SAN FRANCISCO ESTUARY & WATERSHED SCIENCE
Sponsored by the Delta Science Program and the UC Davis Muir Institute

RESEARCH

# Counting the Parts to Understand the Whole: Rethinking Monitoring of Steelhead in California's Central Valley

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## ABSTRACT

Steelhead (*Oncorhynchus mykiss* expressing an anadromous life history) in the Sacramento and San Joaquin rivers and their tributaries in California's Central Valley (CCV) belong to a Distinct Population Segment (DPS) that is listed as threatened under the US Endangered Species Act. Although contemporary management and recovery plans include numerous planned and ongoing efforts seeking to aid in DPS recovery—such as gravel augmentation, manipulation of spring flows, and restoration of rearing and spawning habitat—a paucity of data precludes the possibility of evaluating the effect of these actions on populations of Steelhead in CCV streams. Knowledge gaps relating to historic and current abundance, population-specific ratios of resident and anadromous life-history expression, and the influence of hatchery-reared fish remain largely unaddressed. This is partly a result of aspects of Steelhead biology that make them difficult to monitor, including the multitude of factors that contribute to the expression of anadromy, polymorphic populations, and migration periods that coincide with challenging field conditions. However, these gaps in understanding are also partly the result of an institutional focus on Chinook Salmon (*Oncorhynchus tshawytscha*) and a pervasive notion that actions benefiting Chinook populations will also benefit Steelhead populations. To evaluate these gaps and to suggest approaches for assessing DPS recovery actions, we review available data and existing monitoring efforts, and consider the actions necessary to inform the development of targeted *O. mykiss* monitoring programs. Current management and recovery goals focus on abundance estimates of Steelhead only, yet current monitoring is insufficient for reliable estimates. We argue that a reallocation of monitoring resources to better understand the interaction between resident *O. mykiss* and Steelhead would provide better data to estimate the vital rates needed to evaluate the effects of recovery actions.

## KEY WORDS

Steelhead, *Oncorhynchus mykiss*, Central Valley, monitoring, life history

**SFEWS Volume 20 | Issue 1 | Article 2**
*https://doi.org/10.15447/sfews.2022v20iss1art2*

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## INTRODUCTION

Freshwater resident Rainbow Trout and anadromous Steelhead are two forms of the same species (*Oncorhynchus mykiss*) expressing different life-history strategies (Figure 1). The superficially binary division of populations into migrants and residents belies the multifarious and flexible life histories of *O. mykiss*, which are among the most complex of all salmonids. Thorpe (1998, 2007) identified 32 possible life-history pathways ranging from truly anadromous to completely resident; Hodge et al. (2016) identified 38. This high degree of life-history plasticity creates additional challenges to monitoring and management compared to other Pacific salmonids (*Oncorhynchus* spp.).

The Sacramento and San Joaquin river systems and their associated tributaries in California's Central Valley (CCV) are home to one of the southernmost populations in the native range of anadromous *O. mykiss* (Figure 2). In addition to experiencing higher temperatures and more variable precipitation than more northerly portions of the natural range of *O. mykiss* (Dettinger et al. 2011; Ralph and Dettinger 2012), the riverine environment of the CCV has been dramatically altered from its natural state. The construction of numerous dams throughout the watershed has led to the loss of more than 82% of the system's historic Steelhead spawning and rearing habitat (Lindley et al. 2006). Additionally, historically dynamic hydrographs have been homogenized through the reduction of winter-spring flows and increases in summer-fall flows, which creates cool and relatively stable flows year-round in tailwater habitats that remain accessible to anadromous species (Brown and Bauer 2009; He and Marcinkevage 2017). Downstream of these dams, total annual diversions from the Sacramento–San Joaquin Delta (hereafter "the Delta") equate to 18 million acre-feet (~22.2 $km^3$), or approximately 40% of all flow that would have historically passed through the Delta during an average water year (Lund et al. 2007). Further, introductions of non-native species have irreversibly altered the species composition of the aquatic community, and some have negatively affected native salmonid populations through predation and competition (Katz et al. 2012; Sabal et al. 2016).

Faced with these challenges, CCV salmonid populations have experienced stark declines, and several species and runs have been listed under the Endangered Species Act (ESA), including the CCV Steelhead Distinct Population Segment (DPS; Fed Regist 1998). Although resident *O. mykiss* in anadromous waters are afforded legal protection, they are rarely the focus of monitoring or management efforts. Much of the basic understanding of CCV *O. mykiss* is based on a 6-year study conducted in the 1950s (Hallock et al. 1961), and although many decades have passed since this foundational study, subsequent research on CCV *O. mykiss* has done little to improve monitoring practices, inform management, or evaluate the efficacy of recovery actions. For example, reliable estimates of population abundance—the parameter for gauging progress toward the goals established in recovery plans (Table 1)—have not been generated. In large part, this results from a lack of data on the key demographic factors that dictate abundance, such as juvenile survival, annual production, ratios of anadromous and resident life histories, and the effects of hatchery practices. Although monitoring plans to address these knowledge gaps have been developed (Eilers et al. 2010), some of the monitoring recommendations have yet to be implemented (e.g., spatial distribution surveys across the CCV). The few monitoring and research programs that have been implemented to date have struggled to achieve their stated objectives. For example, the Mainstem Sacramento Mark–Recapture Project set out to estimate the population of adult Steelhead in the Sacramento River watershed (CDFW c2020). Despite concerted trapping effort since 2015, low annual catch has prevented accurate estimates of abundance. However, in recognition of the challenges associated with assessment and management of the anadromous life history form of *O. mykiss*, federal agencies, including the United States Bureau of Reclamation, are funding and coordinating efforts to accurately estimate population vital rates, which are currently in the initial stages of

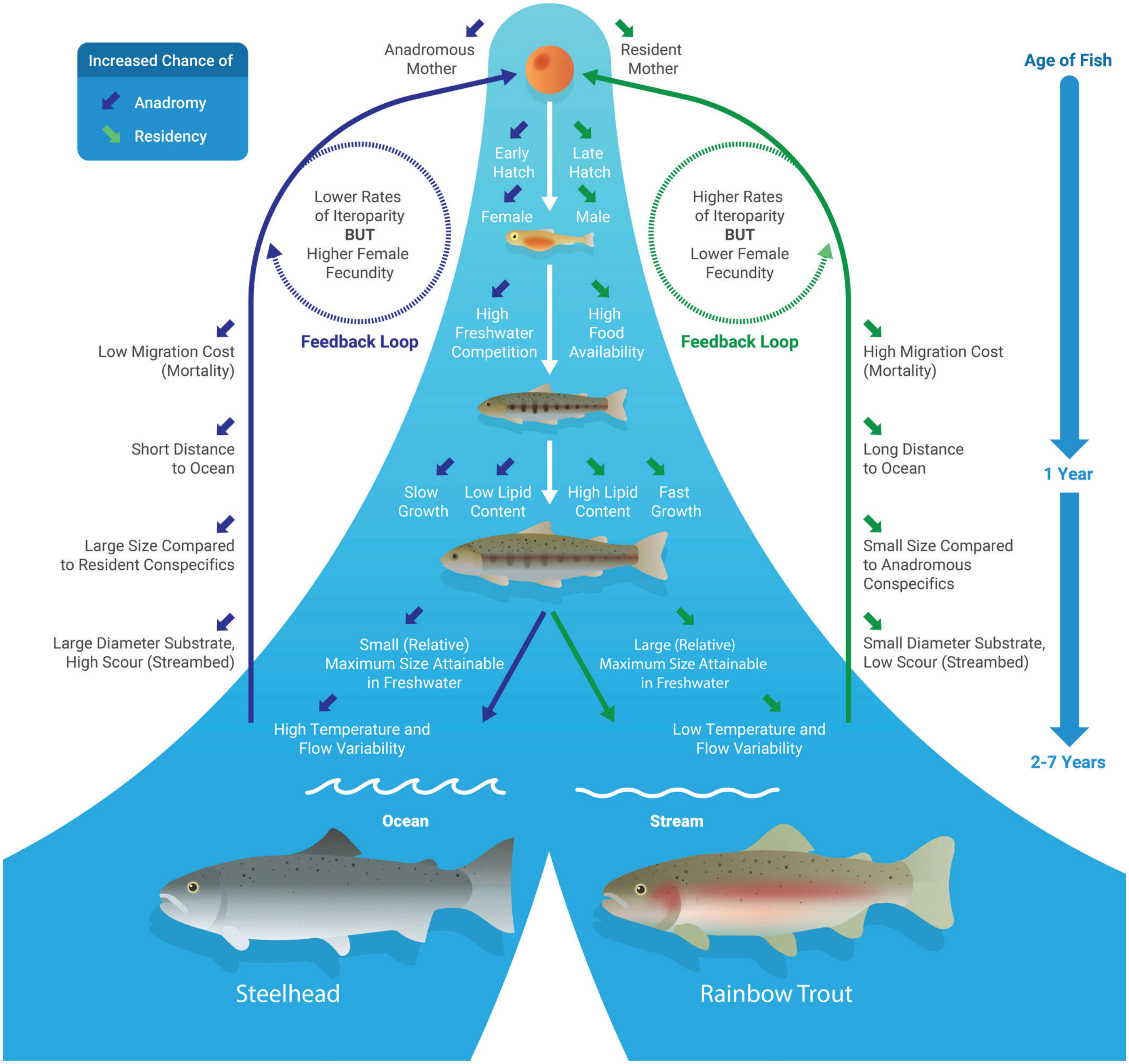

**Figure 1** A generalized life history diagram of anadromous and resident *O. mykiss*, including factors demonstrated to influence life history pathways. Many of these factors are under partial genetic control, and as such, the genetics of an individual play an important role in determining life history expression.

implementation. These efforts include rigorous monitoring of anadromous adult escapement and evaluation of their reproductive success on the Stanislaus River and are intended to provide an important foundation for informed evaluation and management of the CCV *O. mykiss* population.

Among the most significant of the difficulties associated with monitoring anadromous *O. mykiss* is that resident and anadromous individuals form polymorphic populations within rivers where they may spawn with one another (Zimmerman et al. 2009; Baerwald et al. 2016) and identifying

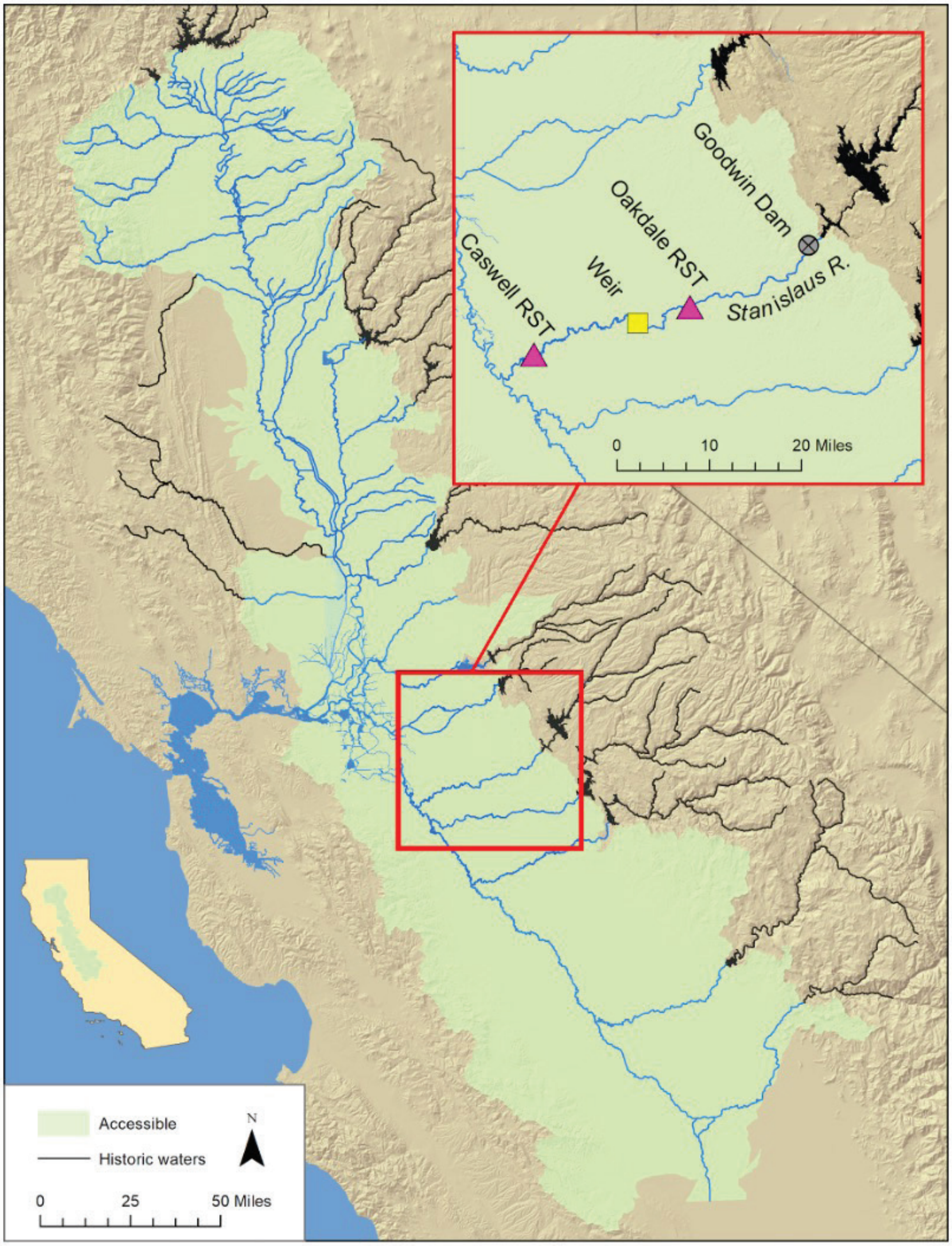

**Figure 2** The historic range and currently accessible habitat (*green*) of anadromous *O. mykiss* (Steelhead) in California's Central Valley. Inset map depicts locations of juvenile trapping sites in the Stanislaus River (see Case Study: The Stanislaus River). Note that the historic distribution is not shown in its entirety.

Steelhead before smolting is nearly impossible. Furthermore, anadromous individuals are rare compared to their resident conspecifics in some CCV rivers. This is true of the Stanislaus River, for example, where Zimmerman et al. (2009) detected only a single migratory Steelhead in a sample of 157 *O. mykiss*. Research is also limited in part by difficulties inherent to the ecology of the species.

**Table 1** Regulatory documents guiding contemporary management and recovery actions for the CCV Steelhead DPS

| Plan | Description | Goals | Required metrics |
|---|---|---|---|
| Central Valley Project Improvement Act[a] | Management plan created to offset the impacts of the Central Valley Project | 13,000 individuals across the entire Central Valley | Abundance |
| National Marine Fisheries Service Recovery Plan[b] | Management plan outlining steps for recovery of the CCV Steelhead DPS | One population in the Northwestern California Diversity Group at low risk of extinction<br>Two populations in the Basalt and Porous Lava Flow Diversity Group at low risk of extinction<br>Four populations in the Northern Sierra Diversity Group at low risk of extinction<br>Two populations in the Southern Sierra Diversity Group at low risk of extinction<br>Maintain multiple populations at moderate risk of extinction<br>Populations considered at low risk of extinction if their census population size is >2,500 adults or effective population size is >500 | Abundance<br>Changes in abundance<br>Genetic diversity |
| Scientific Evaluation Process[c] | Management plan focused on the Stanislaus River | Abundance goals based on the NMFS Recovery Plan<br>Minimum adult escapement of 2,500 individuals over three years<br>Effective freshwater population of 500<br>Full range of life history diversity expression in the population<br>Free from the influence of hatchery fish | Abundance<br>Genetic diversity<br>Proportion of anadromy and residency |
| Biological Opinion on Long Term Operation of the Central Valley project and the State Water Project[d] | Document detailing NMFS' Opinion on the effects of the CVP and SWP operation on Sacramento River Winter-Run Chinook Salmon, Central Valley Spring-Run Chinook Salmon, and California Central Valley Steelhead | Minimize negative impacts of CVP and SWP operation on ESA-listed species, including Steelhead belonging to the CCV DPS | N/A |

a. Central Valley Project Improvement Act 1992.
b. National Marine Fisheries Service 2014.
c. Ferguson et al. 2019.
d. National Marine Fisheries Service 2019.

For instance, adult Steelhead tend to migrate and spawn during periods of high flow (McEwan 2001). Further, out-migrating Steelhead smolts may be able to avoid detection in rotary screw traps (RSTs) because of their strong swimming ability (Tattam et al. 2013). Low sampling efficiency, rarity of anadromous fish, and the resulting low detection rates lead to a high degree of uncertainty associated with collected data.

Contemporary CCV *O. mykiss* populations in anadromous waters are composed of some (largely unknown) proportion of individuals that exhibit the resident life history and some that express anadromy, and it remains unclear how each life-history form contributes to population resilience. Although the numerous factors that influence the expression of anadromy in *O. mykiss* have been the focus of extensive research, very few studies have focused on evaluating the relative significance of these factors in CCV *O. mykiss* populations (Table 2). Whereas several studies have shown that survival of anadromous salmonids can be low as a result of factors such as predation (Sabal et al. 2016), route selection into low survival reaches (Perry et al. 2010), or poor ocean conditions (Lindley et al. 2009; Welch et al. 2021), survival and lifetime reproductive effort of resident individuals are unknown. Current understanding of the trade-offs involved with these two life-history strategies suggests that promoting anadromous individuals may come at the expense of resident individuals (Railsback et al. 2014).

Evaluating the possible outcomes of management actions requires a rigorous monitoring framework that accounts for life-history variability in *O. mykiss* populations. Here, we provide an overview of region-specific studies that relate to the expression of anadromy and residency of CCV *O. mykiss*, and identify the impediments

**Table 2** Summary of intrinsic and extrinsic factors associated with the expression of anadromy in *O. mykiss* and associated studies. Studies are split into whether or not they are CCV specific. Note that this list is not exhaustive, and there may be additional factors influencing *O. mykiss* life history expression that are unstudied or undiscovered.

| Factor | Influence on anadromy | CCV studies | Non-CCV studies |
|---|---|---|---|
| **Genetics** | Life history traits are heritable[1,2,3]<br>Genetic basis for smolt phenotypic traits (e.g., coloration and growth) are distributed across multiple genomic regions[4,5]<br>Close association between life history and the *Omy5* region of the *O. mykiss* genome[5,6]<br>*Omy5* genotype is not deterministic; individuals with resident genotypes may still express anadromy and vice versa[7]<br>Genetic variation associated with anadromy persists in land-locked populations[8] for decades or centuries[9]<br>When residency is strongly favored, anadromous genotypes can decrease in relative frequency over time periods relevant for conservation[6,9] | 8 | 1, 2, 3, 4, 5, 6, 7, 9 |
| **Sex** | Life history trajectory of offspring is associated with maternal life history[10]<br>Sex ratios in resident adults skew towards males and towards females in anadromous individuals[7,11,12]<br>Complete dominance of *Omy5* variants in females and partial dominance in males explains the sex differences in expression of the migratory life history[6,13] | None | 6, 7, 10, 11, 12, 13 |
| **Growth** | Differences in body condition that influence the expression of anadromy may be apparent up to a year prior to expressed life history strategy[14,15,16]<br>Juveniles with higher condition factor have a propensity for maturing in freshwater compared to individuals that eventually smolt[15]<br>Individual size and growth may influence life history strategy across multiple thresholds [17,18,19,20]<br>Ability to attain a large body size in freshwater is associated with an increased prevalence of resident individuals[18,21,22] | 14, 18 | 15, 16, 17, 19, 20, 21, 22 |
| **Prey resources** | Residency is more prevalent in rivers with high productivity[23]<br>Abundant, high-quality prey in rearing streams may discourage anadromy[24] | None | 23, 24 |
| **Reproduction** | Anadromous and resident adults can form joint spawning aggregations[25]<br>Iteroparity rates can be higher among freshwater residents than anadromous individuals[26]<br>Post-spawn kelts can remain anadromous or residualize in freshwater[27]<br>Repeat anadromous spawners are relatively rare and typically female[28,29] | 27 | 25, 26, 28, 29 |

**Table 2** Summary of intrinsic and extrinsic factors associated with the expression of anadromy in *O. mykiss* and associated studies. Studies are split into whether or not they are CCV specific. Note that this list is not exhaustive, and there may be additional factors influencing *O. mykiss* life history expression that are unstudied or undiscovered. (*Continued)*

| Factor | Influence on anadromy | CCV studies | Non-CCV studies |
|---|---|---|---|
| **Survival** | Low survival during outmigration, ocean residence, and/or spawning migration may decrease fitness benefits of anadromy[18,30,31]<br>Reduced ocean survival may contribute to a higher proportion of individuals expressing a resident life history[17]<br>The response of smolting rates to changing freshwater survival appears to be dependent on the maximum attainable size in freshwater; a limited maximum size is predicted to drive females to smolt across a wide range of estimated freshwater survival rates[17] | 18 | 17, 30, 31 |
| **Density dependence** | Positive relationships between density and expression of migratory life history have been observed for other salmonid species<br>▪ White-spotted Char (*Salvelinus leucomaenis*)[32]<br>▪ Brown Trout (*Salmo trutta*)[33,34]<br>▪ Atlantic Salmon (*Salmo salar*)[35,36]<br>▪ Sockeye Salmon (*Oncorhynchus nerka*)[37]<br>Increasing density can have negative effects on individual *O. mykiss* growth rates by increasing competition for prey resources[38], thus increasing the probability for juveniles to pursue a migratory life history[39,40] | None | 32, 33, 34, 35, 36, 37, 38, 39, 40 |
| **Water temperature** | Warmer water temperature regimes, associated with increased growth rates and reduced body lipid content (i.e., energy storage), may lead to higher rates of anadromy compared to cooler temperature regimes[15,41]<br>Cooler water temperatures are correlated with an increased prevalence of residency[15,42,43] | None | 15, 41, 42, 43 |
| **Discharge** | Magnitude of flood pulse events combined with substrate characteristics (e.g., substrate size) may influence distribution and viability of redds constructed by anadromous and resident females[44,45]<br>Flow regimes with low discharge during summer months may cause more individuals to smolt and outmigrate[43,46] | None | 43, 44, 45, 46 |
| **Habitat size** | Resident life history more prevalent in rivers where feeding habitat capacity is equal to or greater than spawning habitat capacity[23]<br>Anadromy is more common in smaller, confined rivers with simple channels; residency is more common in drainages with longer mainstem rivers and broad floodplains[23,47] | None | 23, 47 |
| **Drainage area** | Over broad spatial scales, anadromy is more prevalent in smaller watersheds and residency more prevalent in larger watersheds[48] but this association may not hold at smaller spatial scales[49] | None | 48, 49 |

**Citations**

1. Hayes et al. 2012
2. Neave 1944
3. Ruzycki et al. 2009
4. Nichols et al. 2008
5. Hecht et al. 2012
6. Pearse et al. 2014
7. Kelson et al. 2019
8. Pearse and Campbell 2018
9. Phillis et al. 2016
10. Berejikian et al. 2014
11. Rundio et al. 2012
12. Ohms et al. 2014
13. Pearse et al. 2019
14. Beakes et al. 2010
15. McMillan et al. 2012
16. Pavlov et al. 2007
17. Satterthwaite et al. 2009
18. Satterthwaite et al. 2010
19. Satterthwaite et al. 2012
20. Sloat et al. 2014
21. Sogard et al. 2012
22. Kendall et al. 2015
23. Pavlov et al. 2008b
24. Benjamin et al. 2013
25. Kuzishchin et al. 2007
26. Fleming 1998
27. Null et al. 2013
28. Busby et al. 1996
29. Keefer et al. 2008
30. Hendry et al. 2004
31. Sahashi and Morita 2013
32. Morita et al. 2000
33. Olsson and Greenberg 2004
34. Olsson et al. 2006
35. Gibson 1978
36. Prévost et al. 1992
37. Krogius 1981
38. Holm et al. 1990
39. Imre et al. 2004
40. Keeley 2001
41. Sloat and Reeves 2014
42. Berjikian et al. 2013
43. Courter et al. 2009
44. Lapointe et al. 2000
45. Montgomery et al. 1999
46. Pearsons et al. 2008
47. Pavlov et al. 2001
48. McPhee et al. 2014
49. Harvey et al. 2021

to effective CCV DPS monitoring, which in turn preclude effective management and recovery. To help illustrate the challenges of existing monitoring efforts, we provide a case study on current *O. mykiss* monitoring in the Stanislaus River as an example of the limited utility of existing data and describe how an *O. mykiss*-focused approach could may be applied to inform the development of forthcoming monitoring efforts. We suggest a framework focused on individual life-cycle transition rates, which may be designed to complement existing Steelhead life-history models (e.g., Satterthwaite et al. 2009) by guiding monitoring efforts to acquire data needed to estimate life-cycle transition rates. We argue that monitoring efforts singularly focused on the anadromous component will not yield information that represents CCV *O. mykiss* populations as a whole. Instead, monitoring of both resident and anadromous individuals is important to understand the drivers behind the expression of different life-history forms and the potential management actions that may promote anadromy.

### Factors Associated with Anadromy

No single factor has been conclusively identified as the most important driver of *O. mykiss* anadromy. The occurrence of the anadromous ecotype in an *O. mykiss* population is driven by intrinsic factors at the individual and population levels, as well as by extrinsic environmental conditions. Influential biotic factors include genetics, sex, growth, food resources, reproduction, freshwater and marine survival rates, and density-dependent interactions (Table 2). Genetic control over life-history expression is recognized, and the majority of offspring follow the same life-history path as their parents (Nichols et al. 2008; Hayes et al. 2012; Hecht et al. 2012; Pearse et al. 2014; Phillis et al. 2016), but neither parental life history nor genotype is a deterministic predictor of life-history expression in the offspring. A chromosomal rearrangement on the *Omy5* chromosome resulted in two forms: one associated with anadromous life history and the other with resident life history (Pearse et al. 2019). Additionally, the *Omy5* chromosome contains genes involved with migratory behavior and seasonal maturation, such as adiposity, photoreception, circadian rhythm, and age at maturity (Pearse et al. 2019). However, individuals that possess the resident variant may still express a migratory life-history strategy, and vice versa (Kelson et al. 2019), which may explain the persistence of the anadromous strategy in populations cut off from anadromous waters (Pascual et al. 2001; Hayes et al. 2012; Pearse and Campbell 2018). Both environmental and genetic factors influence individual growth. Similar to migratory behavior, the genetic factors that contribute to an individual's growth are heritable, yet the genes that influence these traits are broadly distributed throughout the *O. mykiss* genome (Hecht et al. 2012). Using CCV Steelhead smolts, Beakes et al. (2010) found that fish that later became residents exhibited higher condition factors in the November before the year of smolting, compared to those that later became smolts. This suggests *O. mykiss* have specific time-periods when they are sensitive to hormonal cues, and these periods are when growth, body condition, and lipid content are most important in determining life history. Modeling studies suggest size and growth thresholds may influence life-history expression, and multiple thresholds with alternating effects on expression may exist (Satterthwaite et al. 2009, 2010, 2012). Lack of growth benefits through anadromy may result in selection against ocean migration (Sloat et al. 2014). This is supported by studies from regions where resident and anadromous individuals achieve similar adult sizes and anadromy is relatively rare (e.g., Quinn and Myers 2004; Kuzishchin et al. 2007; Pavlov et al. 2008b). Closely associated with growth conditions, prey availability is a major determinant of patterns in salmonid migration and residency, because it controls growth, size, condition, and survival (Railsback and Rose 1999). Therefore, a change in the quantity or quality of prey may affect the proportion of anadromous or resident individuals.

Although Steelhead are capable of repeated spawning, iteroparity rates are low in many populations. Repeated spawning by anadromous *O. mykiss* is more common in Oregon and

California than in more northerly regions, but individuals infrequently spawn more than twice, and the majority of those that do are female (maximum observed five times; Busby et al. 1996; Keefer et al. 2008). Few studies on iteroparity of Steelhead in CCV streams have been conducted, but an average iteroparity rate of 3.9% was reported for the spawning population in Battle Creek (Null et al. 2013). Because resident CCV *O. mykiss* are not subject to the mortality associated with migration, they may be more likely to live to spawn multiple times. However, empirical data on their iteroparity rates are not available. This may further reduce the fitness benefits conferred by adopting an anadromous life history, because iteroparity of resident individuals may allow females to match or exceed the total lifetime fecundity of anadromous females.

The cumulative mortality experienced for ocean-migrating individuals exacts a cost that applies to both out-migrating juveniles and post-spawn adults, and has the potential to select for the resident life history. Satterthwaite et al. (2010) found survival during out-migration was a critical factor when predicting life-history strategies of female *O. mykiss*. However, the response of smolting rates to changing freshwater survival appears to depend on the maximum attainable size in freshwater, because a limited maximum size is predicted to drive females to smolt across a wide range of estimated freshwater survival rates (Satterthwaite et al. 2009). Reduced ocean survival rates can also contribute to a higher proportion of individuals that exhibit a resident life history (Gross et al. 1988; Satterthwaite et al. 2009), but the effects of ocean survival rates on life-history expression can be difficult to study because of the long time-scale at which selection affects anadromy (decades to centuries; Kendall et al. 2015). Moreover, the effects of ocean survival rates on life-history expression can be confounded by many other variables such as freshwater growth and survival rates, size and age at smoltification, upstream sources of residents, and physical freshwater habitat conditions (Pavlov et al. 2001, 2008a; Berejikian et al. 2008; Satterthwaite et al. 2010).

Very little information on density-dependence effects on anadromy for *O. mykiss* exists. Theoretically, increasing competition for resources should increase the proportion of individuals expressing anadromy, because it would release the migrating individuals from competition and lead to better growth opportunities. Studies have shown that increasing density can negatively affect individual *O. mykiss* growth rates by increasing competition for prey resources (Holm et al. 1990), which in turn can lead to increased out-migration (Keeley 2001; Imre et al. 2004). Other salmonids such as White-spotted Char (*Salvelinus leucomaenis*), Brown Trout (*Salmo trutta*), Atlantic Salmon (*Salmo salar*), and Sockeye Salmon (*Oncorhynchus nerka*) have shown positive relationships between density and migrants (Gibson 1978; Krogius 1981; Prévost et al. 1992; Morita et al. 2000; Olsson and Greenberg 2004; Olsson et al. 2006). However, other researchers have found no relationship between density and anadromy in Atlantic Salmon (Baum et al. 2004; Aubin–Horth et al. 2006), suggesting the need for further research in this area.

Significant abiotic factors include water temperature, stream discharge, and stream size (Table 2). Water temperature is among the most influential factors that contribute to the expression of life-history patterns in *O. mykiss* because it either directly or indirectly affects biotic factors (e.g., food supply, growth opportunities, and survival). Warmer, though tolerable, stream temperature regimes are associated with higher somatic growth rates and lower lipid levels, leading to higher rates of anadromy (McMillan et al. 2012; Sogard et al. 2012; Sloat and Reeves 2014). Conversely, cooler stream thermal regimes are correlated with an increased prevalence of residency as a result of lower somatic growth rates and higher lipid accumulation that provides the energy for maturation (Courter et al. 2009; McMillan et al. 2012; Berejikian et al. 2013). Discharge affects all life stages of *O. mykiss* and can influence which life-history types are present, or prevalent, in certain streams. Streams that experience higher discharge during spawning season may select for larger females (typically anadromous) that can construct redds that are not scoured or mobilized as easily as those built by smaller females (Montgomery et al. 1999; Lapointe et al. 2000). As juveniles grow, decreasing discharge during the drier summer months may drive them to adopt an anadromous life history as a result of a lack of usable habitat in their natal stream (Pearsons et al. 2008; Courter et al. 2009). Thus, positive correlations between residency and stable summer discharge, and between anadromy and variable summer discharge, have been observed in watersheds where both types of hydrological regimes exist (Zimmerman and Reeves 2002; Zimmerman and Ratliff 2003; Berejikian et al. 2013). In general, streams not large enough to support adult residents will force anadromy, whereas larger streams with suitable habitat will select for residency (Pavlov et al. 2001, 2008a). Furthermore, Pavlov et al. (2001) found that anadromy was more common in smaller, confined rivers with simple channels, whereas residency was more common in drainages with longer mainstem rivers and broad floodplains. Similar results were reported by McPhee et al. (2014), who found drainage area to be the best predictor of anadromy, with the proportion of anadromous individuals highest in small rivers. However, these relationships were not confirmed in the Eel River watershed (Harvey et al. 2021), emphasizing the need for population-specific studies on the influence of stream and watershed size on anadromy.

Abiotic factors may be further broken down temporally into “priming” and “releasing” factors (as defined by Spence and Dick 2014). Priming factors are the environmental conditions during freshwater rearing—such as changing stream temperatures and discharge—that trigger a fish to undergo the behavioral and physiological changes that prepare them for smolting and out-migration. After this preparatory phase, releasing factors are the environmental conditions that trigger initiation of the migratory phase. This dynamic, along with a high degree of plasticity, does not pose a challenge for monitoring Steelhead, per se, but it does mean that monitoring annual smolt production and adult escapement in relation to a few environmental variables will not provide data sufficient to understand the complicated biotic and abiotic interactions that lead to life-history expression.

## Anadromy on an Altered Landscape

Historically, the factors discussed above likely played a role in driving the expression of anadromy or residency in CCV *O. mykiss*. Given that present-day conditions are vastly different from historical conditions and recognizing that the degree of anadromy varies among rivers across the CCV, several lines of evidence suggest that the current conditions in many CCV rivers favor residency over anadromy, and these are related to growth and size, discharge and water temperature conditions, and survival.

First, the apparent overlap in maximum attainable size of resident and anadromous *O. mykiss* in CCV streams, coupled with potentially higher rates of iteroparity for residents, suggests that adopting a migratory life history may not yield an advantage in lifetime fecundity. Average sizes of returning CCV Steelhead adults and CCV resident adults show a high degree of overlap, compared to other regions. For example, Zimmerman et al. (2009) used otolith analysis to identify returning Steelhead in CCV rivers, and although the sample size was low (n = 5), fork lengths for confirmed age-4 Steelhead ranged from 455 to 700 mm (mean = 568). In this study, 212 age-4 residents were confirmed with fork lengths that ranged from 390 to 730 mm (mean = 466). In the Klamath River, where anadromy is more prevalent, mean fork length of age-4 resident fish was 368 (Hodge et al. 2016). In contrast, mean fork length for age-4 Steelhead was 637, 582, and 458, depending on whether individuals smolted at age-1, -2, or -3, respectively (Hodge et al. 2016). The availability of ample prey resources may be among the factors that enable resident *O. mykiss* to attain large adult size. In CCV rivers, *O. mykiss* benefit from the invertebrate prey production below reservoirs (Merz 2002; Sogard et al. 2012), which may encourage them to grow and mature in freshwater as residents. In addition, the dams that limit upstream migration of *O. mykiss* also preclude passage of Chinook Salmon, forcing them to spawn downstream of dams. The resulting supply of salmon eggs, a high-lipid food source, could favor a resident life history among *O. mykiss*, as has been shown in other populations (e.g., Pavlov et al. 2007, 2010; Benjamin et al. 2013).

Second, CCV reservoirs are generally operated to maintain a tolerable or favorable thermal environment for *O. mykiss* and other salmonids below the dams year-round (CVPIA 1992; NMFS 2019). Historically, unregulated flows in many CCV streams tapered off during the warm summer and fall months and stream temperatures increased, sometimes exceeding the thermal tolerance of *O. mykiss* (Brown and Bauer 2009). However, cool hypolimnetic releases from reservoirs where sufficient cold water storage exists, in conjunction with the higher thermal tolerance of resident *O. mykiss* in CCV streams compared with their conspecifics in the northern part of the species' range (Verhille et al. 2016), may limit thermal cues for out-migration of individuals.

In CCV reservoir tailwaters, *O. mykiss* appear to grow faster than in other systems. For example, *O. mykiss* in the American River in the Sacramento Basin had growth rates up to ten times higher than *O. mykiss* inhabiting Central California Coast streams with unimpaired hydrographs (Sogard et al. 2012). Similarly, *O. mykiss* in the Mokelumne River in the San Joaquin Basin grew approximately five times faster than *O. mykiss* in Central California Coast streams (Sogard et al. 2012). Further, *O. mykiss* in CCV tailwaters showed the highest growth during the summer and fall months, whereas in coastal streams where Steelhead are more prevalent, fish showed the highest growth during winter and spring (Sogard et al. 2012). This means that the summer to fall period in most CCV streams, which was historically the most stressful period to *O. mykiss* as the result of decreasing flow and increasing water temperatures, now provides near-optimum growing conditions because of dam releases. The similarity in anadromous and resident adult sizes in certain CCV streams suggests that the growth and reproductive potential of an anadromous life history may not differ from those of a resident ecotype, thereby providing little selective advantage to expressing an anadromous life history (e.g., Phillis et al. 2016).

Third, out-migrating smolts in the highly modified CCV experience low survival regardless of individual size, with individual success related to factors such as flow, migratory route, and predation. Del Real et al. (2012) found fewer than 10% of tagged Steelhead smolts from the Lower Mokelumne River reached the ocean at the Golden Gate Bridge. Singer et al. (2013) found that only 25% of hatchery *O. mykiss* smolts released in the Sacramento River near the City of Sacramento reached the ocean, with reach-specific survival rates varying between the years studied. Sandstrom et al. (2020) reported a mean survival of only 5.6% over 5 years from the upper Sacramento River (below Keswick Dam) to the Pacific Ocean. In the San Joaquin Basin, overall survival of tagged, hatchery-raised juvenile Steelhead smolts migrating from Buckley Cove through the South Delta to Chipps Island was estimated to be 50.2% (Delaney et al. 2014), but survival varied by route. Survival was 56.7% in the mainstem San Joaquin River where most (77.6%) of the fish migrated, whereas survival probabilities outside of the mainstem San Joaquin were low and ranged from 0.5% to 31.7% (Delaney et al. 2014). Buchanan (2018) obtained similar estimates of survival in the San Joaquin River, with 19% to 46% of smolts surviving from Mossdale to Chipps Island. Most recently, Buchanan et al. (2021) found overall survival of Steelhead smolts through the Delta to be highly variable between and within years (6% to 69% from 2011 to 2016). No single factor was identified as driving survival across all reaches of the Delta, but important drivers appeared to have reach-specific effects. For example, river discharge into the Delta was significantly correlated with survival in upstream reaches, whereas migratory route was more important for downstream reaches (Buchanan et al. 2021).

Nearly all survival studies have used acoustic-tagged hatchery-origin smolts, which are generally larger than their wild counterparts. Although hatchery fish are often used as surrogates for estimating survival of wild fish, studies of Chinook Salmon have found that hatchery juveniles may exhibit higher juvenile survival despite having lower smolt-to-adult ratios (or overall survival) than their wild counterparts (Buchanan et al. 2010). Therefore, actual survival rates of natural-origin Steelhead smolts may differ from those estimated from studies of hatchery smolts. Data on ocean survival of CCV Steelhead are nonexistent. In an effort to counteract this selective pressure against anadromy, reconditioning programs are used to improve kelt survival rates, increase the number of repeat spawners, and contribute to the recovery of Steelhead populations (Trammell et al. 2016). In the CCV, the Coleman National Fish Hatchery on Battle Creek has conducted Steelhead kelt reconditioning since 2001, and the survival of kelts in this program has been estimated to be between 36% and 48% (Null et al. 2013).

### Population Status and Monitoring of California Central Valley *O. mykiss*

Data on the historical distribution and abundance of CCV *O. mykiss* are scarce. It is generally accepted that Steelhead were widely distributed throughout CCV river systems, but that they were less abundant in the San Joaquin Basin as a result of natural migration barriers (Lindley et al. 2006). Some estimates suggest that historical run sizes may have been between 50,000 and 100,000 (Moyle et al. 2017), although others suggest runs may have exceeded one million adults (McEwan 2001). Spawning stock estimates between 1960 and 1965 suggest that annual abundance had fallen under 30,000 by the 1960s (CDFG 1965). The total number of naturally spawning female Steelhead throughout the entire region between 1998 and 2000 was estimated at 3,628 (Good et al. 2005), and as of 2016, the average number of adults returning annually was estimated at 4,600 (NMFS 2016). Importantly, these estimates are based on significant assumptions regarding survival and fecundity, and therefore carry a high degree of uncertainty (Moyle et al. 2017). Data at the overall DPS level are limited, but annual sampling downstream of the Delta (US Fish and Wildlife Service Chipps Island Midwater Trawl) suggests that the natural production of CCV Steelhead declined continuously through 2010 (Williams et al. 2016). This sampling also indicated that production remained very low from 2011 to 2015, and a concurrent increase in the adipose-clipped (i.e., hatchery-origin) proportion of the Chipps Island trawl catch suggests a continued decline in natural production of juvenile Steelhead (Swank and Cranford 2016). River-specific abundance estimates are also limited, but substantial declines in recent years have been noted in those systems where run size data are available. For example, in Battle Creek (Sacramento Basin), data suggest that a 17% per year decline in run size of natural-origin Steelhead occurred between 2000 and 2010 (Williams et al. 2016).

Scarce documentation of historical abundances warrants caution when estimates of historical population sizes are considered. Even contemporary estimates of abundance are associated with high uncertainty, limiting the use of these values to set specific population-recovery goals. This uncertainty is the result of a lack of data, which is largely attributable to monitoring efforts that target the small anadromous component of the CCV *O. mykiss* population, and effectively sample an even smaller fraction. In addition to the rarity of adult Steelhead in some CCV systems (e.g., Zimmerman et al. 2009), out-migrating juveniles are also challenging to sample because of their strong swimming ability and associated trap avoidance (Tattam et al. 2013), as well as the high-velocity flows associated with presumed periods of their peak movement (McEwan 2001). As a result, the samples provided by monitoring programs solely focused on anadromous individuals do not represent the population as a whole, and the limited number of captured individuals precludes any confident estimates of population abundance or other demographic parameters. Developing estimates with a reasonable degree of confidence will require monitoring approaches that can yield sufficient captures to provide a representative sample of the population, including the non-migratory contingent.

The National Marine Fisheries Service has delineated more than 80 demographically independent populations of CCV Steelhead as well as a number of smaller dependent populations. Because many of these exist above impassable barriers, they are no longer considered part of the DPS (Williams et al. 2016). Monitoring of populations in anadromous waters has been limited, and this has been the case for many decades. For example, in 1999 the Interagency Ecological Program Steelhead Project Work Team reviewed a total of 82 distinct monitoring and research programs focused on anadromous fish in the CCV; of these, 42 (51%) were salmon exclusive (i.e., characterized by sampling periods and methodologies that do not acquire data on Steelhead), 12 (15%) were focused on salmon but provided some useful Steelhead data, and only eight (10%) were Steelhead-focused (IEP Steelhead Project Work Team 1999). As of 2010, at least 63 monitoring programs collected at least some data on *O. mykiss*, but again, the majority of these were focused on monitoring Chinook Salmon and none provided data sufficient to estimate *O. mykiss* juvenile production or abundance (Eilers et al. 2010). Despite recent efforts to address this shortfall and develop Steelhead-focused monitoring to collect the data necessary to answer basic questions about the population, what Steelhead monitoring exists is biased toward the northern watersheds of the Sacramento River Basin (Beakes et al. 2021). Although several projects are underway in the Sacramento Basin as part of the Central Valley Steelhead Monitoring Program, as well as in the San Joaquin Basin, these programs are in their infancy and have produced limited findings to date. In addition, increased coordination among different programs is needed for research and monitoring and to facilitate data integration among programs (Beakes et al. 2021).

Obtaining the data to quantify the expression of anadromy is difficult. This is especially true in CCV populations where the proportion of migrating fish can potentially be low, such as the Stanislaus River (see Case Study: The Stanislaus River). A major shortcoming of ongoing approaches to CCV *O. mykiss* monitoring is that programs rely on a few stationary sampling methodologies—RSTs, fyke traps, and weirs—which all have limitations (Table 3). Used for sampling juveniles, RSTs generally only capture migratory individuals (smolts), and therefore provide no information on juvenile resident populations. Steelhead smolts typically out-migrate at larger body sizes and have stronger swimming abilities than Chinook Salmon. In addition, Steelhead smolt movement is generally associated with periods of higher stream discharge (Delaney et al. 2014), and they move quickly using main channel areas (Delaney et al. 2014; Chapman et al. 2015), which reduces capture probabilities. Low and often unmeasurable Steelhead smolt capture efficiencies prevent estimates of abundance. Data collected by RSTs may provide information on out-migration timing, and capturing individuals provides an opportunity to collect scales, tissue samples, and morphometric data that may be used to learn more about what factors contributed to the expression of anadromy. However, they provide little information on the proportion of the population that did not smolt or the factors that led them to adopt a resident life history. Fyke traps and weirs, which target adults, face similar challenges. Fyke traps also suffer from low efficiencies and low recaptures of tagged individuals, and a network of many fykes is required to sample the vast area of the Delta and CCV rivers. Weirs that span the width of a river and funnel migrating individuals through a narrow chute with a counting device can provide accurate abundance estimates (Eilers et al. 2010). However, weirs are only feasible on smaller rivers with limited small watercraft traffic and cannot be safely operated during high flow periods when peak Steelhead movement is expected. Despite these weaknesses, adjustments to these monitoring techniques may improve sampling efficiency for migratory *O. mykiss*, and they may be supplemented with other methods that can provide more insight into resident components of the population.

### Case Study: The Stanislaus River

The Stanislaus River is among the most intensively monitored rivers in the CCV. The CDFW has performed carcass surveys annually (typically October through January) since 1953 to

**Table 3** The strengths and weaknesses of *O. mykiss* sampling techniques

| Gear type | Method | Strengths | Weaknesses |
|---|---|---|---|
| Active | Hook and Line | ▪ Broad range of habitats can be sampled<br>▪ Allows for physical capture of fish for measuring, tagging, and/or collection of specimens | ▪ Size selectivity unknown<br>▪ Sampling effort difficult to quantify and/or standardize<br>▪ Higher risk of fish injury or mortality than other methods |
| Active | Backpack Electrofishing | ▪ Allows for physical capture of fish for measuring, tagging, and/or collection of specimens | ▪ Limited to shallow, wadeable areas<br>▪ Higher risk of fish injury or mortality than other methods |
| Active | Boat/Raft Electrofishing | ▪ Allows for physical capture of fish for measuring, tagging, and/or collection of specimens<br>▪ Can be conducted in habitats that are too deep for wading | ▪ Limited to river sections that are passable by boat<br>▪ Higher risk of fish injury or mortality than other methods |
| Active | Seine | ▪ Allows for physical capture of fish for measuring, tagging, and/or collection of specimens | ▪ Limited to shallow areas<br>▪ Requires sloping banks for efficient sampling<br>▪ Typically biased towards smaller fish |
| Active | Midwater Trawl | ▪ Allows for physical capture of fish for measuring, tagging, and/or collection of specimens<br>▪ Can be conducted in habitats that are too deep for wading | ▪ Limited to river sections that are passable by boat<br>▪ Limited to river sections that are free of debris in the water column<br>▪ Less likely to catch fish that are strong swimmers |
| Active | Kodiak Trawl | ▪ Allows for physical capture of fish for measuring, tagging, and/or collection of specimens<br>▪ Can be conducted in habitats that are too deep for wading<br>▪ Use of a live box can limit risk of fish injury and mortality | ▪ Limited to river sections that are passable by boat<br>▪ Limited to river sections that are free of debris in the water column<br>▪ Requires multiple vessels<br>▪ Targets smaller fish<br>▪ Less likely to catch fish that are strong swimmers |
| Active | Snorkel Survey | ▪ Can be conducted in habitats that are too deep for wading | ▪ Does not allow for the capture of fish for measuring, tagging, and/or collection of specimens<br>▪ Can only be conducted during periods of low flow<br>▪ Only feasible in areas with low turbidity |
| Passive | Rotary Screw Trap (RST) | ▪ Allows for physical capture of outmigrating juveniles for measuring, tagging, and/or collection of specimens | ▪ May not effectively capture juvenile Steelhead, as they are typically larger and better swimmers than other salmonid smolts<br>▪ Challenging to maintain during the high flows typical during Steelhead migration<br>▪ Trap efficiencies may be overestimated for Steelhead smolts as they are often based on release of marked juvenile Chinook Salmon |

**Table 3** The strengths and weaknesses of *O. mykiss* sampling techniques (*Continued*)

| Gear type | Method | Strengths | Weaknesses |
|---|---|---|---|
| Passive | Fish Counting Weir | ▪ Can allow for physical capture of migrating adults for measuring, tagging, and/or collection of specimens (if an associated trap is used)<br>▪ Can serve as a platform for automated monitoring systems (e.g., Vaki Riverwatcher, ARIS, PIT tag antenna) | ▪ Steelhead have a greater jumping ability than other Pacific salmonids and may be able to jump over the weir panels<br>▪ Challenging to maintain during the high flows typical during Steelhead migration |
| Passive | Fyke Trap | ▪ Allows for physical capture of fish for measuring, tagging, and/or collection of specimens | ▪ Fish may be able to avoid the trap<br>▪ Small fish may pass through the mesh on larger traps<br>▪ Requires a bank that is suitable for securing the trap |
| Passive | Redd surveys | ▪ Non-invasive sampling<br>▪ Provides data that can be used to develop production estimates<br>▪ Characterize spatio-temporal distribution of spawning | ▪ Does not allow for physical capture of fish for measuring, tagging, and/or collection of specimens<br>▪ Distinguishing species origin of redd can be challenging in rivers with other salmonid species<br>▪ Distinguishing among Rainbow Trout and Steelhead redds poses a potential challenge<br>▪ Challenging in areas of high flow that are often the location of Steelhead redds |
| Passive | eDNA | ▪ Non-invasive sampling that requires no permitting<br>▪ Inexpensive means of assessing the spatial distribution of *O. mykiss*<br>▪ Can be applied to confirm redd identity | ▪ Does not allow for physical capture of fish for measuring, tagging, and/or collection of specimens<br>▪ Only provides presence/absence data<br>▪ Cannot distinguish between Rainbow Trout and Steelhead presence |

estimate fall-run Chinook Salmon escapement. Two RSTs have been operated annually (typically January through May) by private contractors and the Pacific States Marine Fisheries Commission since 1996 to catch out-migrating fall-run Chinook Salmon and Steelhead at two locations: immediately below the known spawning reach and near the confluence with the San Joaquin River (Figure 2). In addition to providing data on relative abundance of out-migrating juveniles and associated length frequencies (Figure 3A and 3B), RSTs have allowed biological samples to be collected, including scale samples for age and growth estimation. Since 2003, a resistance-board weir with infrared and video counting devices has been operated at the lower end of the spawning reach (approximately 50 river kilometers upstream of the San Joaquin River confluence) to enumerate and obtain length measurements of adult Chinook Salmon and Steelhead (Figure 3C and 3D) that migrate upstream to spawn (weir monitoring typically occurs from September through December; see Appendix A). Redd surveys (typically mid-October to mid-December) have been performed since 2009 to characterize annual timing and spatial distribution of fall-run Chinook Salmon spawning (Peterson et al. 2020). Summer snorkel surveys (July and August) have been conducted annually since 2009 to monitor resident adult and juvenile *O. mykiss* densities, abundance, and distribution within the known rearing reach below Goodwin Dam. As a Central Valley Project stream, flows in the lower Stanislaus River are prescribed by a Biological Opinion for the benefit of ESA-listed anadromous

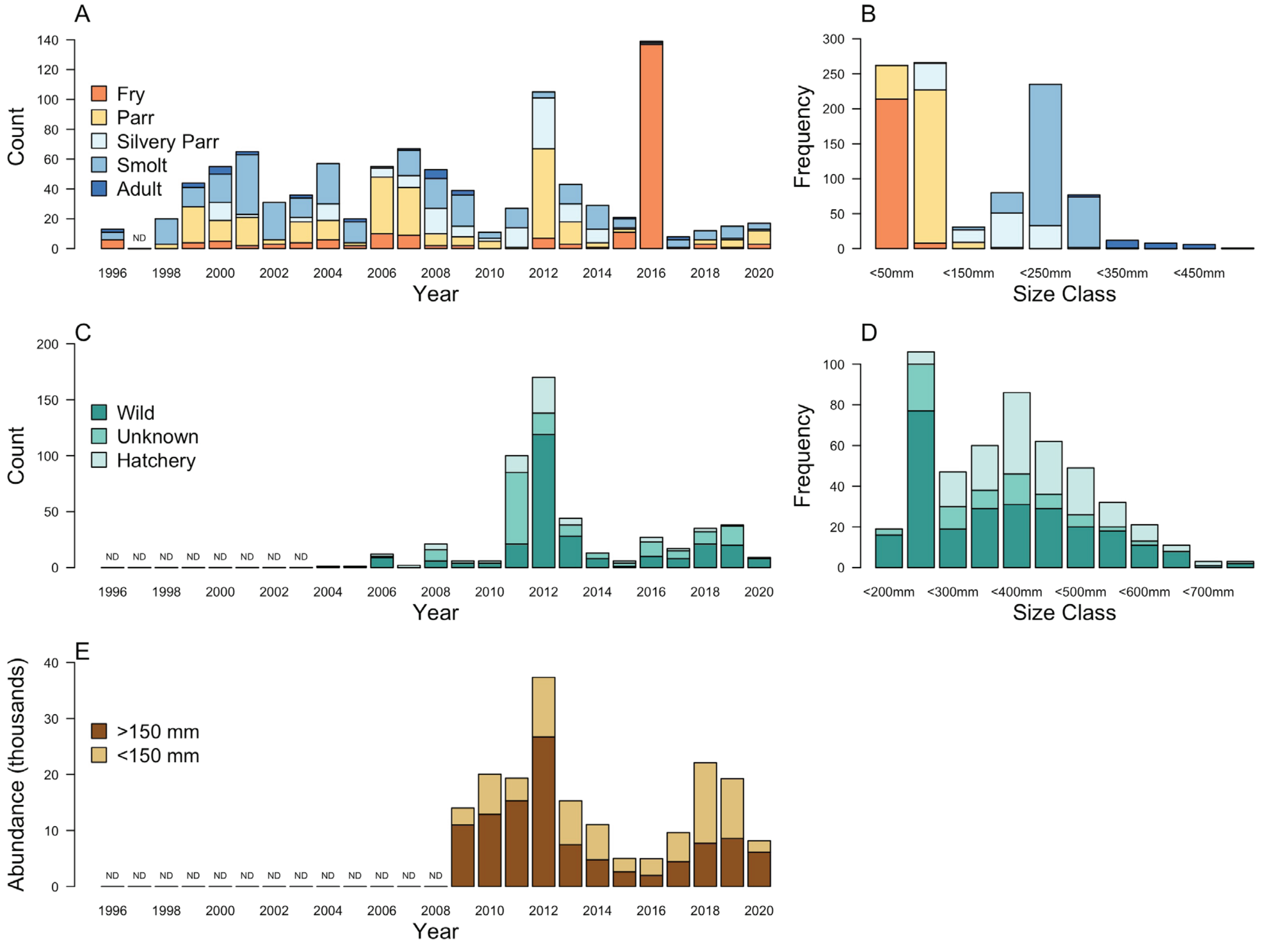

**Photo 1**

**Photo 2**

**Photo 3**

**Figure 3** Summary of *O. mykiss* monitoring on the Stanislaus River. **Panel A**–Annual detections of outmigrating *O. mykiss* at the rotary screw trap (RST) near Oakdale, CA (**Photo 1**), which has been operated every year since 1996 except for 1997 color coded by assigned life stage (*IEP 2008*). Typical operation period is from January into June. **Panel B**–The frequency of individuals in each size class captured by the RST (total n = 1,034), also color coded by assigned life stage. **Panel C**–Annual upstream passages of *O. mykiss* at the fish counting weir located near Riverbank, CA (**Photo 2**), from 2004 through 2019. Color coding indicates fish origin based on whether the presence of an adipose fin clip could be clearly discerned. The typical weir operation period is from September through December. **Panel D**–The frequency of individuals per 50 mm total length bin detected by the weir, with color coding indicating origin. Note the first size bin is 150 to 199 mm and that fish smaller than approximately 200 mm total length have low detection at the weir. Based on length, 180 individuals were classified as Steelhead (i.e., > 406 mm [> 16 inches]), of which 89 had an intact adipose fin, 75 had a clipped adipose fin, and 16 were inconclusive. **Panel E**–*O. mykiss* abundance estimates from summer snorkel surveys that have been conducted in reaches above Oakdale since 2009 (**Photo 3**).

species (USBR 2019). Except for the summer snorkel surveys, the monitoring time-frames and sampling gears used were specifically designed to capture anadromous individuals during periods of peak Chinook Salmon migrations.

Although monitoring efforts have centered on fall-run Chinook Salmon, limited captures of *O. mykiss* provide insight into the seasonality of *O. mykiss* movements. Data from the RST and weir suggest that both up- and downstream movement of *O. mykiss* is infrequent in this system (Figure 3A and 3C), but upstream migration of anadromous adults is greatest from October through February (Appendix A). Downstream adult movement after spawning is highest from December through February, although at greatly reduced numbers compared to upstream migration. Because monthly weir operation has varied over time, monthly escapement was standardized by dividing the cumulative upstream passage of *O. mykiss* by the number of days with active weir operation since the beginning of the weir program. For fish greater than 406 mm FL (16 inches; considered the size cut-off to classify individuals as Steelhead; CFGC c2021), standardized passage rates suggest peak passage in October (0.11 fish day$^{-1}$). For smaller individuals (< 406 mm), peak passage occurred from January through March (0.19 to 0.23 fish day$^{-1}$). Based on RST data, downstream juvenile movement is highest from April through June for parr, January through March for silvery parr, and January through March for smolts (see Appendix B). Juvenile *O. mykiss* have been captured during every month of the year except August and September, the only 2 months when the RST has never been operated (Appendix B). This suggests that out-migration may occur across a broad temporal scope rather than a clearly defined season, as with fall-run Chinook Salmon. In addition, the data are too sparse to be able to assess environmental factors associated with the timing of captures.

Data from current monitoring programs and otolith studies suggest that Steelhead are rare in the Stanislaus River. Low numbers of migrating Steelhead smolts and adults detected at the RST and weir, respectively, indicate that a large proportion of the population follows the resident life-history strategy. Steelhead escapement estimates for years with complete (or near-complete) temporal coverage has numbered in the tens of fish. Extended weir monitoring from September through June occurred in 4 years: 2006–07, 2008–09, 2009–10, and 2012–13. Escapement counts of *O. mykiss* measuring 406 mm or greater total length ranged from two in 2009–10 to 10 in 2008–09. In 2006–07 and 2012–13, Steelhead escapement was eight individuals. Zimmerman et al. (2009) used otolith microchemical analysis to reconstruct migration history of 157 adult *O. mykiss* in the Stanislaus River and found a single anadromous individual. However, 17 individuals from multiple age classes had mothers of anadromous origin (Appendix 1 in Zimmerman et al. 2008, 2009). This research indicates that although Steelhead are rare in the Stanislaus River, they do contribute to juvenile *O. mykiss* production.

Analysis of scale samples collected at the Oakdale RST has provided age information on *O. mykiss* and indicates a diverse age composition. The majority of aged fish captured in the RST were determined to be age-0 (n = 167), followed by age–2 (n = 116), age–1 (n = 35), age–3 (n = 21), age–4 (n = 6), age–5 (n = 4), and age–6 (n = 1; Figure 4; Appendix B). However, not all of these fish appeared to be actively migrating to the marine environment, because many were classified as parr and some were classified as adult *O. mykiss* with no indication of anadromous life-history expression. Individuals definitively identified as smolts also comprised multiple age classes. A small portion (3.7%) had completed one winter in freshwater, but the majority of smolts (80.7%) were determined to be age 2 at time of capture. Age-3 smolts comprised 14.7% of individuals, and a single age–4 smolt was observed. Size-at-age relationships within assigned life stages were not different (Appendix B), indicating highly variable growth rates among individuals, which limits the applicability of size-at-age relationships to predict if juveniles will become anadromous.

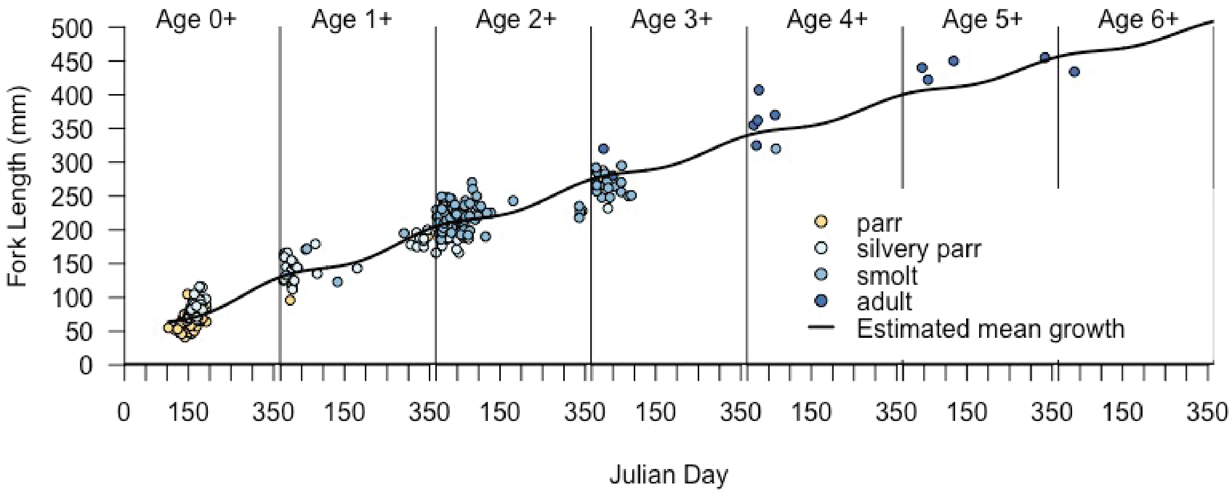

**Figure 4** Growth and age composition of *O. mykiss* (n = 350) captured in the Stanislaus River rotary screw trap near Oakdale, CA. Individuals are color coded by assigned life stage (IEP 2008). *Solid black line* is the estimated seasonally fluctuating von Bertalanffy growth through time. Typical operation of the trap is from January into June, but the trap was occasionally operated in December.

Although snorkel surveys provide coarse length and age information, they are an efficient, non-invasive method for assessing the status of juvenile and adult *O. mykiss* present in freshwater. Details on snorkel survey methods and abundance estimates are provided in Appendix C. From 2009 to 2012, the freshwater component residing in the Stanislaus River over summer was large (>10,000) and mostly composed of individuals of larger size classes (Figure 3E; Appendix C). Estimated summer abundance declined during the 2012–2016 drought, from 14,014 in 2012 to 4,968 in 2016. After the drought, summer abundance increased, but the proportion of smaller individuals also increased relative to the larger size class, suggesting strong recruitment after the drought (Figure 3E). The snorkel survey program is useful for characterizing *O. mykiss* population dynamics; however, mechanisms for the decline and changes in seasonal survival remain elusive. Since no mass die-offs were reported, worsening freshwater conditions during the drought may have caused individuals to out-migrate, although no noticeable increase in catch at the RST was observed (note: RST operations ran from January through June in those years; Appendix B).

Video and infrared weir monitoring has allowed individuals with clipped adipose fins (indicating hatchery origin) to be identified, which has revealed that a sizable fraction of adult escapement to the Stanislaus River consists of hatchery-origin fish. From 2004 through 2019, nearly half (45.7%) of *O. mykiss* (total length >406 mm) with identifiable presence/absence of adipose fin observed passing upstream through the weir were hatchery-origin (Figure 3C and 3D). A third (33%) of *O. mykiss* smaller than 406 mm were identified as being hatchery-origin fish. Although these fish were not physically sampled to permit identification of their natal hatchery, it is reasonable to assume that most of these strays originated from the Mokelumne River Hatchery, because it is the geographically closest facility and the only hatchery in the San Joaquin Basin that produces Steelhead. The upstream passage of hatchery-origin juveniles through the weir suggests that some hatchery-produced fish may residualize, or at least extend their freshwater rearing, in non-natal streams after release from the hatchery. For the fish <406 mm with intact adipose fins, it is unknown whether they originated in the Stanislaus River and moved back upstream through the weir after previous downstream dispersal or originated from nearby tributaries.

Although available data on *O. mykiss* in the Stanislaus River comprises a far richer data set than is available for *O. mykiss* populations elsewhere in the CCV, we cannot confidently estimate the anadromous portion of the Stanislaus River *O. mykiss* population for several reasons:

1. an apparent overlap in the size of resident and anadromous adults complicates Steelhead identification,
2. the uncertainty in the number of fish that return from the ocean and contribute to juvenile production, and
3. a lack of a definitive, non-lethal method to assess future life-history trajectory (smolting vs. freshwater maturation).

An enhanced monitoring plan that specifically targets all *O. mykiss* ecotypes and life stages present in the Stanislaus River is needed. Extended weir and RST operations are justified, given the extended time-periods over which Steelhead migrate in and out of the river. However, infrequent observations and catch may need to be balanced against added labor costs for extended operations of these gears. Continuation of the summer snorkel survey seems warranted in that it can be used to track the status of the freshwater component of the population. Although redd surveys are useful for characterizing spatio-temporal distribution of spawning, their utility for understanding anadromous contribution is limited, owing to the difficulty in determining if a redd was constructed by an anadromous or resident female. Additional capture methods such as electrofishing, seining, and/or hook-and-line could be implemented to collect biological samples for age and growth, genetic analysis, and injection of passive integrated transponder (PIT) tags. Strategic collection of otoliths from a representative sample of age-0 fish (the most abundant life stage), would provide data to estimate anadromous contribution to juvenile production. Genotyping individuals at *Omy5* would provide baseline information on the genetic capacity for anadromy in the Stanislaus River. Frequencies of the genotype associated with anadromy could be compared between samples collected during electrofishing/seining surveys and samples of smolts from the RST, to estimate the influence of *Omy5* genotype on expression of anadromy (i.e., to test whether the anadromy-associated variant is in higher frequency in RST-captured smolts). Lastly, mark-recapture or resighting analyses of PIT-tagged individuals could be used to estimate survival and transition probabilities, as well as to detect returning adults.

The US Bureau of Reclamation is funding and coordinating efforts to enhance the current monitoring of Steelhead on the Stanislaus River, and several of the enhanced methods described above are expected to be implemented. The data generated by these efforts may in turn allow for better

- evaluation of trends in the population over time,
- estimates of Steelhead production with reasonable levels of certainty,
- evaluation of smolt-to-adult ratios,
- estimates of survival rates, and
- understanding of the factors that influence the expression of the anadromous life-history strategy.

Comprehensive data collection from both *O. mykiss* ecotypes is needed to assess Steelhead-specific recovery actions, which include extensive gravel augmentation, construction of additional rearing habitat, and stepped releases from New Melones Reservoir (USBR 2019).

### Recommendations to Improve Understanding of Anadromy in Central Valley *O. mykiss*

Numerous factors can influence the expression of anadromy at the individual and population levels. The complexity of these variables combined with the challenges associated with monitoring Steelhead in some CCV rivers make obtaining the data to quantify the anadromous proportion of an

*O. mykiss* population difficult. Current monitoring in the CCV targets migrating Steelhead (Table 3) as per recovery programs (Table 1), and while there is limited data on CCV Steelhead from some important tributaries, there are practically no data available to assess the status of resident and juvenile *O. mykiss* in anadromous waters. Enacting the full recommendations set forth in the Comprehensive Monitoring Plan (Eilers et al. 2010) and recovery plan (NMFS 2014) would be prudent, specifically the CCV-wide Steelhead distribution surveys would provide a complete account of *O. mykiss* populations in anadromous waters. Enhanced monitoring and complementary studies are needed to evaluate the relationship between resident and anadromous forms of *O. mykiss*, because this will inform our understanding of the relative importance of life-history diversity (in both resident and anadromous strategies) for the resilience and persistence of the CCV DPS.

Priority enhancements to CCV *O. mykiss* monitoring include an expanded monitoring season, monitoring resident and juvenile individuals, and an increased collection of biological samples. Rivers with monitoring programs centered around the timing of Chinook Salmon migrations may be missing small but important migrations of Steelhead. In the Stanislaus River, observations of smolts and adult Steelhead are few but occur over a longer time-period each year compared to fall-run Chinook Salmon migrations. In rivers where the proportion of anadromous individuals is potentially low (such as the Stanislaus River), a critical review of the data obtained from gears with sparse numbers of captured or observed Steelhead may be advisable. If warranted, a reallocation of resources could be used to monitor resident and juvenile individuals using snorkel and electrofishing surveys. This approach has been suggested by others, including Eilers et al. (2010) who noted the statistical challenges related to the paucity of Steelhead in the San Joaquin River basin and recommended that electrofishing surveys for juvenile *O. mykiss* be performed.

Monitoring of CCV *O. mykiss* populations would also benefit from increased collection and utilization of biological samples, such as tissue for genetic analysis, otoliths, and scales. Tissue samples collected from resident, juvenile, and anadromous individuals provide material for genetic monitoring that is needed to identify the frequency of *Omy5* variants in each river, and to assess hatchery introgression and associated effects on genetic diversity in naturally reproducing populations (Schwartz et al. 2007). Extraction of otoliths requires lethal sampling, and therefore should only be performed strategically (with clear research goals in mind) or opportunistically. Given that otoliths are an invaluable tool for determining individual movement history and life-history diversity (e.g., Zimmerman et al. 2009; Courter et al. 2013; Harvey et al. 2021), concerted efforts are also needed to acquire otoliths from naturally produced Steelhead adults. Individual age and growth information can also be obtained from otoliths, but this information could be acquired for a larger number of individuals using non-lethal collection of scale samples from captured individuals.

In addition to enhanced monitoring, funding for complementary studies is needed to better understand the interaction among resident, juvenile, and anadromous *O. mykiss*. Studies using otoliths are needed to elucidate the full range of life-history diversity of CCV *O. mykiss* (e.g., Courter et al. 2013; Hodge et al. 2016). Whereas mark–recapture efforts to estimate abundance of Steelhead escapement are limited by few recaptures, mark–recapture studies of resident and juvenile fish may be used to estimate river-specific survival and transition probabilities. Parameterized life-history models could be used to simulate a polymorphic population with known survival and transition rates and used to assess accuracy and precision of estimates derived from empirical data. Population-specific data such as the frequency of the *Omy5* variants, individual growth rates, food and habitat availability, and survival of the resident and juvenile component of the population, are needed to assess variation in levels of anadromy among CCV rivers. Lastly, researchers should leverage the flow-control infrastructure present in many CCV rivers to test hypotheses related to expression of anadromy, and to identify potential management actions related to flow and temperature that could encourage the expression of anadromy.

## CONCLUSIONS

In conclusion, the unique plasticity in life-history expression attributable to facultative anadromy requires a tailored monitoring approach that differs from Chinook Salmon monitoring. Monitoring of the anadromous, freshwater resident, and juvenile components of CCV *O. mykiss* populations is needed for comprehensive status assessments and evaluation of population trends. Further, it is needed to quantify the capacity of each CCV river to support anadromous individuals and whether conditions can be altered to increase the expression of anadromy. Management agencies tasked with the recovery of the anadromous life-history strategy will benefit from enhanced monitoring and CCV-specific studies of anadromy, because these will result in better estimates of both Steelhead and resident *O. mykiss* abundance, increased understanding of the intrinsic (genotypes and individual growth) and extrinsic (environmental conditions) factors related to the expression of anadromy, and reduced chances for unintended negative consequences from management actions singularly focused on promoting one life-history strategy. Previous life-history models suggest that increasing the number of anadromous individuals may come at the cost of decreasing numbers of resident fish (Railsback et al. 2014). This could reduce population resilience by promoting the movement of fish into highly-variable, low-survival environments (i.e., the Delta and ocean), while decreasing the number of fish in a fairly stable environment (i.e., dam tailwaters). Further, resident individuals may produce offspring that later adopt an anadromous life history (Christie et al. 2011; Donohoe et al. 2021), and the importance of this contribution to maintaining the Steelhead contingent of *O. mykiss* populations in anadromous waters is not well understood. Assuming it is possible to implement actions that increase the fraction of anadromous individuals in CCV rivers, data from existing monitoring may limit the ability to detect if recovery goals have been met. Monitoring strategies that are informed through consideration of *O. mykiss* life history will not only provide data to better understand biological diversity but will also ensure that future data collection is appropriate for assessing recovery actions and goals.

## ACKNOWLEDGEMENTS

The long-term data sets used in the Stanislaus Case Study and the development of this manuscript were funded by the Tri-Dam Project, consisting of the Oakdale and South San Joaquin Irrigation Districts. The United States Fish and Wildlife Service provided the weir used on the Stanislaus River since 2002 and funded operations through 2006. Numerous people have contributed to field efforts to collect data from the Oakdale rotary screw trap and weir over two decades. Stockton East Water District provided funds to analyze previously collected monitoring data and accompanying biological samples. We thank Dee Thao for her assistance with Figure preparation, John Montgomery for the steelhead distribution map, Chrissy Sonke for database management, and Chad Alderson for the initial draft of Figure 1. The manuscript was greatly improved through critical reviews and discussions with Shaara Ainsley, Adam Herdrich, and Erin Loury as well as three anonymous reviewers. The views and opinions expressed in this article are those of the authors and do not necessarily reflect the official policies or positions of the Oakdale and South San Joaquin Irrigation Districts, the Stockton East Water District, or the US Fish and Wildlife Service.

## REFERENCES

Aubin–Horth N, Bourque JF, Daigle G, Hedger R, Dodson JJ. 2006. Longitudinal gradients in threshold sizes for alternative male life history tactics in a population of Atlantic Salmon (*Salmo salar*). Can J Fish Aquat Sci. [accessed 2021 Jun 8];63(9):2067–2075. *https://doi.org/10.1139/f06-103*

Baerwald MR, Meek MH, Stephens MR, Nagarajan RP, Goodbla AM, Tomalty KMH, Thorgaard GH, May B, Nichols KM. 2016. Migration-related phenotypic divergence is associated with epigenetic modifications in Rainbow Trout. Mol Ecol. [accessed 2021 Jun 8];25(8):1785–1800. *https://doi.org/10.1111/mec.13231*

Baum D, Laughton R, Armstrong JD, Metcalfe NB. 2004. Altitudinal variation in the relationship between growth and maturation rate in Salmon parr. J Anim Ecol. [accessed 2021 Jun 8];73(2):253–260. *https://doi.org/10.1111/j.0021-8790.2004.00803.x*

Beakes MP, Bilski R, Matthias B, Byrne B, Vick P, Goertler P. 2021. Monitoring Steelhead populations in the San Joaquin Basin – *Oncorhynchus mykiss* monitoring and research gap analysis. Sacramento (CA): Delta Stewardship Council. [accessed 2021 Jun 8]. 21 p. Available from: *https://deltacouncil.ca.gov/pdf/science-program/fact-sheets/2021-02-03-monitoring-steelhead-populations-monitoring-and-research-gap-analysis.pdf*

Beakes MP, Satterthwaite WH, Collins EM, Swank DR, Merz JE, Titus RG, Sogard SM, Mangel M. 2010. Smolt transformation in two California Steelhead populations: effects of temporal variability in growth. Trans Am Fish Soc. [accessed 2021 Jun 8];139(5):1263–1275. *https://doi.org/10.1577/T09-146.1*

Benjamin JR, Connolly PJ, Romine JG, Perry RW. 2013. Potential effects of changes in temperature and food resources on life-history trajectories of juvenile *Oncorhynchus mykiss*. Trans Am Fish Soc. [accessed 2021 Jun 8];142(1):208–220. *https://doi.org/10.1080/00028487.2012.728162*

Berejikian BA, Bush RA, Campbell LA. 2014. Maternal control over offspring life history in a partially anadromous species, *Oncorhynchus mykiss*. Trans Am Fish Soc. [accessed 2021 Jun 8];143(2):369–379. *https://doi.org/10.1080/00028487.2013.862181*

Berejikian BA, Campbell LA, Moore ME, Grant J. 2013. Large-scale freshwater habitat features influence the degree of anadromy in eight Hood Canal *Oncorhynchus mykiss* populations. Can J Fish Aquat Sci. [accessed 2021 Jun 8];70(5):756–765. *https://doi.org/10.1139/cjfas-2012-0491*

Berejikian BA, Johnson T, Endicott RS, Lee–Waltermire J. 2008. Increases in Steelhead (*Oncorhynchus mykiss*) redd abundance resulting from two conservation hatchery strategies in the Hamma Hamma River, Washington. Can J Fish Aquat Sci. [accessed 2021 Jun 8];65(4):754–764. *https://doi.org/10.1139/f08-014*

Brown LR, Bauer ML. 2009. Effects of hydrologic infrastructure on flow regimes of California's Central Valley rivers: implications for fish populations. River Res App. [accessed 2021 Jun 8];26(6):751–765. *https://doi.org/10.1002/rra.1293*

Buchanan RA, Buttermore E, Israel J. 2021. Outmigration survival of a threatened Steelhead population through a tidal estuary. Can J Fish Aquat Sci. [accessed 2021 Jun 8];78(12):1869–1886. *https://doi.org/10.1139/cjfas-2020-0467*

Buchanan RA. 2018. 2015 six-year acoustic telemetry Steelhead study: statistical methods and results. Seattle (WA): University of Washington. [accessed 2020 Nov 19]. 174 p. Available from: *http://www.cbr.washington.edu/sites/default/files/papers/UW%206yr%20steelhead%20report%20 2015%20FINAL.pdf*

Buchanan R, Skalski JR, Giorgi AE. 2010. Evaluating surrogacy of hatchery releases for the performance of wild yearling Chinook Salmon from the Snake River Basin. N. Am J Fish Manage. [accessed 2021 Jun 8];30(5):1258–1269. *https://doi.org/10.1577/M09-175.1*

Busby PJ, Wainwright TC, Bryant GJ, Lierheimer LJ, Waples RS, Waknitz FW, Lagomarsino IV. 1996. Status review of West Coast Steelhead from Washington, Idaho, Oregon, and California. Seattle (WA): US Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service. NOAA Technical Memorandum NMFS-NWFSC-27. [accessed 2020 Nov 19]. 275 p. Available from: *https://repository.library.noaa.gov/view/noaa/2986/noaa_2986_DS1.pdf*

[CDFG] California Department of Fish and Game. 1965. California Fish and Wildlife Plan. Volume III: Supporting data. Part B: Inventory (Salmon–Steelhead and Marine Resources). Sacramento (CA): California Department of Fish and Game.

[CDFW] California Department of Fish and Wildlife. c2020. Sacramento (CA): Central Valley Steelhead monitoring. [accessed 2020 August 31]. Available from: *https://wildlife.ca.gov/Drought/Projects/Central-Valley-Steelhead*

[CFGC] California Fish and Game Commission. c2021. Sacramento (CA): California Freshwater Fishing Regulations; [accessed 2021 June 14]. Available from: *https://nrm.dfg.ca.gov/FileHandler.ashx?DocumentID=190456&inline*

[CVPIA] Central Valley Project Improvement Act. 1992. Title 34 of the Reclamation Projects Authorization and Adjustment Act of 1992, Pub. L. No. 102-575, 106 Stat. 4600.

Chapman ED, Hearn AR, Singer GP, Brostoff W, LaCivita P, Klimley AP. 2015. Movements of Steelhead (*Oncorhynchus mykiss*) smolts migrating through the San Francisco Bay Estuary. Environ Biol Fish. [accessed 2021 Jun 8];98(4):1069–1080. *https://doi.org/10.1007/s10641-014-0341-9*

Christie MR, Marine ML, Blouin MS. 2011. Who are the missing parents? Grandparentage analysis identifies multiple sources of gene flow into a wild population. Mol Ecol. [accessed 2021 Jun 8];20(6):1263–1276. *https://doi.org/10.1111/j.1365-294X.2010.04994.x*

Courter II, Child DB, Hobbs JA, Garrison TM, Glessner JJG, Duery S, Fraser D. 2013. Resident Rainbow Trout produce anadromous offspring in a large interior watershed. Can J Fish Aquat Sci. [accessed 2021 Jun 8];70(5):701–710. *https://doi.org/10.1139/cjfas-2012-0457*

Courter II, Justice C, Cramer SP. 2009. Flow and temperature effects on life-history diversity of *Oncorhynchus mykiss* in the Yakima River Basin. Gresham (OR): Cramer Fish Sciences. 46 p.

Del Real SC, Workman M, Merz J. 2012. Migration characteristics of hatchery and natural-origin, *Oncorhynchus mykiss*, from the lower Mokelumne River, California. Environ Biol Fish. [accessed 2021 Jun 8];94(2):363–375. *https://doi.org/10.1007/s10641-011-9967-z*

Delaney D, Bergman P, Cavallo B, Malgo J. 2014. Stipulation study: Steelhead movement and survival in the South Delta with adaptive management of Old and Middle River flows. Sacramento (CA): California Natural Resources Agency, Department of Water Resources.

Dettinger MD, Ralph FM, Das T, Neiman PJ, Cayan DR. 2011. Atmospheric rivers, floods and the water resources of California. Water. [accessed 2021 Jun 8];3(2):445–478. *https://doi.org/10.3390/w3020445*

Donohoe CJ, Rundio DE, Pearse DE, Williams TH. 2021. Straying and life history of adult Steelhead in a small California coastal stream revealed by otolith natural tags and genetic stock identification. N Am J Fish Manage. [accessed 2021 Jun 8];41(3):711–723. *https://doi.org/10.1002/nafm.10577*

Eilers CD, Bergman J, Nielson R. 2010. A comprehensive monitoring plan for steelhead in the California Central Valley. Sacramento (CA): California Department of Fish and Game. Fisheries Branch Administrative Report Number 2010-2. [accessed 2020 Nov 19]. 184 p. Available from: *http://cahatcheryreview.com/wp-content/uploads/2012/08/CV-Steelhead-Monitoring-Plan-2010.pdf*

Federal Register. 1998. Endangered and threatened species: threatened status for two ESUs of steelhead in Washington, Oregon, and California. Thursday, March 19, 1998. Rules and Regulations. Fed Regist [accessed 2020 Nov 19];63953):13347–13371. Available from: *https://www.federalregister.gov/documents/1998/03/19/98-6972/endangered-and-threatened-species-threatened-status-for-two-esus-of-steelhead-in-washington-oregon*

Fleming, IA. 1998. Pattern and variability in the breeding system of Atlantic salmon (*Salmo salar*), with comparisons to other salmonids. Can J Fish Aquat Sci. [accessed 2021 Jun 8];55(S1):59–76. *https://doi.org/10.1139/d98-009*

Gibson JR. 1978. Recent changes in the population of juvenile Atlantic Salmon in the Matamek River, Quebec, Canada. ICES J Mar Sci. [accessed 2021 Jun 8];38(2):201–207. *https://doi.org/10.1093/icesjms/38.2.201*

Good TP, Waples, RS, Adams P. 2005. Updated status of federally listed ESUs of West Coast salmon and steelhead. Seattle (WA): US Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service. NOAA Technical Memorandum NMFS-NWFSC-66. [accessed 2020 Nov 19]. 637 p. Available from: *https://repository.library.noaa.gov/view/noaa/3413/noaa_3413_DS1.pdf*

Gross MR, Coleman RM, McDowall RM. 1988. Aquatic productivity and the evolution of diadromous fish migration. Science. [accessed 2021 Jun 8];239(4845):1291–1293. *https://doi.org/10.1126/science.239.4845.1291*

Hallock RJ, Van Woert WF, Shapovalov L. 1961. An evaluation of stocking hatchery-reared Steelhead Rainbow Trout (*Salmo gairdnerii gairdnerii*) in the Sacramento River System. Red Bluff (CA): California Department of Fish and Game. Fish Bulletin No. 114. [accessed 2020 Nov 19]. 74 p. Available from: *https://escholarship.org/uc/item/3564k9q5*

Harvey BC, Nakamoto RJ, Kent AJ, Zimmerman CE. 2021. The distribution of anadromy and residency in Steelhead/Rainbow Trout in the Eel River, northwestern California. Calif Fish and Wildl J. [accessed 2021 Jun 8];107(2):77–88. *https://doi.org/10.51492/cfwj.107.7*

Hayes SA, Hanson CV, Pearse DE, Bond MH, Garza JC, MacFarlane RB. 2012. Should I stay or should I go? The influence of genetic origin on emigration behavior and physiology of resident and anadromous juvenile *Oncorhynchus mykiss*. N Am J Fish Manage. [accessed 2021 Jun 8];32(4):772–780. *https://doi.org/10.1080/02755947.2012.686953*

He L, Marcinkevage C. 2017. Incorporating thermal requirements into flow regime development for multiple Pacific salmonid species in regulated rivers. Ecol Eng. [accessed 2021 Jun 8];99:141–158. *https://doi.org/10.1016/j.ecoleng.2016.11.009*

Hecht BC, Thrower FP, Hale MC, Miller MR, Nichols KM. 2012. Genetic architecture of migration-related traits in Rainbow and Steelhead Trout, *Oncorhynchus mykiss*. G3. [accessed 2021 Jun 8];2(9):1113–1127. *https://doi.org/10.1534/g3.112.003137*

Hendry AP, Bohlin T, Jonsson B, Berg OK. 2004. To sea or not to sea. In: Hendry AP, Stearns SC, editors. Evolution illuminated: Salmon and their relatives. New York (NY): Oxford University Press. p. 92–125.

Hodge BW, Wilzbach MA, Duffy WG, Quiñones RM, Hobbs JA. 2016. Life history diversity in Klamath River steelhead. Trans Am Fish Soc. [accessed 2021 Jun 8];145(2):227–238. *https://doi.org/10.1080/00028487.2015.1111257*

Holm JC, Refstie T, Bø S. 1990. The effect of fish density and feeding regimes on individual growth rate and mortality in Rainbow Trout (*Oncorhynchus mykiss*). Aquaculture. [accessed 2021 Jun 8];89(3-4):225–232. *https://doi.org/10.1016/0044-8486(90)90128-A*

Interagency Ecological Program Steelhead Project Workteam. 1999. Monitoring, assessment, and research on Central Valley Steelhead: status of knowledge, review of existing programs, and assessment of needs. In: Comprehensive monitoring, assessment, and research program plan technical appendix VII–A–11.

Imre I, Grant JW, Keeley ER. 2004. The effect of food abundance on territory size and population density of juvenile Steelhead Trout (*Oncorhynchus mykiss*). Oecologia. [accessed 2021 Jun 8];138(3):371–378. *https://doi.org/10.1007/s00442-003-1432-z*

Katz J, Moyle PB, Quiñones RM, Israel J, Purdy S. 2012. Impending extinction of Salmon, Steelhead, and Trout (Salmonidae) in California. Environ Biol Fish. [accessed 2021 Jun 8];96(10):1169–1186. *https://doi.org/10.1007/s10641-012-9974-8*

Keefer ML, Wertheimer RH, Evans AF, Boggs CT, Peery CA. 2008. Iteroparity in Columbia River summer-run Steelhead (*Oncorhynchus mykiss*): implications for conservation. Can J Fish Aquat Sci. [accessed 2021 Jun 8];65(12):2592–2605. *https://doi.org/10.1139/F08-160*

Keeley ER. 2001. Demographic responses to food and space competition by juvenile Steelhead Trout. Ecology. [accessed 2021 Jun 8];82(5):1247–1259. *https://doi.org/10.1890/0012-9658(2001)082[1247:DRTFAS]2.0.CO;2*

Kelson SJ, Miller MR, Thompson TQ, O'Rourke SM, Carlson SM. 2019. Do genomics and sex predict migration in a partially migratory salmonid fish, *Oncorhynchus mykiss*? Can J Fish Aquat Sci. [accessed 2021 Jun 8];76(11):2080–2088. *https://doi.org/10.1139/cjfas-2018-0394*

Kendall NW, McMillan JR, Sloat MR, Buehrens TW, Quinn TP, Pess GR, Kuzishchin KV, McClure MM, Zabel RW. 2015. Anadromy and residency in Steelhead and Rainbow Trout (*Oncorhynchus mykiss*): a review of the processes and patterns. Can J Fish Aquat Sci. [accessed 2021 Jun 8];72(3):319–342. *https://doi.org/10.1139/cjfas-2014-0192*

Krogius FV. 1981. The role of resident fish in the reproduction of anadromous Sockeye Salmon, *Oncorhynchus nerka*. J Ichthyol. 21:14–21.

Kuzishchin KV, Mal'tsev AY, Gruzdeva MA, Savvaitova KA, Pavlov DS, Stanford DA. 2007. On joint spawning of anadromous and resident mykiss *Parasalmo mykiss* in rivers of Western Kamchatka. J Ichthyol. [accessed 2021 Jun 8];47(5):348–352. *https://doi.org/10.1134/S0032945207050037*

Lapointe M, Eaton B, Driscoll S, Latulippe C. 2000. Modelling the probability of salmonid egg pocket scour due to floods. Can J Fish Aquat Sci. [accessed 2021 Jun 8];57(6):1120–1130. *https://doi.org/10.1139/f00-033*

Lindley ST, Grimes CB, Mohr M, Peterson W, Stein J, Anderson JT, Botsford LW, Bottom DL, Busack CA, Collier TK, et al. 2009. What caused the Sacramento River fall Chinook stock collapse? Santa Cruz (CA): US Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service. NOAA Technical Memorandum NMFS-SWFSC-447. [accessed 2020 Nov 19]. 125 p. Available from: *https://repository.library.noaa.gov/view/noaa/3664/noaa_3664_DS1.pdf*

Lindley ST, Schick RS, Agrawal A, Goslin M, Pearson TE, Mora E, Anderson JJ, May B, Greene S, Hanson C, et al. 2006. Historical population structure of Central Valley Steelhead and its alteration by dams. San Franc Estuary Watershed Sci. [accessed 2021 Jun 8];4(1). *https://doi.org/10.15447/sfews.2006v4iss1art3*

Lund J, Hanak E, Fleenor W, Howitt R, Mount J, Moyle P. 2007. Envisioning futures for the Sacramento–San Joaquin Delta. San Francisco (CA): Public Policy Institute of California. [accessed 2020 Nov 19]. 325 p. Available from: *https://www.ppic.org/publication/envisioning-futures-for-the-sacramento-san-joaquin-delta/*

McEwan DR. 2001. Central Valley Steelhead. In: Brown RL, editor. Fish B-NOAA Bulletin 179. Contributions to the biology of Central Valley Ssalmonids. Volumes 1 & 2. Sacramento (CA): State of California, California Department of Fish and Game. p. 1–44. *https://escholarship.org/uc/item/6sd4z5b2*

McMillan JR, Dunham JB, Reeves GH, Mills JS, Jordan CE. 2012. Individual condition and stream temperature influence early maturation of Rainbow and Steelhead Trout, *Oncorhynchus mykiss*. Environ Biol Fish. [accessed 2021 Jun 8];93(3):343–355. *https://doi.org/10.1007/s10641-011-9921-0*

McPhee MV, Whited DC, Kuzishchin KV, Stanford JA. 2014. The effects of riverine physical complexity on anadromy and genetic diversity in Steelhead or Rainbow Trout *Oncorhynchus mykiss* around the Pacific Rim. J Fish Biol. [accessed 2021 Jun 8];85(1):132–150. *https://doi.org/10.1111/jfb.12286*

Merz JE. 2002. Seasonal feeding habits, growth, and movement of Steelhead Trout in the lower Mokelumne River, California. California Fish and Game. [accessed 2021 Jun 8];88(3):95–111. Available from: *https://www.csus.edu/indiv/m/merzj/research%20projects/published%20literature/steelheaddietpaper.pdf*

Montgomery DR, Beamer EM, Pess GR, Quinn TP. 1999. Channel type and salmonid spawning distribution and abundance. Can J Fish Aquat Sci. [accessed 2021 Jun 8];56(3):377–387. *https://doi.org/10.1139/f98-181*

Morita K, Yamamoto S, Hoshino N. 2000. Extreme life history change of White-spotted Char (*Salvelinus leucomaenis*) after damming. Can J Fish Aquat Sci. [accessed 2021 Jun 8];57(6):1300–1306. *https://doi.org/10.1139/f00-050*

Moyle PB, Lusardi RA, Samuel PJ, Katz JVE. 2017. State of the salmonids: status of California's emblematic fishes 2017. San Francisco (CA): Center for Watershed Sciences, University of California, Davis. A report commissioned by California Trout. [accessed 2020 Nov 19]. 579 p. Available from: *https://watershed.ucdavis.edu/files/content/news/SOS%20II_Final.pdf*

[NMFS] National Marine Fisheries Service. 2019. Biological Opinion on long-term operation of the Central Valley Project and the State Water Project. Sacramento (CA): US Department of Commerce, National Oceanic and Atmospheric Administration, NMFS. [accessed 2021 Jul 1]. 900 p. Consultation # WCR-2016-00069.n Available from: *https://repository.library.noaa.gov/view/noaa/22046*

[NMFS] National Marine Fisheries Service. 2016. 5-year review: summary and evaluation of south-central California coast Steelhead Distinct Population Segment. Santa Rosa (CA): US Department of Commerce, National Oceanic and Atmospheric Administration, NMFS. [accessed 2021 Jul 1]. 73 p. Available from: *https://www.fisheries.noaa.gov/resource/document/5-year-review-south-central-southern-california-coast-steelhead-recovery-planning*

[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. Sacramento (CA): US Department of Commerce, National Oceanic and Atmospheric Administration, NMFS. [accessed 2020 Nov 19]. 1561 p. Available from: *https://www.fisheries.noaa.gov/resource/document/recovery-plan-evolutionarily-significant-units-sacramento-river-winter-run*

Neave F. 1944. Racial characteristics and migratory habits in *Salmo gairdneri*. J Fish Res Board Can. [accessed 2021 Jun 8];6c(3):245–251. *https://doi.org/10.1139/f42-030*

Nichols KM, Edo AF, Wheeler PA, Thorgaard GH. 2008. The genetic basis of smoltification-related traits in *Oncorhynchus mykiss*. Genetics. [accessed 2021 Jun 8];179(3):1559–1575. *https://doi.org/10.1534/genetics.107.084251*

Null RE, Niemela KS, Hamelberg SF. 2013. Post-spawn migrations of hatchery-origin *Oncorhynchus mykiss* kelts in the Central Valley of California. Environ Biol Fish. [accessed 2021 Jun 8];96(2):341–353.*https://doi.org/10.1007/s10641-012-0075-5*

Ohms HA, Sloat MR, Reeves GH, Jordan CE, Dunham JB. 2014. Influence of sex, migration distance, and latitude on life-history expression in Steelhead and Rainbow Trout (*Oncorhynchus mykiss*). Can J Fish Aquat Sci. [accessed 2021 Jun 8]; 71(1):70–80. *https://doi.org/10.1139/cjfas-2013-0274*

Olsson IC, Greenberg LA. 2004. Partial migration in a landlocked Brown Trout population. J Fish Biol. [accessed 2021 Jun 8];65(1):106–121. *https://doi.org/10.1111/j.0022-1112.2004.00430.x*

Olsson IC, Greenberg LA, Bergman E, Wysujack K. 2006. Environmentally induced migration: the importance of food. Ecol Lett. [accessed 2021 Jun 8];9(6):645-651. *https://doi.org/10.1111/j.1461-0248.2006.00909.x*

Pascual M, Bentzen P, Rossi CR, Mackey G, Kinnison MT, Walker R. 2001. First documented case of anadromy in a population of introduced Rainbow Trout in Patagonia, Argentina. Trans Am Fish Soc. [accessed 2021 Jun 8];130(1):53–67. *https://doi.org/10.1577/1548-8659(2001)130<0053:FDCOAI>2.0.CO;2*

Pavlov DS, Savvaitova KA, Kuzishchin KV. 2001. Theoretical aspects of the problem of the distribution pattern and formation of life-history strategy of mikizha (*Parasalmo mykiss* (Walbaum), Salmonidae, Salmoniformes) on the Kamchatka Peninsula. Dokl Biol Sci. [accessed 2021 Jun 8];379(1):344–346. *https://doi.org/10.1023/A:1011652230060*

Pavlov DS, Nemova NN, Kirillov PI, Kirillova EA, Nefedova ZA, Vasil'eva OB. 2007. Lipid status and feeding habits of salmonid juveniles in the year preceding seaward migration as factors controlling their future smoltification. J Ichthyol. [accessed 2021 Jun 8];47(3):241–245. *https://doi.org/10.1134/S003294520703006X*

Pavlov DS, Mikheev VN, Lupandin AI, Skorobogatov MA. 2008a. Ecological and behavioural influences on juvenile fish migrations in regulated rivers: a review of experimental and field studies. Hydrobiologia. [accessed 2021 Jun 8];609(1):125–138. *https://doi.org/10.1007/s10750-008-9396-y*

Pavlov DS, Savvaitova KA, Kuzishchin KV, Gruzdeva MA, Mal'tsev AY, Stanford JA. 2008b. Diversity of life strategies and population structure of Kamchatka mykiss *Parasalmo mykiss* in the ecosystems of small salmon rivers of various types. J Ichthyol. [accessed 2021 Jun 8];48(1):37–44. *https://doi.org/10.1134/S0032945208010049*

Pavlov DS, Nemova NN, Nefedova ZA, Ruokolainen TR, Vasil'eva OB, Kirillov PI, Kirillova EA. 2010. The lipid status of young of the year mykiss *Parasalmo mykiss* and Coho Salmon *Oncorhynchus kisutch*. J Ichthyol. [accessed 2021 Jun 8];50(1):116–126. *https://doi.org/10.1134/S0032945210010145*

Pearse DE, Miller MR, Abadia–Cardoso A, Garza JC. 2014. Rapid parallel evolution of standing variation in a single, complex, genomic region is associated with life history in Steelhead/Rainbow Trout. P Roy Soc B-Biol Sci. [accessed 2021 Jun 8];281(1783):20140012. *https://doi.org/10.1098/rspb.2014.0012*

Pearse, DE, Campbell, MA. 2018. Ancestry and adaptation of Rainbow Trout in Yosemite National Park. Fisheries. [accessed 2021 Jun 8];43(10):472–484. *https://doi.org/10.1002/fsh.10136*

Pearse DE, Barson NJ, Nome T, Gao G, Campbell MA, Abadía–Cardoso A, Anderson EC, Rundio DE, Williams TH, Naish KA, et al. 2019. Sex-dependent dominance maintains migration supergene in Rainbow Trout. Nat Ecol Evol. [accessed 2021 Jun 8];3(12): 1731–1742. *https://doi.org/10.1038/s41559-019-1044-6*

Pearsons TN, Temple GM, Fritts AL, Johnson CL, Webster TD. 2008. Ecological interactions between non-target taxa of concern and hatchery-supplemented salmon. Olympia (WA): State of Washington, Washington Department of Fish and Wildlife. 2007 Annual Report, Project No. 1995-063-25. [accessed 2020 Nov 20]. 178 p. Available from: *http://pisces.bpa.gov/release/documents/documentviewer.aspx?doc=P106758*

Perry RW, Skalski JR, Brandes PL, Sandstrom PT, Klimley AP, Ammann A, MacFarlane B. 2010. Estimating survival and migration route probabilities of juvenile Chinook Salmon in the Sacramento–San Joaquin River Delta. N Am J Fish Manage. [accessed 2021 Jun 8];30(1):142–156. *https://doi.org/10.1577/M08-200.1*

Peterson, ML, Lee DJ, Montgomery J, Hellmair M, Fuller A, Demko D. 2020. Stability in reproductive timing and habitat usage of Chinook Salmon across six years of varying environmental conditions and abundance. Fish Manage Ecol. [accessed 2021 Jun 8];27(4):399–416. *https://doi.org/10.1111/fme.12421*.

Phillis CC, Moore JW, Buoro M, Hayes SA, Garza JC, Pearse DE. 2016. Shifting thresholds: rapid evolution of migratory life histories in Steelhead/Rainbow Trout, *Oncorhynchus mykiss*. J Hered. [accessed 2021 Jun 8];107(1):51–60. *https://doi.org/10.1093/jhered/esv085*

Prévost E, Chadwick EMP, Claytor RR. 1992. Influence of size, winter duration and density on sexual maturation of Atlantic Salmon (*Salmo salar*) juveniles in Little Codroy River (southwest Newfoundland). J Fish Biol. [accessed 2021 Jun 8];41(6):1013–1019. *https://doi.org/10.1111/j.1095-8649.1992.tb02728.x*

Quinn TP, Myers KW. 2004. Anadromy and the marine migrations of Pacific Salmon and Trout: Rounsefell revisited. Rev Fish Biol Fisher. [accessed 2021 Jun 8];14(4):421–442. *https://doi.org/10.1007/s11160-005-0802-5*

Railsback SF, Harvey BC, White JL. 2014. Facultative anadromy in salmonids: linking habitat, individual life-history decisions, and population-level consequences. Can J Fish Aquat Sci. [accessed 2021 Jun 8];71(8):1270–1278. *https://doi.org/10.1139/cjfas-2014-0091*

Railsback SF, Rose KA. 1999. Bioenergetics modeling of Stream Trout growth: temperature and food consumption effects. Trans Am Fish Soc. [accessed 2021 Jun 8];128(2):241–256. *https://doi.org/10.1577/1548-8659(1999)128<0241:BMOSTG>2.0.CO;2*

Ralph FM, Dettinger MD. 2012. Historical and national perspectives on extreme West Coast precipitation associated with atmospheric rivers during December 2010. B Am Meteorol Soc. [accessed 2021 Jun 8];93(6):783–790. *https://doi.org/10.1175/BAMS-D-11-00188.1*

Rundio DE, Williams TH, Pearse DE, Lindley ST. 2012. Male-biased sex ratio of nonanadromous *Oncorhynchus mykiss* in a partially migratory population in California. Ecol Freshw Fish. [accessed 2021 Jun 8];21(2):293–299. *https://doi.org/10.1111/j.1600-0633.2011.00547.x*

Ruzycki JR, Clarke LR, Flesher MW, Carmichael RW, Eddy DL. 2009. Performance of progeny from steelhead and rainbow trout crosses. Salem (OR): State of Oregon, Oregon Department of Fish and Wildlife, Oregon Fish Research and Development, Northeast Region. [accessed 2020 Nov 20]. 42 p. Available from: *https://digital.osl.state.or.us/islandora/object/osl%3A18473*

Sabal MC, 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. N Am J Fish Manage. [accessed 2021 Jun 8];36(2):309–320. *https://doi.org/10.1080/02755947.2015.1121938*

Sahashi G, Morita K. 2013. Migration costs drive convergence of threshold traits for migratory tactics. P Roy Soc B-Biol Sci. [accessed 2021 Jun 8];280(1773):20132539. *https://doi.org/10.1098/rspb.2013.2539*

Sandstrom PT, Ammann AJ, Michel C, Singer G, Chapman ED, MacFarlane RB, Lindley ST, Klimley AP. 2020. Low river survival of juvenile Steelhead in the Sacramento River watershed. Environ Biol Fish. [accessed 2021 Jun 8];103(5):531–541. *https://doi.org/10.1007/s10641-020-00954-z*

Satterthwaite WH, Beakes MP, Collins EM, Swank DR, Merz JE, Titus RG, Sogard SM, Mangel M. 2009. Steelhead life history on California's Central Coast: insights from a state-dependent model. Trans Am Fish Soc. [accessed 2021 Jun 8];138(3):532–548. *https://doi.org/10.1577/T08-164.1*

Satterthwaite WH, Beakes MP, Collins EM, Swank DR, Merz JE, Titus RG, Sogard SM, Mangel M. 2010. State-dependent life-history models in a changing (and regulated) environment: Steelhead in the California Central Valley. Evol Appl. [accessed 2021 Jun 8];3(3):221–243. *https://doi.org/10.1111/j.1752-4571.2009.00103.x*

Satterthwaite WH, Hayes SA, Merz JE, Sogard SM, Frechette DM, Mangel M. 2012. State-dependent migration timing and use of multiple habitat types in anadromous salmonids. Trans Am Fish Soc. [accessed 2021 Jun 8];141(3):781–794. *https://doi.org/10.1080/00028487.2012.675912*

Schwartz MK, Luikart G, Waples RS. 2007. Genetic monitoring as a promising tool for conservation and management. Trends Ecol Evol. [accessed 2021 Jun 8];22(1):25–33. *https://doi.org/10.1016/j.tree.2006.08.009*

Singer GP, Hearn AR, Chapman ED, Peterson ML, LaCivita PE, Brostoff WN, Bremner A, Klimley AP. 2013. Interannual variation of reach specific migratory success for Sacramento River hatchery yearling late-fall run Chinook Salmon (*Oncorhynchus tshawytscha*) and Steelhead Trout (*Oncorhynchus mykiss*). Environ Biol Fish. [accessed 2021 Jun 8];96(2):363–379. *https://doi.org/10.1007/s10641-012-0037-y*

Sloat MR, Fraser DJ, Dunham JB, Falke JA, Jordan CE, McMillan JR, Ohms HA. 2014. Ecological and evolutionary patterns of freshwater maturation in Pacific and Atlantic salmonines. Rev Fish Biol Fisher. [accessed 2021 Jun 8];24(3):689–707. *https://doi.org/10.1007/s11160-014-9344-z*

Sloat MR, Reeves GH. 2014. Individual condition, standard metabolic rate, and rearing temperature influence Steelhead and Rainbow Trout (*Oncorhynchus mykiss*) life histories. Can J Fish Aquat Sci. [accessed 2021 Jun 8];71(4):491–501. *https://doi.org/10.1139/cjfas-2013-0366*

Sogard SM, Merz JE, Satterthwaite WH, Beakes MP, Swank DR, Collins EM, Titus RG, Mangel M. 2012. Contrasts in habitat characteristics and life-history patterns of *Oncorhynchus mykiss* in California's Central Coast and Central Valley. Trans Am Fish Soc. [accessed 2021 Jun 8];141(3):747–760. *https://doi.org/10.1080/00028487.2012.675902*

Spence BC, Dick EJ. 2014. Geographic variation in environmental factors regulating outmigration timing of Coho Salmon (*Oncorhynchus kisutch*) smolts. Can J Fish Aquat Sci. [accessed 2021 Jun 8];71(1):56–69. *https://doi.org/10.1139/cjfas-2012-0479*

Swank DR, Cranford A. 2016. Central Valley Recovery Domain 5-year review: summary and evaluation California Central Valley Steelhead Distinct Population Segment. Sacramento (CA): US Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service. [accessed 2021 Jun 23]. 44 p. available from: *https://www.fisheries.noaa.gov/resource/document/5-year-review-summary-and-evaluation-california-central-valley-steelhead-distinct*

Tattam IA, Ruzycki JR, Bayley PB, Li HW, Giannico GR. 2013. The influence of release strategy and migration history on capture rate of *Oncorhynchus mykiss* in a rotary screw trap. N Am J Fish Manage. [accessed 2021 Jun 8];33(2):237–244. *https://doi.org/10.1080/02755947.2012.758202*

Thorpe JE. 1998. Salmonid life-history evolution as a constraint on marine stock enhancement. B Mar Sci. 62(2):465–475.

Thorpe JE. 2007. Maturation responses of salmonids to changing developmental opportunities. Mar Ecol Prog Ser. [accessed 2021 Jun 8];335:285–288. *https://doi.org/10.3354/meps335285*

Trammell JLJ, Fast DE, Hatch DR, Bosch WJ, Branstetter R, Pierce AL, Blodgett JW, Frederiksen CR. 2016. Evaluating Steelhead kelt treatments to increase iteroparous spawners in the Yakima River Basin. N Am J Fish Manage. [accessed 2021 Jun 8];36(4):876–887. *https://doi.org/10.1080/02755947.2016.1165767*

[USBR] US Bureau of Reclamation. 2019. Reinitiation of consultation on the coordinated long-term operation of the Central Valley Project and State Water Project. Sacramento (CA): US Department of the Interior, Reclamation. Final Environmental Impact Statement. [accessed 2020 Nov 20]. 871 p. Available from: *https://www.usbr.gov/mp/nepa/includes/documentShow.php?Doc_ID=41664*

Verhille CE, English KK, Cocherell DE, Farrell AP, Fangue NA. 2016. High thermal tolerance of a Rainbow Trout population near its southern range limit suggests local thermal adjustment. Conserv Physiol. [accessed 2021 Jun 8];4(1):cow057. *https://doi.org/10.1093/conphys/cow057*

Welch DW, Porter AD, Rechisky EL. 2021. A synthesis of the coast-wide decline in survival of West Coast Chinook Salmon (*Oncorhynchus tshawytscha*, Salmonidae). Fish Fisheries. [accessed 2021 Jun 8];22(1):194–211. *https://doi.org/10.1111/faf.12514*

Williams TH, Spence BC, Boughton DA, Johnson RC, Crozier LG, Mantua NJ, O'Farrell MR, Lindley ST. 2016. Viability assessment for Pacific Salmon and Steelhead listed under the Endangered Species Act: Southwest. Santa Cruz (CA): US Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service. NOAA Technical Memo NMFS-SWFSC-564. [accessed 2020 Nov 20]. 170 p. Available from: *https://repository.library.noaa.gov/view/noaa/12013*

Zimmerman CE, Reeves GH. 2002. Identification of Steelhead and resident Rainbow Trout progeny in the Deschutes River, Oregon, revealed with otolith microchemistry. Trans Am Fish Soc. [accessed 2021 Jun 8];131(5):986–993. *https://doi.org/10.1577/1548-8659(2002)131<0986:IOSARR>2.0.CO;2*

Zimmerman CE, Ratliff DE. 2003. Controls on the distribution and life history of fish populations in the Deschutes River: geology, hydrology, and dams. In: O'Connor JE, Grant GE, editors. A peculiar river: geology, geomorphology, and hydrology of the Deschutes River, Oregon. Washington (DC): American Geophysical Union. p. 51–70.

Zimmerman CE, Edwards G, Perry K. 2008. Maternal origin and migratory history of *Oncorhynchus mykiss* captured in rivers of the Central Valley, California. Sacramento (CA): State of California, California Department of Fish and Game. Final Report, Contract P0385300. [accessed 2020 Nov 20]. 54 p. Available from: *http://www.tuolumnerivertac.com/Documents/Zimmerman%20Rpt%20Mar2008.pdf*

Zimmerman CE, Edwards GW, Perry K. 2009. Maternal origin and migratory history of Steelhead and Rainbow Trout captured in rivers of the Central Valley, California. Trans Am Fish Soc. [accessed 2021 Jun 8];138(2):280–291. *https://doi.org/10.1577/T08-044.1*