelhead trout. Conservation Biology 19:446–454.

McMichael, G.A., Sharpe, C.S. and Pearsons, T.N., 1997. Effects of residual hatchery-reared steelhead on growth of wild rainbow trout and spring chinook salmon. Transactions of the American Fisheries Society, 126(2), pp.230-239.

McMichael, G.A., Rakowski, C.L., James, B.B., and Lukas, J.A. 2005. Estimated fall Chinook salmon survival to emergence in dewatered redds in a shallow side channel of the Columbia River. North American Journal of Fisheries Management, 25:876–884. doi:10. 1577/M04-168.1.

McMillan, J.R., Katz, S.L. and Pess, G.R. 2007. Observational evidence of spatial and temporal structure in a sympatric anadromous (winter steelhead) and resident rainbow trout mating system on the Olympic Peninsula, Washington. Transactions of the American Fisheries Society 136:736-748.

McMillan, J.R., Dunham, J., Reeves, G.H., Mills, J.S., and Jordan, C.E. 2012. Individual condition and stream temperature influence early maturation of rainbow and steelhead trout, Oncorhynchus mykiss. Environmental Biology of Fishes 93:343–355. doi:10.1007/s10641-011-9921-0.

Merz, J.E., and Setka, J.D. 2004. Evaluation of a spawning habitat enhancement site for Chinook Salmon in a regulated California river. North American Journal of Fisheries Management 24:397-407.

Merz, J.E., Setka, J.D., Pasternack, G.B., and Wheaton, J.M. 2004. Predicting benefits of spawning-habitat rehabilitation to salmonid (Oncorhynchus spp.) fry production in a regulated California river. Canadian Journal of Fisheries and Aquatic Sciences 61:1433-1446. doi: 10.1139/F04-077.

Metcalfe, N. B., F. A. Huntingford, and J. E. Thorpe. 1988. Feeding intensity, growth rates, and the establishment of life history patterns in juvenile Atlantic salmon Salmo salar. Journal of Animal Ecology 57:463–474.

Michel, C.J. 2018. Decoupling outmigration from marine survival indicates outsized influence of streamflow on cohort success for California's Chinook Salmon populations. Canadian Journal of Fisheries and Aquatic Sciences 76:1398–1410. https://doi.org/10.1139/cjfas-2018-0140

Michel, C.J., Smith, J.M., Lehman, B.M., Demetras, N.J., Huff, D.D., Brandes, P.L., Israel, J.A., Quinn, T.P., Hayes, S.A. 2020. Limitations of active removal to manage predatory fish populations. North American Journal of Fisheries Management 40:3-16. DOI: 10.1002/nafm.10391

Michel, C.J., Ammann, A.J., Chapman, E.D., Sandstrom, P.T., Fish, H.E., Thomas, M.J., Singer, G.P., Lindley, S.T., Klimley, A.P., and MacFarlane, R.B. 2013. The effects of environmental factors on the migratory movement patterns of Sacramento River yearling late-fall run Chinook salmon (Oncorhynchus tshawytscha). Environmental Biology of Fishes 96:257–271. doi:10.1007/s10641-012-9990-8.

Miller, M. R., Brunelli, J. P., Wheeler, P. A., Liu, S., Rexroad, C. E., Palti, Y., Doe, C. Q., & Thorgaard, G. H. (2012). A conserved haplotype controls parallel adaptation in geographically distant salmonid populations. Molecular Ecology, 21(2), 237–249. https://doi.org/10.1111/j.1365-294X.2011.05305.x

Miller, J.A, Teel, D.J., Baptista, A., and Morgan, C.A. 2013. Disentangling bottom-up and top-down effects on survival during early ocean residence in a population of Chinook salmon (Oncorhynchus tshawytscha). Canadian Journal of Fisheries and Aquatic Science 70:617-629.

Montgomery, D.R., Buffington, J.M., Peterson, N.P., Schuett-Holmes, D., and Quinn, T.P. 1996. Stream-bed scour, egg burial depths, and the influence of salmonid spawning on bed surface mobility and embryo survival. Canadian Journal of Fisheries and Aquatic Science 53:1061-1070.

Moore, J.W., Yeakel, J.D., Peard, D., Lough, J. and Beere, M. 2014. Life-history diversity and its importance to population stability and persistence of a migratory fish: steelhead in two large North American watersheds. Journal of Animal Ecology 83:1035-1046.

Morinville G.R. and Rasmussen J.B. 2003. Early juvenile bioenergetic differences between anadromous and resident brook trout (*Salvelinus fontinalis*). Can. J. Fish. Aquat. Sci. 60(4): 401–410.

Moyle, P. B. 2002. Inland Fishes of California, 2nd edition. Berkeley, CA: University of California Press.

Murphy, K., Hanson, L., Harris, M., and Schroyer, T. 2001a. Central Valley salmon and steelhead harvest monitoring project – 1999 angler survey. California Department of Fish and Game. Unpublished Annual Report, 29 p.

Murphy, K., Schroyer, T., Harris, M., and Massa, D. 2001b. Central Valley salmon and steelhead harvest monitoring project – 2000 angler survey. California Department of Fish and Game. Unpublished Annual Report, 29 p.

Myrvold, K.M. and Kennedy, B.P., 2015. Variation in juvenile steelhead density in relation to instream habitat and watershed characteristics. Transactions of the American Fisheries Society, 144(3), pp.577-590.

Myrvold, K.M. and Kennedy, B.P., 2016. Juvenile steelhead movements in relation to stream habitat, population density, and body size: consequences for individual growth rates. Canadian Journal of Fisheries and Aquatic Sciences, 73(10), pp.1520-1529.

Myrick, C.A., and Cech, J.J. 2000. Temperature influences on California rainbow trout physiological performance. Fish Physiology and Biochemistry 22:245-254.

Myrick C.A., and J.J. Cech. 2001. Temperature Effects on Chinook Salmon and Steelhead: a Review Focusing on California's Central Valley Populations. Bay-Delta Modeling Forum. Technical Publication 01-1. 57pp.

Myrick, C.A. and Cech, J.J. 2005. Bay-Delta Modeling Forum Technical Publication 01-1: Temperature effects on Chinook salmon and steelhead: A review focusing on California's Central Valley Populations. Obtained from https://www.cwemf.org/Pubs/TempReview.pdf

Naman, S.M., Rosenfeld, J.S., Neuswanger, J.R., Enders, E.C. and Eaton, B.C. 2019. Comparing correlative and bioenergetics-based habitat suitability models for drift-feeding fishes. Freshwater Biology 64:1613-1626.

Narum S.R., Hatch, D., Talbot, A., Moran, P., and Powell, M. 2008. Iteroparity in complex mating systems of steelhead Oncorhynchus mykiss (Walbaum). Journal of Fish Biology 72:45–60.

Newman, K.B., and Rice, J. 2002. Modeling the survival of Chinook Salmon smolts outmigrating through the lower Sacramento River system. Journal of the American Statistical Association 97:983–993.

Nichols K.M., Edo A.F., Wheeler P.A., and Thorgaard G.H. 2008. The genetic basis of smoltification-related traits in *Oncorhynchus mykiss*. Genetics, 179: 1559–1575.

NMFS (National Marine Fisheries Service). 2009. Biological Opinion and Conference Opinion on the Long-term Operation of the Central Valley Project and the State Water Project. Consultation Tracking Number: SWR-2008/09022.

NMFS (National Marine Fisheries Service). 2014. Recovery Plan for the Evolutionarily Significant Units of Sacramento River Winter-run Chinook Salmon and Central Valley Spring-run Chinook Salmon and the Distinct Population Segment of California Central Valley Steelhead. National Marine Fisheries Service, California Central Valley Area Office, Sacramento, California.

NMFS (National Marine Fisheries Service). 2016. 5-Year Review: Summary and Evaluation of California Central Valley Steelhead Distinct Population Segment. National Marine Fisheries Service, West Coast Region.

NMFS (National Marine Fisheries Service). 2019. Biological Opinion on Long-term Operation of the Central Valley Project and the State Water Project Consultation. Consultation Tracking Number: WCRO-2016-00069. DOI: https://doi.org/10.25923/f6tw-rkl 9.

Nobriga, M., and Cadrett, P. 2001. Differences Among Hatchery and Wild Steelhead: Evidence from Delta Fish Monitoring Programs. Interagency Ecological Program Newsletter 14(3): 30-38.

Nordeng, H. 1977. A pheromone hypothesis for homeward migration in anadromous salmonids. Oikos 28:155-159. DOI: https://doi.org/10.2307/3543965.

Notch, J.J., McHuron, A.S., Michel, C.J., Cordoleani, F., Johnson, M., Henderson, M.J., and Ammann, A.J. 2020. Outmigration survival of wild Chinook Salmon smolts through the Sacramento River during historic drought and high water conditions. Environmental Biology of Fishes 103:561–576. https://doi.org/10.1007/s10641-020-00952-1

NPAFC (North Pacific Anadromous Fish Commission). 2020. North Pacific Anadromous Fish Commission Annual Report 2020. Available at: https://npafc.org/wp-content/uploads/Public-Documents/2020/AR2020.pdf.

O'Neal, J.S., 2007. Snorkel surveys. Salmonid field protocols handbook, pp.325-339.

Oregon Department of Fish and Wildlife (ODFW) and U.S. Fish and Wildlife Service (USFWS). 1996. Integrated Hatchery Operations Team — operation plans for anadromous fish production facilities in the Columbia River Basin. Vol. II. Oregon. BPA Proj. No. 92-043, Bonneville Power Administration, Portland, OR.

Patterson, J., J.Thomas, L. Rosenfeld, J. Newton, L. Hazard, J. Scianna, R. Kudela, E. Mayorga, C. Cohen, M. Cook, M. Otero, and J. Adelaars. 2012. Addressing ocean and coastal issues at the West Coast scale through regional ocean observing system collaboration. 1-8. 10.1109/OCEANS.2012.6404937.

Pearse, D. E, & Garza, J. C. (2015). You Can't Unscramble an Egg: Population Genetic Structure of Oncorhynchus mykiss in the California Central Valley Inferred from Combined Microsatellite and Single Nucleotide Polymorphism Data. San Francisco Estuary and Watershed Science, 13(4). doi:https://doi.org/10.15447/sfews.2015v13iss4art3

Pearse, D.E., Miller, M.R., Abadía-Cardoso, A. and Garza, J.C., 2014. Rapid parallel evolution of standing variation in a single, complex, genomic region is associated with life history in steelhead/rainbow trout. Proceedings of the Royal Society B: Biological Sciences, 281(1783), p.20140012.

Pearsons, T.N., McMichael, G.A., Bartrand, E.L., Fisher, M., Monahan, J.T., Leider, S.A., Strom, G.R., and Murdoch, A.R. 1993. Yakima species interactions study, 1992 annual report. Washington Department of Fish and Wildlife.

Pearsons, T.N., Temple, G.M., Fritts, A.L., Johnson, C.L., and Webster, T.D. 2008. Ecological interactions between non-target taxa of concern and hatchery supplemented salmon, 2007 Annual Report Project number 1995-063-25. Washington Department of Fish and Wildlife.

Penney, Z. L., and Moffitt, C.M. 2014a. Histological assessment of organs in sexually mature and post-spawning steelhead trout and insights into iteroparity. Reviews in Fish Biology and Fisheries 24:781–801.

Penney, Z. and Moffitt, C. 2014b. Proximate composition and energy density of stream-maturing adult steelhead during upstream migration, sexual maturity, and kelt emigration. Transactions of the American Fisheries Society 143:399-413.

Perry, R.W., Plumb, J.M. and W. Huntington, C. 2015. Using a laboratory-based growth model to estimate mass-and temperature-dependent growth parameters across populations of juvenile Chinook salmon. Transactions of the American Fisheries Society 144:331-336.

Perry, R.W., Pope, A.C., Romine, J.G., Brandes, P.L., Burau, J.R., Blake, A.R., Ammann, A.J., and Michel, C.J. 2018. Flow-mediated effects on travel time, routing, and survival of juvenile Chinook Salmon in a spatially complex, tidally forced river delta. Canadian Journal of Fisheries and Aquatic Sciences 75:1886–1901. https://doi.org/10.1139/cjfas-2017-0310

Peterson, W., Morgan, C., Peterson, J., Fisher, J., Burke, B. and Fresh, K. 2013. Ocean Ecosystem Indicators of Salmon Marine Survival in the Northern California Current. Fish Ecology Division, Northwest Fisheries Science Center, National Marine Fisheries Service and Cooperative Institute for Marine Resource Studies, Hatfield Marine Science Center, Oregon State University.

PFMC (Pacific Fisheries Management Council). 2022. Preseason Report Ii Proposed Alternatives and Environmental Assessment Part 2 For 2022 Ocean Salmon Fishery Regulations Regulation Identifier Number 0648- BK78. Pacific Fishery Management Council. Portland, OR 97220-1384. March 2022.

Phillips, R.W., and Koski, K.V. 1969. A fry trap method for estimating salmonid survival from egg deposition to fry emergence. Journal of the Fisheries Research Boar of Canada 26: 133-141.

Phillis, C.C., Moore, J.W., Buoro, M., Hayes, S.A., Garza, J.C. and Pearse, D.E. 2016. Shifting thresholds: rapid evolution of migratory life histories in steelhead/rainbow trout, Oncorhynchus mykiss. Journal of Heredity 107:51-60.

Pulido, F. 2011. Evolutionary genetics of partial migration–the threshold model of migration revis (it) ed. Oikos, 120(12), pp.1776-1783.

Quinn, T.P. and Dittman, A.J. 1990. Pacific salmon migrations and homing mechanisms and adaptive significance. Trends in Ecology and Evolution 5:174-177. DOI: http://dx.doi.org/10.1016/0169-5347(90)90205-R

Quinn, T.P. 2005. The behavior and ecology of Pacific salmon and trout. University of Washington Press, Seattle, Wash.

Quinn, T.P. 2018. The behavior and ecology of Pacific salmon and trout. Second edition. University of Washington Press, Seattle, Washington.

R Core Team. 2023. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Raleigh, R.F. 1984. Habitat suitability information: rainbow trout. Western Energy and Land Use Team, Division of Biological Services, Research and Development, Fish and Wildlife Service, US Department of the Interior.

Reiser, D.W.; Bjornn, T.C. 1979. Influence of forest and rangeland management on anadromous fish habitat in Western North America: habitat requirements of anadromous salmonids. Gen. Tech. Rep. PNW-GTR-096. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station: 1-54

Rikardsen, A.H., Haugland, M., Bjørn, P.A., Finstad, B., Knudsen, R., Dempson, J.B., Holst, J.C., Hvidsten, N.A. and Holm, M. 2004. Geographical differences in marine feeding of Atlantic salmon post-smolts in Norwegian fjords. Journal of Fish Biology, 64:1655-1679.

Robards, M.D. and Quinn, T.P. 2002. The Migratory Timing of Adult Summer-Run Steelhead in the Columbia River over Six Decades of Environmental Change. Transactions of the American Fisheries Society 131:523–536.

Roberts, B.C., and White, R.G. 1992. Effects of angler wading on survival of trout eggs and pre-emergent fry. North American Journal of Fisheries Management 12:450–459.

Roni, P., Pess, G.R., Beechie, T.J. and Hanson, K.M., 2014. Fish-habitat relationships and the effectiveness of habitat restoration.

Roper, B.B., Scarnecchia, D.L. and La Marr, T.J., 1994. Summer distribution of and habitat use by chinook salmon and steelhead within a major basin of the South Umpqua River, Oregon. Transactions of the American Fisheries Society, 123:3, pp.298-308.

Ruzzante, D.E., McCracken, G.R., Førland, B., MacMillan, J., Notte, D., Buhariwalla, C., Mills Flemming, J. and Skaug, H., 2019. Validation of close-kin mark–recapture (CKMR) methods for estimating population abundance. Methods in Ecology and Evolution, 10:9, pp.1445-1453.

Sabal, M., Hayes, S., Merz, J., & Setka, J. (2016). Habitat Alterations and a Nonnative Predator, the Striped Bass, Increase Native Chinook Salmon Mortality in the Central Valley, California. North American Journal of Fisheries Managementt, 36(2), 309–320. https://doi.org/10.1080/02755947.2015.1121938

Saiki, M.K., Jennings, M.R., and Brumbaugh, W.G. 1993. Boron, molybdenum, and selenium in aquatic food chains from the lower San Joaquin River and its tributaries, California. Archives of environmental contamination and toxicology 24:307-319. https://doi.org/10.1007/bf01128729

San Joaquin River Restoration Program (SJRRP). 2013. PIT tag monitoring for emigrating juvenile Chinook salmon at three flow conditions. Prepared by USBR and USFWS for the San Joaquin River Restoration Program. Sacramento, CA. 13 p. http://www.restoresjr.net/download/data-reporting/data-reporting-2013/SanJoaquin%20River%20PIT%20Tag%20Monitoring%20Summary.pdf

Satterthwaite, W.H., Beakes, M.P., Collins, E.M., Swank, D.R., Merz, J.E., Titus, R.G., Sogard, S.M. and Mangel, M. 2009. Steelhead life history on California's central coast: insights from a state-dependent model. Transactions of the American Fisheries Society 138:532-548.

Satterthwaite, W.H., Beakes, M.P., Collins, E.M., Swank, D.R., Merz, J.E., Titus, R.G., Sogard, S.M. and Mangel, M. 2010. State-dependent life history models in a changing (and regulated) environment: steelhead in the California Central Valley. Evolutionary Applications 3:221-243.

Schroeder, R. K., Lindsay, R. B., & Kenaston, K. R. (2001). Origin and Straying of Hatchery Winter Steelhead in Oregon Coastal Rivers. Transactions of the American Fisheries Society, 130(3), 431–441. https://doi.org/10.1577/1548-8659(2001)130<0431:oasohw>2.0.co;2

Seber, G.A.F., 1982. The estimation of animal abundance and related parameters.

Shapovalov, L. and Taft, A.C. 1954. The life histories of the steelhead rainbow trout (*Salmo gairdneri gairdneri*) and silver salmon (*Oncorhynchus kisutch*): with special reference to Waddell Creek, California, and recommendations regarding their management (p. 575). Sacramento, California, USA: California Department of Fish and Game.

Shelton, A.O., Satterthwaite, W.H., Beakes, M.P., Munch, S.B., Sogard, S.M. and Mangel, M. 2013. Separating intrinsic and environmental contributions to growth and their population consequences. The American Naturalist 181:799-814.

Silver, S.J., Warren, C.E., and Doudoroff, P. 1963. Dissolved oxygen requirements of developing steelhead trout and Chinook Salmon embryos at different water velocities. Transactions of the American Fisheries Society 92:327-343.

Simenstad, C.A., and J.R. Cordell. 2000. Ecological assessment criteria for restoring anadromous salmon habitat in Pacific Northwest Estuaries. Ecological Engineering, vol. 15, pp. 283-302.

Singer, G. P., Chapman, E. D., Ammann, A. J., Klimley, A. P., Rypel, A. L., & Fangue, N. A. (2020). Historic drought influences outmigration dynamics of juvenile fall and spring-run Chinook Salmon. Environmental Biology of Fishes, 103(5), 543–559. https://doi.org/10.1007/s10641-020-00975-8

Sloat, M.R. and Osterback, A.M.K. 2013. Maximum stream temperature and the occurrence, abundance, and behavior of steelhead trout (*Oncorhynchus mykiss*) in a southern California stream. Canadian Journal of Fisheries and Aquatic Sciences 70:64-73.

Sloat, M.R., and Reeves, G.H. 2014. Individual condition, standard metabolic rate, and rearing temperature influence steelhead and rainbow trout (*Oncorhynchus mykiss*) life histories. Canadian Journal of Fisheries and Aquatic Sciences 71:491–501. doi:10.1139/cjfas-2013-0366.

Sogard, S.M., Merz, J.E., Satterthwaite, W.H., Beakes, M.P., Swank, D.R., Collins, E.M., Titus, R.G. and Mangel, M. (2012), Contrasts in Habitat Characteristics and Life History Patterns of Oncorhynchus mykiss in California's Central Coast and Central Valley. Transactions of the American Fisheries Society, 141: 747-760. https://doi.org/10.1080/00028487.2012.675902

Sommer, T., Harrell, B., Nobriga, M., Brown, R., Moyle, P., Kimmerer, W. and Schemel, L. (2001), California's Yolo Bypass: Evidence that flood control Can Be compatible with fisheries, wetlands, wildlife, and agriculture. Fisheries, 26: 6-16. https://doi.org/10.1577/1548-8446(2001)026<0006:CYB>2.0.CO;2

State Water Resources Control Board (SWRCB). 2003. Revised Water Right Decision 1644 in the Matter of Fishery Resources and Water Right Issues of the Lower Yuba River.

Sturrock, A.M., Satterthwaite, W.H., Cervantes-Yoshida, K.M., Huber, E.R., Sturrock, H.J.W., Nussle, S., and Carlson, S.M. 2019. Eight Decades of Hatchery Salmon Releases in the California Central Valley: Factors Influencing Straying and Resilience. Fisheries 44:433–444.

Tatara, C.P., Larsen, D.A., Cooper, M.R., Swanson, P., Middleton, M.A., Dickey, J.T., Harstad, D., Humling, M., Pasley, C.R., and Berejikian, B. 2019. Age at Release, Size, and Maturation Status Influence Residualism in Hatchery Steelhead. North American Journal of Fisheries Management 39:468–484.

Teo, S.L., Sandstrom, P.T., Chapman, E.D., Null, R.E., Brown, K., Kimley, A.P., and Block, B.A. 2013. Archival and acoustic tags reveal the post-spawning migrations, diving behavior, and thermal habitat or hatchery-origin Sacramento River steelhead kelts. Environmental Biology of Fishes 96. DOI:10.1007/s10641-011-9938-4.

Thayer, J.A., Field, J.C., and Sydeman, W.J. 2014. Changes in California Chinook salmon diet over the past 50 years: relevance to the recent population crash. Marine Ecology Progress Series 498:249-261.

Thompson, S. K. 2012. Sampling, third edition. John Wiley & Sons, Inc., Hoboken, NJ, USA.

Thorpe, J. E., Mangel, M., Metcalfe, N.B., and Huntingford, F.A. 1998. Modeling the proximate basis of life history variation, with application to Atlantic salmon, Salmo salar L. Evolutionary Ecology 121:581–600.

Thorpe, J.E. 2007. Maturation responses of salmonids to changing developmental opportunities. Marine Ecology Progress Series 335:285–288.

Thorpe, W., 2020. Steelhead (*Oncorhynchus mykiss*) rearing habitat heterogeneity in the Lower American River influences presence and density patterns observed in oversummering juveniles (Doctoral dissertation).

Thrower, F.P., Hard, J.J. and Joyce, J.E. 2004. Genetic architecture of growth and early life-history transitions in anadromous and derived freshwater populations of steelhead. Journal of Fish Biology, 65:286-307.

Tomkins, J.L. and Hazel, W. 2007. The status of the conditional evolutionarily stable strategy. Trends in Ecology & Evolution, 22:522-528.

Ueda, H. 2012. Physiological mechanisms of imprinting and homing migration in Pacific salmon *Oncorhynchus* spp. Journal of Fish Biology 81:543-558.

Voss, S. D., and W. R. Poytress. 2020. Brood year 2018 juvenile salmonid production and passage indices at the Red Bluff Diversion Dam. Report of U.S. Fish and Wildlife Service to U.S. Bureau of Reclamation, Sacramento, CA

Wagner, H. 1969. Effect of stocking location on juvenile steelhead trout, Salmo gairdnerii, on adult catch. Transactions of the American Fisheries Society 98:27-34.

Walker, M.M., Diebel, C.E., Haugh, C.V., Pankhurst, P.M., Montgomery, J.C., and Green, C.R. 1997. Structure and function of the vertebrate magnetic sense. Nature. 390(6658):371–376. https://doi.org/10.1038/37057

Waples, R.S., Ford, M.J., Nichols, K., Kardos, M., Myers, J., Thompson, T.Q., Anderson, E.C., Koch, I.J., McKinney, G., Miller, M.R., Naish, K., Narum, S.R., O'Mally, K.G., Pearse, D.E., Pess, G.R., Quinn, T.R., Seamons, T.R., Spidle, A., Warheit, K.I., Willis, S.C. 2022. Implications of Large-Effect Loci for Conservation: A Review and Case Study with Pacific Salmon. Journal of Heredity, 113(2): 121–144

Waters, C.D., Clemento, A., Aykanat, T., Garza, J.C., Naish, K.A., Narum, S. and Primmer, C.R., 2021. Heterogeneous genetic basis of age at maturity in salmonid fishes. Molecular Ecology, 30(6), pp.1435-1456.

Washington State Department of Ecology (WDOE). 2002. Evaluating Criteria for the Protection of Freshwater Aquatic Life in Washington's Surface Water Quality Standards: Dissolved Oxygen. Draft Discussion Paper and Literature Summary. Publication Number 00-10- 071. 90pp.

Wells, B.K., Grimes, C.B., Field, J.C., and Reiss, C.S. 2006. Covariation between the average lengths of mature coho (Oncorhynchus kisutch) and Chinook salmon (O. tshawytscha) and the ocean environment. Fisheries Oceanography 15:67-79.

Wells, B.K., Santora, J.A., Schroeder, I.D., Mantua, N., Sydeman, W.J., Huff, D.D., et al. 2016. Marine ecosystem perspectives on Chinook salmon recruitment: a synthesis of empirical and modeling studies from a California upwelling system. Marine Ecological Progress Series 552:271–284.

West, D., Winkowski, J., Seamons, T., and Litz, M. 2021. Chehalis River smolt production, 2020, FPA 21-06. Washington Department of Fish and Wildlife, Olympia, Washington.

Westley, P.A.H., Quinn, T.P., and Dittman, A.H. 2013. Rates of straying by hatchery-produced Pacific salmon. Canadian Journal of Fisheries and Aquatic Sciences 746:735–746.

Willey, R. G. 1986. HEC-5Q: System Water Quality Modeling. United States: U.S. Army Corps of Engineers, Hydrologic Engineering Center.

Williams, J.G. 2006. Central Valley salmon: a perspective on Chinook and steelhead in the Central Valley of California. San Francisco Estuary and Watershed Science, 4, 416 p.

Williams, T.H., Spence, B.C., Boughton, D.A., Johnson, R.C., Crozier, L., Mantua, N., O'Farrell, M., and Lindley, S.T. 2016. Viability assessment for Pacific salmon and steelhead listed under the Endangered Species Act: Southwest. 2 February 2016 Report to National Marine Fisheries Service – West Coast Region from Southwest Fisheries Science Center, Fisheries Ecology Division 110 Shaffer Road, Santa Cruz, California 95060.

Windell, S., Brandes, P.L., Conrad, J.L., Ferguson, J.W., Goertler, P.A., Harvey, B.N., Heublein, J.C., Israel, J.A., Kratville, D.W., Kirsch, J.E. and Perry, R.W. 2017. Scientific framework for assessing factors influencing endangered Sacramento River winter-run Chinook salmon (*Oncorhynchus tshawytscha*) across the life cycle. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-SWFSC-586. 49 p. https://doi.org/10.7289/V5/TM-SWFSC-586

Woodson, L., Wells, B.K., Weber, P.K., MacFarlane, R.B., Whitman, G.E., and Johnson, R.C. 2013. Size, growth, and origin-dependent mortality of juvenile Chinook salmon Oncorhynchus tshawytscha during early ocean residence. Marine Ecology Progress Series 487:163-175.

Yoshiyama, R.M., Fisher, F.W., and Moyle, P.B. 1998. Historical abundance and decline of Chinook salmon in the Central Valley region of California. North American Journal of Fisheries Management 18:487-521.

Zeug, S.C., Sellheim, K., Watry, C., Rook, B., Hannon, J., Zimmerman, J., Cox, D. and Merz, J. (2013), Gravel augmentation increases spawning utilization by anadromous salmonids: A case study from California, USA. River Res. Applic., 30: 707-718. https://doi.org/10.1002/rra.2680

Zeug, S., Sellheim, K., Watry, C., Rook, B., Hannon, J., Zimmerman, J., Cox, D., and Merz, J. 2014. Gravel augmentation increases spawning utilization by anadromous salmonids: A case study from California, USA. River Research and Applications. 30. 10.1002/rra.2680.

Zeug, S., A. Brodsky, W. Thorpe, B. Flores, A. Constandache, S. Blankenship, and J. Weisenfeld. 2024. *Oncorhynchus mykiss* in anadromous waters of the Stanislaus River. Report prepared for U.S. Bureau of Reclamation. 58 pages.

Zimmerman, C.E., Edwards, G.W. and Perry, K., 2009. Maternal origin and migratory history of steelhead and rainbow trout captured in rivers of the Central Valley, California. Transactions of the American Fisheries Society, 138(2), pp.280-291.