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Seventy years of diminishing biocomplexity of California Central Valley hatchery steelhead, *Oncorhynchus mykiss*

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Abstract

The California Central Valley steelhead (*Oncorhynchus mykiss*) has declined precipitously since Euro-American colonization and has been listed as threatened under the United States Endangered Species Act since 1998. Hatchery-origin fish now dominate the population, and hatchery management is a key listing factor. However, scant release metric information is available. We compiled a time series of *O. mykiss* hatchery release data for all four Central Valley hatcheries releasing *O. mykiss* between 1948 and 2017. The biocomplexity of released fish has declined since the early 1980s. Individuals have been released at increasingly similar numbers, biomass, body sizes, times, and locations over time. Moreover, yearling fish have been released at larger sizes, leading to the near-exclusive release of age-1 smolts in February and March since the late 1990s and early 2000s. Pervasive reductions in release portfolios have likely occurred for other hatchery-supported Pacific salmonid stocks throughout the Pacific Rim region. In an increasingly variable environment, such reductions in intraspecific diversity could significantly affect population stability and resilience.

Key words: biocomplexity, life history, *Oncorhynchus mykiss*, phenotypic diversity, portfolio effect, stocking

Introduction

The steep decline of Pacific salmonids (*Oncorhynchus* spp.) since the mid-19th century presents a conservation crisis of considerable economic, ecological, cultural, and political importance (Ruckelshaus et al. 2002; Moyle et al. 2017). To supplement declining populations, fishery enhancement hatcheries around the Pacific Rim release billions of artificially propagated *Oncorhynchus* spp. annually (Mahnken et al. 1998; Naish et al. 2007). The enhancement programs support and sustain commercial and recreational fisheries (Brannon et al. 2004; Lynch et al. 2016), but they also have unintentional consequences and contribute to the decline of wild populations (recently summarized by McMillan et al. 2023). Potential impacts include the effects of domestication selection (Araki et al. 2009; Christie et al. 2012*a*), genetic introgression (Waples 1991; Reisenbichler and Rubin 1999), offsite releases and straying (Flagg et al. 2000; Sturrock et al. 2019), inbreeding (Wang et al. 2002), reductions in effective population sizes (Christie et al. 2012*b*), exceedance of habitat carrying capacities (Beamish et al. 1997; Levin et al. 2001), predation (Naman 2008), overexploitation (Flagg et al. 2000), and disease transmission (Fryer and Lannan 1993), among others (McMillan et al. 2023).

Among Pacific salmonids, *O. mykiss* may exhibit the highest degree of life history diversity (Shapovalov and Taft 1954; Thorpe 1998; Moore et al. 2014). Both anadromous (steelhead) and freshwater resident (rainbow trout) forms of *O. mykiss* can produce the other life history form, and the degree to which progeny express different migratory phenotypes varies within and between watersheds (Zimmerman and Reeves 2000; Zimmerman et al. 2009; Courter et al. 2013). Unlike most species of Pacific salmonids, *O. mykiss* is iteroparous, and some individuals may spawn multiple times (Moyle 2002). The diversity of spawning and rearing habitats used by *O. mykiss* combined with the high degree of phenotypic plasticity contribute to the expression of diverse life histories (i.e., biocomplexity, *sensu* Hilborn et al. 2003), which is expected to buffer *O. mykiss* population complexes against environmental variation through a "portfolio effect" (McEwan 2001; Schindler et al. 2010; Lusardi et al. 2023). Like financial portfolios, where investment in a wide assortment of assets stabilizes returns and reduces the risk of catastrophic losses, intraspecific diversity enhances population resilience and helps stabilize ecosystems and fisheries (Schindler et al. 2015).

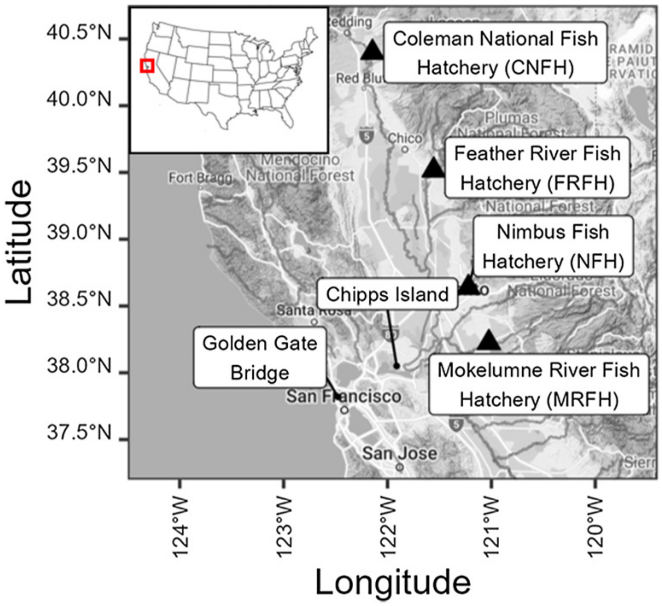


Fig. 1. Map of our study area with hatcheries (▲) indicated. Chipps Island represents the transition point between the upstream Sacramento-San Joaquin Delta and the downstream San Francisco Estuary. All anadromous *O. mykiss* must exit the San Francisco Estuary through the Golden Gate. Base map ©2023 Google using a WGS84 projection. Inset map sourced from Vecteezy.com.

In the California Central Valley, steelhead run sizes have declined from coarse estimates of one to two million adults before Euro-American colonization to approximately 40,000 adults in Central Valley drainages by the 1960s and no more than 10,000 adults for the entire system, including hatcheries, by the 1990s (reviewed by McEwan 2001). The stock complex was proposed to be listed as endangered under the United States Endangered Species Act (ESA) in 1996 and ultimately was listed as threatened in 1998 (63 FR 13347).

Today, the Central Valley *O. mykiss* population complex is supported mainly by four hatcheries (Fig. 1). Long-term monitoring suggests that hatchery-origin *O. mykiss* comprise an increasing proportion of the overall Central Valley *O. mykiss* population and currently constitute the majority of the distinct population segment (DPS) (Lindley et al. 2007; Johnson et al. 2022). Best-available estimates suggest that hatchery-origin *O. mykiss* in this system represented from 3% to 18% of adult returns during the 1950s (Hallock et al. 1961) but 63% to 92% of adult returns at the turn of the 21st century (NMFS 2003). More robust information has been available since brood year 1998, when the practice of 100% marking of all hatchery-origin *O. mykiss* with an adipose fin clip commenced. Long-term monitoring from 1998 to 2021 reveals that hatchery-origin *O. mykiss* comprised the vast majority of catches (∼84%) at the San Francisco Estuary entry, primarily due to their preponderance (∼94%) in the Sacramento River (based on catches at the Delta entry from that system) (Interagency Ecological Program et al. (IEP) 2022). According to genetic analyses (Garza and Pearse 2008; Pearse and Garza 2015), broodstock history records, and out-of-basin egg and fish transfers, only steelhead produced at the CNFH, MRFH, and FRFH (see Materials and Methods for hatchery abbreviation definitions) are assigned to the California Central Valley steelhead DPS (63 FR 13347, 85 FR 81822). The NFH stock is not included in the DPS due to the influence of the genetically divergent Northern California steelhead on the genetic composition of the modern NFH broodstock.

Here, we characterize patterns in Central Valley *O. mykiss* hatchery practices over 70 years (1948 to 2017) and assess changes in population and life history metrics associated with biocomplexity. We characterized temporal variation in juvenile release metrics, including the number and biomass of fish released, the timing and location of release, as well as the size, age, growth, and life history stage of released fish. The analyses presented herein provide valuable insight into shifting patterns within this population complex over the 70 year period. We discuss the potential unintended consequences of shifting hatchery release strategies and review factors that could influence Central Valley *O. mykiss* biocomplexity and resiliency in a changing environment. We conclude with a discussion of the implications for hatchery-supported systems more generally.

Materials and methods

Study system

California's Central Valley experiences a Mediterranean-montane climate with cool, wet winters and hot, dry summers in the Sacramento-San Joaquin Valley and cold winters and warm to cool summers in the Sierra Nevada and Cascade Mountains. In the study region, steelhead typically spend one to three years in freshwater and one to three years in the ocean but may return earlier; sexually immature "half-pounder" fish spend two to four months at sea before returning to freshwater to overwinter; and small and sexually mature "jack" males rear for a few months in fresh, brackish, or marine environments (Hallock et al. 1961; Moyle 2002; Williams 2006).

Dams were built during the 20th century on major tributaries of the Sacramento and San Joaquin rivers to promote water management. These dams and associated infrastructure currently supply drinking water for approximately 30 million California residents and irrigation water for over 6 million acres of farmland (Gartrell et al. 2022). Central Valley *O. mykiss* hatcheries (Fig. 1) were constructed to legally comply with mitigation requirements for habitat loss associated with the construction of the impassable dams (reviewed by JHRC 2001), including the Coleman National Fish Hatchery on Battle Creek (CNFH), the Nimbus Fish Hatchery on the American River (NFH), the Feather River Fish Hatchery (FRFH), and the Mokelumne River Fish Hatchery (MRFH). The CNFH, NFH, and FRFH are located on Sacramento River tributaries, whereas the MRFH, to the south, is located on a major San Joaquin River tributary (Fig. 1). Hatchery program management is primarily determined by the federal (CNFH) or state (NFH, FRFH, and MRFH) operators (USFWS 2008). Annual production goals for each hatchery (CA HSRG 2012, Appendix VIII), including total number of fish planted, size-at-release, release month(s), and primary stocking location, are presented in Table A1.

Hatchery release database

We compiled release data from 135 annual reports provided by the California Department of Fish and Wildlife (CDFW) for state-operated hatcheries. The state hatchery annual reports spanned one fiscal year from 1 July to 30 June of the following year: NFH (54 reports, 1956–57 to 2009–10), FRFH (40 reports, 1969–70 to 2009–10), and MRFH (41 reports, 1964–65 to 2007–08). From 1988–2001, release records were obtained for MRFH from the California Hatchery Scientific Review Group (CA HSRG 2012, Appendix VI) instead of annual reports because the former dataset is more detailed and complete. From 2001 to 2017 for the FRFH and 2003 to 2017 for the NFH and MRFH, an electronic dataset from CDFW's statewide inventory system was used instead of annual reports or California Hatchery Scientific Review Group data (CA HSRG 2012, Appendix VIII). Hatchery release data were considered "draft" or non-finalized from 1994–2017 for the NFH, 1992–2017 for the FRFH, and 1988–2017 for the MRFH. Release data for the CNFH from 1948 to winter 1975 were obtained from an electronic database provided by the US Fish and Wildlife Service (USFWS), and data from spring 1975 to 2017 were obtained from the Regional Mark Information System (RMIS, http://www.rmpc.org/; retrieved on 21 May 2020).

The basic reporting unit for all data sources was a cohort of similarly sized fish released together in a stated release location over a specified time (hereafter referred to as a "release group"). Information about brood year (same as emergence year for winter-run *O. mykiss*), total number of fish planted, average or range of fish size(s)-at-release (usually expressed as fish·lb^{-1}), release timing (from single days to months), and descriptions and (or) geographic coordinates of release locations were reported for release groups.

The final release database is available from the Dryad Data Repository (Huber et al. 2023). Note that we focus our interpretation on the combined data set to emphasize the larger spatiotemporal patterns, but we report the results for individual hatcheries separately in Supplement 1.

Objective 1: temporal trends in juvenile releases

Number released

We present annual release data according to the California water year (i.e., 1 October to 30 September, hereafter "release year") since the water year period is more relevant to the Central Valley *O. mykiss* life cycle than the calendar year (e.g., upstream migration in fall and winter, spawning and emergence in winter, rearing in spring and summer [Williams 2006]). When the release period spanned two water years (5.1% of the total number released, 90.5% of which occurred before the water year 1976), the water year possessing the largest share of the release period was assigned as the release year. In rare instances when the release period spanned two water years and was split equally between the first and second water years (0.2% of all releases), the second year was set as the release year. A 3-year centered moving average was applied to the annual numerical release data to highlight longer term trends.

Biomass released

Release group biomass was calculated as the product of the total number of fish released and the mean fish mass for that release group. The mean annual fish mass-at-release for a hatchery was used as the mean mass-at-release for any release group's missing weight, length, or life history stage-at-release information (3.8% of all releases). A 3-year centered moving average was also applied to the annual biomass release data to smooth the time series data.

Release timing

We analyzed release timing on a monthly scale because the release day-of-month was missing for 63.5% of all releases. The release period usually occurred within the same calendar month (80.3% of all releases), but occasionally a range of calendar months were reported (16.7% of all releases). In limited cases, only one release year was reported (3.0% of all releases). Due to these inconsistencies, we restrict all release timing and growth rate analyses to cases where the release start and end months are the same.

Release location

Geographic coordinates of release locations and river km distances from the releasing hatchery to the release location were obtained from Sturrock et al. (2019) (92.0% of all releases), RMIS (1.4% of all releases), or the electronic database provided by CDFW (0.7% of all releases). An additional 5.7% of release location coordinates and hatchery distances were newly determined using the methods described by Sturrock et al. (2019). Coordinates and distances are unavailable for 0.2% of all released fish due to insufficient descriptions of release site locations.

Size-at-release

Fish sizes were reported as mean mass (75.2% of all releases) or length (19.5% of total) for each release group. Length-at-release was converted to mass-at-release (and vice versa) according to a relationship for Sacramento River *O. mykiss* (Hallock et al. 1961) to facilitate dataset comparisons:

$$\ln(M) = \ln\left(8.80 \cdot 10^{-6}\right) + 3.06 \cdot \ln(\mathrm{FL}) \tag{1}$$

where mass (M) is measured in grams and fork length (FL) in millimeters. Note that eq. 1 is modified from the original version to permit the use of metric units instead of English units. Also, note that this relationship was determined for fish with FLs ≥ 325 mm but predicts masses for smaller fish within 5% deviation from a similar length-weight transformation reported for California Central Coast *O. mykiss* (Huber 2018; 53–442 mm FL range; $R^2 = 0.99$) across nearly the entire *O. mykiss* size range encountered in this investigation (97.0% of all hatchery fish with reported lengths smaller than 325 mm FL were larger than 53 mm FL).

When size ranges were reported, the midpoint was assigned as the mean length or mass for the release group. Occasionally, missing size data could be gleaned from written descriptions of the release group's life history stage (e.g., "fry", "fingerlings", and "yearlings"). In these cases (1.5% of all releases), the midpoint of the life stage-at-release mass range (see "Life-stage-at-release" below) was used.

Age-at-release

All age information was estimated based on an assumed 1 February spawn date (Satterthwaite et al. 2010) and, therefore, should be considered apparent ages. Age analyses were restricted to cases when the release group's beginning and end months of release were identical (80.3% of all releases). Apparent ages were estimated as the difference between the release month midpoint and 1 February of the brood year.

Life stage-at-release

We explored coarse- and fine-scale trends in life-stages-at-release composition. We first classified *O. mykiss* as subyearling (y−) or yearling or older fish (y+). We followed hatchery program guidelines (CA HSRG 2012, Appendix VIII) and assumed *O. mykiss* became yearlings once they grew to 71.2 g (~180 mm FL). We further classified life history stage-at-release diversity according to fish sizes and standardized nomenclature guidelines (Interagency Ecological Program Steelhead Project Work Team (IEP Steelhead PWT) 1998): "yolk-sac fry" were defined as fish with masses <0.3 g; "fry": ≥0.3 to <1.4 g; "parr": ≥1.4 g to <26.3 g; "silvery parr": ≥26.3 g to <71.2 g; "small smolts": ≥71.2 g to <131.6 g; "large smolts": ≥131.6 g to <219.6 g; "subadults": ≥219.6 g to <954.0 g; and "adults": ≥954.0 g. For cases where size data were missing but life-stage-at-release was described, "fed fry" were assumed to be fry, "fingerlings" were assumed to be parr, "advanced fingerlings" were assumed to be silvery parr, and "smolts" were assumed to be small smolts.

Objective 2: temporal variation in juvenile release metrics

Life stage diversity

We characterized life stage diversity by calculating the reciprocal Simpson's index (RSI; Simpson 1949) for each hatchery and all hatcheries combined per release year. The RSI measures the evenness of a community and ranges from 0 (all life stages were equally represented in every release group) to 1 (all fish were planted at the same life stage). The formula used to calculate RSI was:

$$(2)\qquad \mathrm{RSI} = \left(\sum\nolimits_{n}^{i=1}\left(\frac{n_i}{n}\right)^2\right)$$

where n_i is the number of individuals in life stage i and n is the pooled number of individuals across all life stages.

Interannual variation in release metrics

To investigate interannual variation in release practices, we divided the 70-year time series (1948 to 2017) into seven 10-year intervals and calculated the decadal coefficient of variation (CV_{10}) for six metrics associated with hatchery releases summarized annually at each hatchery program and for all *O. mykiss* hatchery programs combined. The metrics examined included (1) total number released, (2) total biomass released, (3) mean release month, (4) mean release distance downstream of the hatchery, (5) mean mass-at-release, and (6) mean age-at-release:

$$(3)\qquad \mathrm{CV}_{10} = \frac{\mathrm{SD}_{10}}{\bar{x}}$$

where $\bar{x}$ is the 10-year or decadal mean of the release metric annual totals or means for each hatchery or all hatcheries combined, and SD_{10} is the decadal standard deviation for each hatchery or all hatcheries combined:

$$(4)\qquad \mathrm{SD}_{10} = \left(p\sum\nolimits_{10}^{i=1}(x_i-\bar{x})^2\right)^{1/2}$$

where p equals 1/10, x_i equals the annual release metric mean for release year i, and $\bar{x}$ is the decadal mean of the annual release metric means for each hatchery or all hatcheries combined.

Statistical analyses

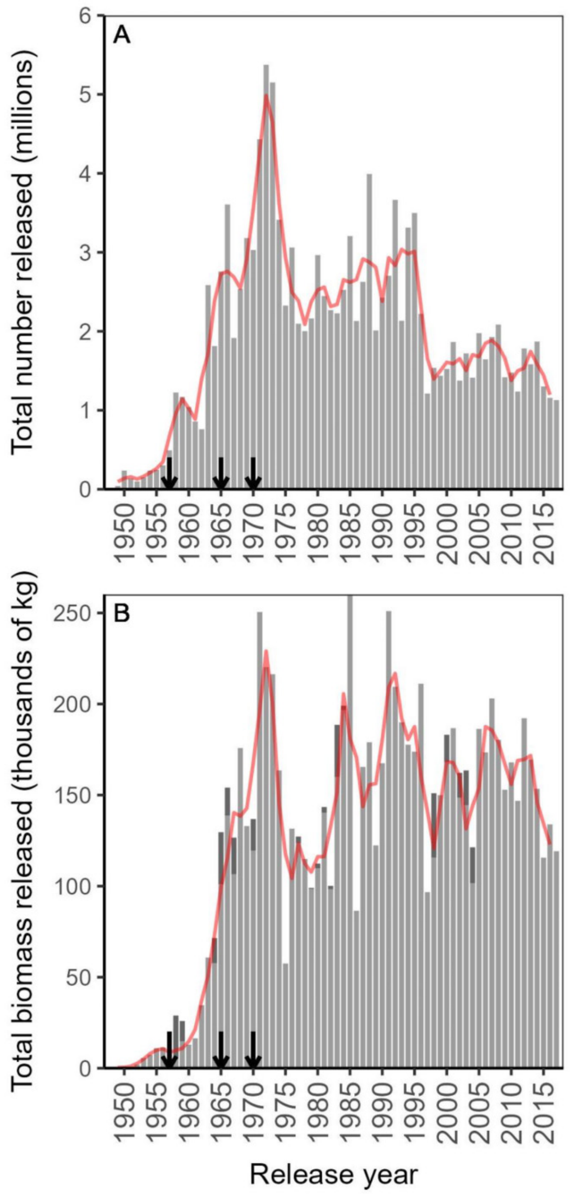
Prior to data analysis, we removed all release groups from the final database known to be for research purposes (usually numbering in the 10s or 100s of fish), out-of-basin releases, and (or) releases in landlocked waters because these fish were not part of the California Central Valley *O. mykiss* population (0.3% of all releases). All annual and overall mean values presented for release metrics were weighted according to the total number of fish released across all release groups for each hatchery or all *O. mykiss* hatchery programs combined. Temporal trends of release metrics were quantified using a combination of post hoc (1) calculations of means of annual means and CVs (standard deviation divided by mean), (2) regression analyses, including linear (ordinary least squares), quadratic, and logistic curve fitting, and (3) residual analyses of linear regressions. To explore evidence of a trend through time, we report parameters of ordinary least squares linear regression analysis and report 95% bootstrapped confidence intervals ($N = 1999$ replicates) for slopes significantly different from zero. Statistical analyses were performed using the statistical software R (R Core Development Team 2020) and PAST (version 4.03; Hammer et al. 2001).

Results

Objective 1: temporal trends in juvenile releases

As a reminder, we report the temporal trends in juvenile releases based on all hatcheries combined, but we also present

Fig. 2. Plots of (A) total number of *O. mykiss* individuals released annually and (B) total fish biomass released annually (a light gray stacked bar indicates recorded values and a dark gray stacked bar indicates estimated values). The red lines indicate 3-year-centered running averages. Black arrows indicate when new hatcheries began operation (NFH in 1957; MRFH in 1965; FRFH in 1970).

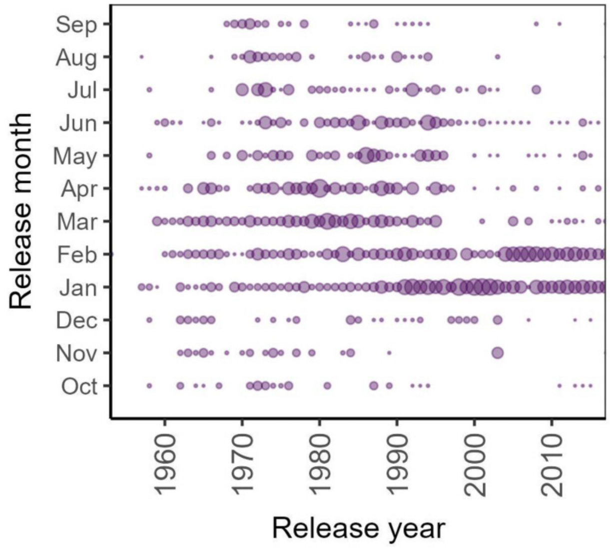


the interpretation of the releases from individual hatcheries in Supplement 1.

Number released

The four main *O. mykiss* Central Valley hatcheries (Fig. 1) released 137.5 million artificially propagated *O. mykiss* in Central Valley waters from 1948 to 2017 (Table A1 and Fig. 2). The number of fish increased rapidly from 1948 to the early 1970s as the experimental program at CNFH became permanent and the NFH, MRFH, and FRFH programs were established in 1957, 1965, and 1970, respectively (Table A1 and Fig. 2). According to an inspection of the plot, release numbers stabilized from 1974 to 1996 ($\bar{x} = 2.7 \times 10^6$ fish·year^{-1}, CV = 22%) before a steep decline to a mean of 1.6×10^6 fish·year^{-1} (CV = 18%) from 1997 to 2017 (Fig. 2).

Fig. 3. The month of release plotted through time. The area of each bubble is proportional to the total number of fish released in a given month and year.



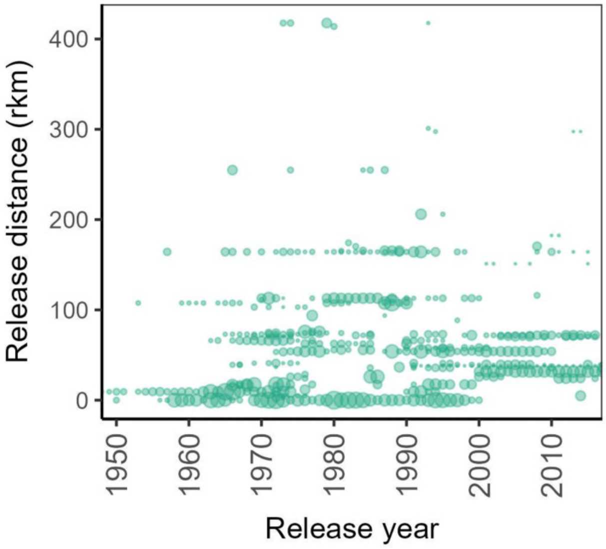
Biomass released

Approximately 8.8 million kg of *O. mykiss* were released from the four hatcheries propagating *O. mykiss* from 1948 to 2017 (Table A1 and Fig. 2A). Note that this value is underestimated because of unreported size-at-release information for 4.8% of all hatchery-year combinations. Total biomass released (Fig. 2B) resembles trends in the abundance data (Fig. 2A) during the early part of the time series (i.e., a rapid rise from 1948 to 1971); however, unlike the abundance data, total biomass released annually did not exhibit a steep decline during the mid-to-late 1990s but held steady and averaged ~1.6×10^5 kg·year^{-1} from 1974 to 2017 (CV = 26%; Fig. 2).

Release timing

Across all hatcheries and all years, the overall mean release date was 12 March. From an inspection of the plot (Fig. 3), there was a noticeable shift in 2003, so we have presented the results before and after that date. The mean annual release date for the period from 2003 to 2017 ($\bar{x}$ = 17 February) was over 1.5 months earlier than the mean date from 1953 to 1995 ($\bar{x}$ = 24 March) (Fig. 3). There was a linear decline in mean annual release date (quantified as months since 1 October) versus release water year for the combined hatchery stock complex in the full time series from 1970 (the first year all four *O. mykiss* release programs operated simultaneously) until 2017 (Fig. 3; $R^2 = 0.68$, slope = -0.07 months·year^{-1}, 95% CI [-0.08, -0.06]).

Fig. 4. Release distances downstream of the releasing hatcheries, in river kilometers (rkm), plotted through time. The area of a bubble is proportional to the total number of fish released at a given release site in a given year.



Release location

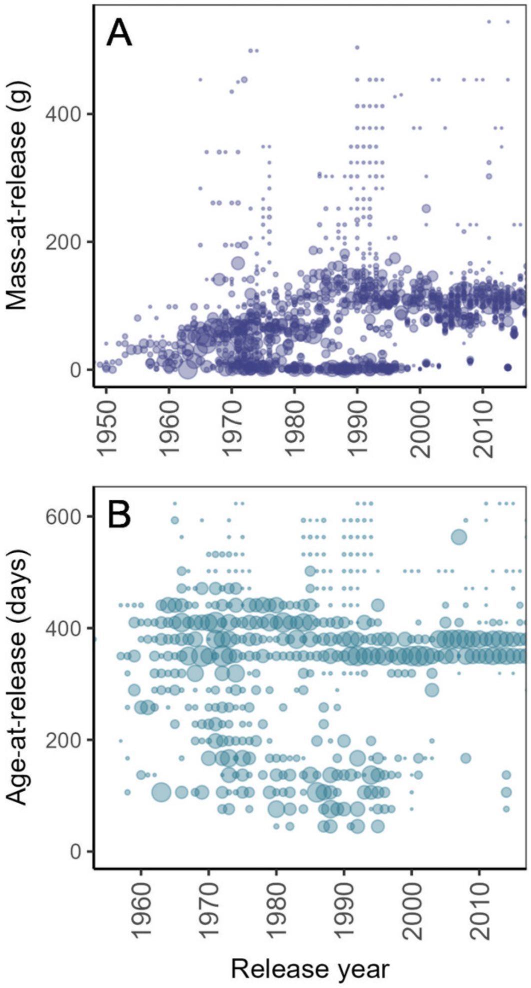
The overall mean of the mean annual release location distances downstream from all hatcheries combined was 40.2 river kilometers (rkm) (CV = 63%; Fig. 4). Based on the plots, average stocking distances from the releasing hatchery (Fig. 1) were above the long-term average (i.e., farther from the hatchery) between 1976 and 2017 ($\bar{x}$ = 50.5 rkm, CV = 42%) but below the long-term average earlier in the time series (1948–1975, $\bar{x}$ = 23.6 rkm, CV = 96%), respectively (Fig. 4). The overall mean of the mean annual release location distances upstream of the Pacific Ocean at the Golden Gate was 337.4 rkm (CV = 24%). Below and above average stocking distances from the Pacific Ocean occurred from 1976 to 2017 ($\bar{x}$ = 308.6 rkm, CV = 16%) and 1948 to 1975 ($\bar{x}$ = 382.4 rkm, CV = 25%), respectively.

The number of unique release sites during the period when all four release programs were operational (i.e., 1970–2017) ranged from six (1978 and 2017) to 21 sites (1974). From 1948 to 1974, as new hatcheries were constructed and early programmatic adjustments were made, the total number of release sites (R^2 = 0.86, slope = 0.73 sites·year^{-1}, 95% CI [0.61, 0.86]) and average number of fish released per site (R^2 = 0.44, slope = 8627 fish·site^{-1}, 95% CI [5233, 12052]) increased linearly. The opposite was observed from release year 1975–2017; the total number of release sites (R^2 = 0.21, slope = −0.09 sites·year^{-1}, 95% CI [−0.15, −0.04]) and average number of fish released per site (R^2 = 0.15, slope = −1774 fish·site^{-1}, 95% CI [−2909, −570]) declined linearly.

Size-at-release

The mean fish mass-at-release across all 70 years was 64.3 g or 174 mm fork length (eq. 1; Table A1 and Fig. 5A). A positive linear relationship for mean annual fish mass-at-release versus release year is observed throughout the 70-year time series (Fig. 5A; R^2 = 0.80, slope = 1.44 g·year^{-1}, 95% CI [1.28, 1.59]).

Fig. 5. The (A) mass-at-release (in grams) for *O. mykiss* release groups and (B) apparent age-at-release (in days since 1 February of the spawn year) plotted through time. The area of a bubble is proportional to the total number of fish released. Data for fish larger than 550 g (1.4% of all releases with size data) and 720 days of apparent age (1.4% of all releases with age data) are not shown for visual display purposes.



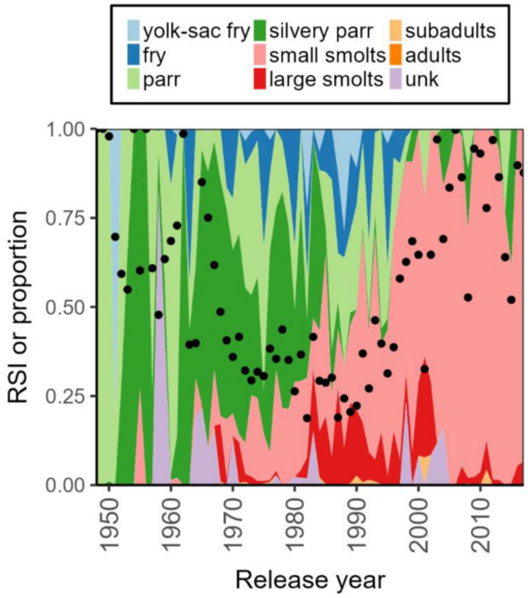
Age-at-release

A bimodal pattern is evident for age-at-release with peaks at ∼120–130 days old (1970s to 1990s) and ∼370–380 days old (all years) (Fig. 5B). Overall, the average annual age-at-release was 322 days (CV = 17%). Generally, fish were released at older and more consistent ages later in the time series (Fig. 5B). From an inspection of the plot, an apparent shift occurred in 1998 (Fig. 5B). In particular, the mean age-at-release from 1998 to 2017 was 359 days (CV = 8%) compared with 305 days for the pre-1998 value (Fig. 5B).

Life stage-at-release

Small smolts, silvery parr, and parr were the most common life stages released and comprised 78.8% of all releases (Table A1 and Fig. 6). As fish at a given time of year were released at

Fig. 6. The relative proportions of different life histories released per year (represented by different colors), with the life history stage-at-release diversity metric included as dots (as quantified by the reciprocal Simpson's index (RSI); see Methods and eq. 2).



larger sizes (Supplement 2, Fig. S2.1), the corresponding life stage composition shifted to smaller smolts and less parr and silvery parr were released (Fig. 6). For example, after 1997, small smolts comprised more than 80% of all *O. mykiss* released (Table A1 and Fig. 6).

Over time, increased growth performance in the hatchery environment produced an apparent "substitution of growth for time" effect (Supplement 2, Fig. S2.1 [left panel]). These factors facilitated a rapid increase in the release of "advanced yearlings" (i.e., *O. mykiss* released at smolt sizes [71.2 g] or larger; Fig. 7). Logistic regression indicates that advanced yearlings comprised 25%, 50%, and 75% of all releases in 1978, 1988, and 1998, respectively (Fig. 7).

Objective 2: temporal variation in juvenile release metrics

The mean annual RSI (eq. 2) was 0.57 (CV = 45%; Table A1 and Fig. 6). Generally, RSI was higher during the early and late parts of the time series and lower during the intermediate years (Fig. 6). Based on an inspection of the plot, apparent shifts occurred in 1968 and 1997; RSI values from 1948 to 1967 ($x = 0.73$, CV = 29%) and 1997 to 2017 ($x = 0.82$, CV = 24%) were 2.2 and 2.5 times greater, respectively, than the average value for the intermediate period (1968–1996; $x = 0.33$, CV = 24%; Fig. 6).

Fig. 7. Proportion of the total number of fish released at advanced yearling sizes (71.2 g) or larger (y+) per water year (dots) as well as the logistic regression curve fit (line) with 95% confidence intervals (gray-shaded area).

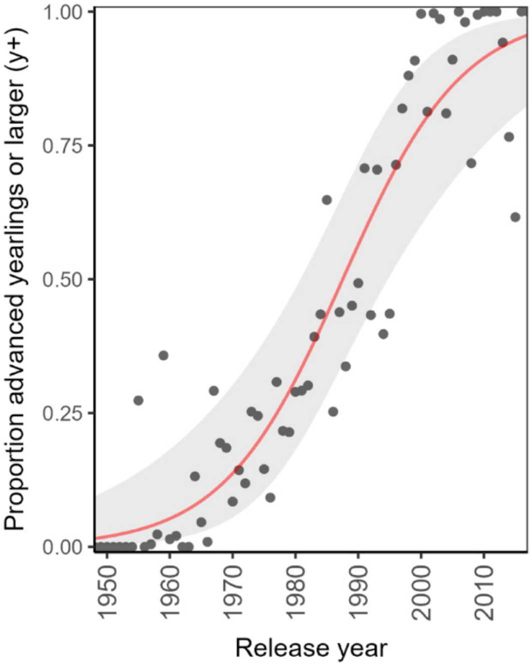
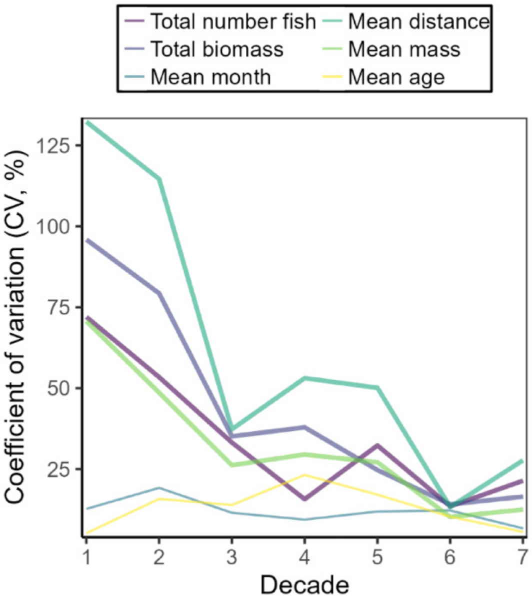


Fig. 8. Portfolio changes of key release metrics, expressed as coefficients of variation (CV) across all hatcheries, calculated for each decade of releases. Thicker lines indicate significant linear declines (see Results).



Interannual release metric variability

The decadal CVs (eqs. 3 and 4) for all six release metrics (total number released, total biomass released, mean release month, mean release distance downstream of the hatchery, mean mass-at-release, and mean age-at-release) decreased through time for the Central Valley *O. mykiss* population complex, as indicated by negative correlations with decade for each release metric (Fig. 8). The linear temporal declines were significant for total number released ($R^2 = 0.71$, slope = $-8.3\%\cdot\text{decade}^{-1}$, 95% CI [−15.2, −2.7]), total biomass released ($R^2 = 0.84$, slope = $-13.5\%\cdot\text{decade}^{-1}$, 95% CI [−21.4, −7.7]), mean release distance downstream of hatchery ($R^2 = 0.75$, slope $= -18.0\%\cdot\text{decade}^{-1}$, 95% CI [$-31.2$, -10.2]), and mean mass-at-release ($R^2 = 0.83$, slope $= -8.9\%\cdot\text{decade}^{-1}$, 95% CI [$-13.6$, -5.3]) (Fig. 8).

Discussion

Our analysis of 70 years of *O. mykiss* juvenile release data (1948 to 2017) for four Central Valley California hatcheries demonstrates how key release metrics have been homogenized through time. Over 135 million *O. mykiss* were released from four Central Valley hatcheries from 1948 to 2017. Our analysis of the patterns in hatchery releases revealed shifts to earlier and narrower release timing, simplification of age structure, and a dominance of a single life history (age-1 "small smolts"). Overall, these results suggest a simplification of the *O. mykiss* hatchery portfolio with possible consequences for risk-spreading and climate resilience (Hilborn et al. 2003; Schindler et al. 2010, 2015).

Due to the controlled nature of hatcheries and aquaculture, there is a tendency to search for "optimization" over "diversification" to maximize survival. However, given the uncertain environmental conditions in California, an attempt to optimize growing and release conditions can be risky given that what is "optimal" may shift through space and time. Provided that the high levels of hatchery *O. mykiss* supplementation continue within the Central Valley, it is critical to focus on efforts that promote and conserve biocomplexity as part of hatchery broodstock collection as well as juvenile rearing and release practices because we cannot predict which strategies will be successful now or under future conditions.

A fundamental principle of ecophysiology is that phenotype influences performance, which then determines survival and, ultimately, fitness (Lailvaux and Husak 2014). Consequently, increased phenotypic diversity within species and populations spreads risk across uncertain environmental conditions. For example, larger juvenile size or early outmigration timing may be advantageous for salmonids during some conditions, whereas smaller size or delayed timing may be advantageous during other conditions. Studies on Central Valley Chinook Salmon (*O. tshawytscha*) have found that slow-growing fish that delayed migration as yearlings were favored during drought conditions (Cordoleani et al. 2021), whereas small, early migrating Chinook Salmon exhibited higher contributions to adult spawning populations during wet conditions (Sturrock et al. 2020). Ultimately, phenotypic diversity within and among populations confers resilience to environmental variation (Schindler et al. 2010). When hatchery practices constrain phenotypic variation, as found with the system-wide release trait homogenization in Central Valley *O. mykiss* hatcheries, the risk of variable performance increases, including the potential for cohort failure (Satterthwaite and Carlson 2015; Willmes et al. 2018; Hagen et al. 2021). More generally, the loss of genetic and phenotypic variation within species due to anthropogenic activities has been described as a "hidden biodiversity crisis" (e.g., Des Roches et al. 2021). Ensuring that the annual release cohort possesses a diversity of traits is fundamental to increasing resilience to extreme hydrologic and thermal conditions associated with California's variable Mediterranean climate, as well as more extreme scenarios predicted under a shifting climate (Moyle et al. 2017; Herbold et al. 2018; Swain et al. 2018).

In many respects, the data presented here suggest that the Central Valley *O. mykiss* complex may be experiencing "threat evolution", as has been documented in intensively managed inland trout populations in California (Lusardi et al. 2015). Initially, dams throughout the Central Valley reduced wild populations of steelhead (initial threat; *sensu* Lusardi et al. 2015), and hatcheries were used to supplement and improve adult returns. However, intensive hatchery steelhead propagation has reduced phenotypic diversity across the Central Valley hatcheries, making the *O. mykiss* population complex less resilient to environmental change and more vulnerable to stochastic processes (secondary threat associated with management actions; *sensu* Lusardi et al. 2015). Below, we discuss factors that may influence Central Valley *O. mykiss* biocomplexity and resiliency under a variable climate.

Management considerations

We hypothesize that the following management actions could improve the biocomplexity and population stability of Central Valley *O. mykiss*. It is important that the management actions, if implemented, are conducted within a scientific framework and that each of these actions is accompanied by a monitoring and evaluation program to test the efficacy of the action in achieving the goal (CA HSRG 2012).

Increase phenotypic diversity at multiple life stages

Increased phenotypic diversity of released fish can be readily achieved by considering changes to broodstock collection schedules, release sites, and rearing conditions. Run timing in salmonids is heritable, and selecting broodstock based on the earliest returning individuals can shift population run timing (Tillotson et al. 2019); therefore, it is important to collect hatchery broodstock over the entire return distribution and hatch fry over periods that track natural temporal patterns, including interannual shifts. Salmonids have evolved to use a mosaic of habitats that vary in temperature, energetic demands, and food resources, resulting in a diversity of growth rates and outmigration timing (Brennan et al. 2015; Lusardi et al. 2020; Cordoleani et al. 2021; Rossi et al. 2022). A diversity of juvenile rearing habitats encourages phenotypic variability in wild salmonids, both in terms of size and migration timing.

Provided continuing hatchery releases, hatchery managers could re-incorporate releasing hatchery juveniles at multiple life stages, including on-site releases of fry and parr that are more likely to use non-natal rearing habitats (e.g., tributaries, side/secondary channels, floodplains, and estuaries) and encourage phenotypic diversity. While smaller (younger) fish often have lower survival and return rates, they can contribute significantly to adult returns when they encounter favorable conditions in non-natal rearing habitats (Phillis et al. 2018; Sturrock et al. 2020). Additionally, with fixed rearing space in hatchery environments, producing a larger proportion of smaller (younger) fish is possible. This practice can also reduce the use of antibiotics or chemical treatments to treat pathogens, buffer against potential losses caused by low fry-to-smolt survival, and reduce the time that fish are subjected to artificial selection.

Due to their conservation status, all hatchery-origin steelhead released in the Central Valley must be marked with an adipose fin clip. Individuals smaller than the minimum size for adipose fin clipping at maximum rates (∼50 mm FL; Skalski et al. 2009) could be identified by parentage-based tagging (Pepping et al. 2020). Unlike mass marking, parentage-based tagging can uniquely identify the offspring of hatchery broodstock. Hatcheries can treat the releases of parentage-based tagged fry and larger (older) fish as "experimental", creating an opportunity to attain valuable information (e.g., outmigration survival, return rates, straying rates, adult return age/size structure, etc.) critical to assess the outcomes of interventions in release practices.

Hatchery infrastructure such as cement raceways with uniform flow and thermal environments and predictable feeding schedules and food quantities can homogenize growth among fish. Conversely, implementing "natural growth regimes" (*sensu* Berejikian et al. 2012) that mimic natural variations in water temperatures, feeding rates, and rearing densities can promote proper smoltification and diversify age structure and size-at-age before release into the environment. The MRFH's "Natural Rearing Enhancement System" (NATUREs) pilot program utilizes naturalized rearing regimes, enriched environments, and predator training to increase post-release *O. mykiss* survival rates (Williams 2006; CA HSRG 2012, Appendix VIII) and serves as a model that could be adopted and expanded elsewhere.

Today, the Central Valley *O. mykiss* population complex is dominated by hatchery-origin fish (NMFS 2003; Lindley et al. 2007). Best available information indicates that natural-origin *O. mykiss* comprise only ∼6% to 16% of the *O. mykiss* in the northern Sacramento-San Joaquin Delta and San Francisco Estuary. While diversifying the portfolio of release practices is expected to benefit stock complex resiliency and stability, it is also important to consider the potential genetic and ecological impacts of releasing hatchery-origin presmolts on natural-origin *O. mykiss* and other life stages of hatchery-origin *O. mykiss*. Genetic risks include inbreeding depression, outbreeding depression, and domestication selection, and ecological risks include competition, predation, and disease (reviewed by Claussen and Philipp 2022). The degree to which these potential unintended consequences outweigh the possible benefits of a diversified release portfolio for Central Valley *O. mykiss* (and native salmonids in hatchery-supplemented systems, more generally) requires further study.

Spreading mortality risk through space and time

Survival to adulthood appears to be extremely low for Central Valley steelhead (CA HSRG 2012, Appendix VIII). Releasing more *O. mykiss* at or near hatcheries (i.e., on-site releases) may improve homing and survival by allowing more individuals to access diverse habitats and environmental conditions during outmigration (CA HSRG 2012). Such habitats likely offer variable growth opportunities and contribute to the expression of diverse life histories (e.g., Bourret et al. 2016). Furthermore, juveniles migrating over a variety of time periods likely spread mortality risk by reducing the chance that a large fraction of fish encounter, for example, stressful thermal conditions or predatory hot spots. Moreover, increased variability in release timing, either within or among hatcheries, could help ensure that some smolts enter nearshore habitats during or after the spring transition and the onset of coastal upwelling (Holtby et al. 1990; Lindley et al. 2009). Normally, productive marine food webs establish in the California Current by mid-March, with occasional delays occurring into late May or June (Barth et al. 2007; Lindley et al. 2009; Satterthwaite et al. 2014). Volitional releases at hatcheries or release of multiple age classes (e.g., age-1 and age-2 smolts; *sensu* Berejikian et al. 2012) would likely diversify maturation schedules and population age structure to better match historical conditions (Hallock et al. 1961; CA HSRG 2012, Appendix VIII) and narrow Central Valley population complex mortality by spreading risk through both space and time. Release programs that mimic size-at-age and outmigration timing variations within natural ranges of variability due to differences in spawning and emergence timing and growth rates are expected to buffer population dynamics and hedge against unpredictable environmental conditions.

Reduce the hatchery dominance of remaining wild fish

One issue that exacerbates hatchery dominance is that program goals often focus on achieving a total number of fish released rather than maximizing biocomplexity and resiliency. Focusing on improving post-release survival and interannual stability in returns may allow fewer fish to be produced and released while sustaining the popular recreational inland fishery and allowing hatchery managers to meet broodstock needs consistently. For instance, reducing smolt release group sizes and diversifying release timing, locations, and sizes could minimize size-based interference competition, density-dependent effects, and (or) predation effects on hatchery- and natural-origin *O. mykiss*. During dry years when minimal outflow occurs and transporting fish is deemed necessary, post-release survival may be improved by continuing and expanding practices such as allowing trucked fish to acclimate to environmental conditions before release, releasing fish closer to in-stream and riparian cover, and matching smolt releases with environmental factors that enhance survival like rain events and turbidity spikes, low light conditions, and (or) reservoir releases.

Increase habitat complexity and connectivity

Historical land use changes have profoundly altered California's Central Valley and reduced environmental variation and biocomplexity for Central Valley salmonids, including steelhead (Lindley et al. 2006; Carlson and Satterthwaite 2011). Restoring habitat complexity and connectivity is essential to promoting life history diversity, particularly in degraded environments. The concept of shifting habitat mosaics (Stanford et al. 2005; Brennan et al. 2019) considers how habitat diversity contributes to population resiliency by providing options that contribute to the expression of diverse life histories. For example, the relative productivity of Sockeye salmon (*O. nerka*) in a large Alaskan watershed varies temporally across locations but is ultimately stable at the basin scale, providing evidence of the importance of the shifting habitat mosaic for stabilizing salmon production across years with different conditions (Brennan et al. 2019). Similarly, juvenile Central Valley fall-run Chinook Salmon exhibited multiple rearing and migration timing strategies, enabling them to utilize spatiotemporal differences in growth opportunities between the American River mainstem and Sacramento-San Joaquin Delta during low and normal/high flow years (Coleman et al. 2022). Ultimately, integrating diversified hatchery release strategies with an increased pace and scale of environmental restoration activities is necessary to reconcile the water demand of humans and aquatic ecosystems in California's Central Valley.

Conclusions

Our aim in conducting this synthesis is to help facilitate the use of science, monitoring, and adaptive management to improve hatchery practices and sustain conservation-sensitive and culturally and economically important fish populations. This synthesis adds to a growing body of information about the ecology of hatchery-produced salmonids throughout the Pacific Rim (Mahnken et al. 1998; Ruggerone et al. 2010; Ruggerone and Irvine 2018), including California's Central Valley (Huber and Carlson 2015; Satterthwaite and Carlson 2015; Sturrock et al. 2019). For example, the temporal pattern of annual *O. mykiss* releases observed here tracks trends observed for hatchery-released Pacific salmonids released in the Pacific Northwest, British Columbia, Alaska, and Japan (Mahnken et al. 1998; Ruggerone et al. 2010; Ruggerone and Irvine 2018), where a steady increase in release abundances is observed from the 1950s through the 1970s until a plateau is reached beginning in the 1980s that continues until the present. Furthermore, the current practice of releasing large numbers of similarly sized *O. mykiss* at restricted times and locations around the turn of the 21st century mirrors the hatchery release management trends for Central Valley fall-run Chinook Salmon (Huber and Carlson 2015). Pervasive reductions in release portfolios have likely occurred in other regions too and deserve further scientific inquiry. Management actions that promote biocomplexity should be approached within a scientific and monitoring framework to assess changes in stock resilience over time. Given continued salmon and steelhead population losses and the pace of global climate change, there is an increasing need for evidence-based adaptive management approaches to conserve populations.

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Supplementary material

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Appendix A

Table A1. Summary table of Central Valley *O. mykiss* hatchery release metrics for all hatcheries combined (ALL), Coleman National Fish Hatchery (CNFH), Nimbus Fish Hatchery (NFH), Feather River Fish Hatchery (FRFH), and Mokelumne River Fish Hatchery (MRFH).

	ALL	CNFH	NFH	FRFH	MRFH
Range of release years	1948–2017	1948–2017	1957–2017	1970–2017	1965–2017
Number of release years	70	69	59	48	51
Mean number of fish released annually (millions)	1.96	0.85	0.71	0.59	0.17
Mean biomass released annually (thousands of kg)	125.71	55.07	40.68	37.50	15.69
Mean release date	12 Mar	24 Feb	21 Mar	6 Apr	27 Feb
Mean release distance from hatchery (rkm)	40.0	33.8	48.2	44.4	110.2
Hatchery distance from SF Estuary (rkm)	–	445.1	138.3	239.0	133.3
Hatchery distance from Pacific Ocean (rkm)	–	517.8	211.0	311.7	206.0
Mean fish mass-at-release (g)	64.3	65.1	57.3	63.0	96.8
Mean fish fork length-at-release (mm)	174	175	168	173	199
Mean apparent age-at-release (days)	322	344	296	320	356
Mean apparent absolute growth rate ($g \cdot day^{-1}$)	0.25	0.23	0.29	0.30	0.34
Mean apparent absolute growth rate ($mm \cdot day^{-1}$)	0.49	0.48	0.52	0.52	0.50
Mean annual reciprocal Simpson's index (RSI)	0.57	0.78	0.60	0.71	0.70
Mean percentage of each life history stage released:					
(1) yolk-sac fry	2.3	0.2	3.3	5.7	0.3
(2) fry	8.3	2.5	18.8	7.0	1.0
(3) parr	19.2	14.1	20.5	28.5	17.4
(4) silvery parr	25.2	46.1	11.0	7.8	9.1
(5) small smolts	34.4	33.8	29.0	40.1	45.5
(6) large smolts	6.4	2.2	8.8	9.3	13.5
(7) sub-adults	0.5	0.2	0.2	0.2	4.5
(8) adults	<0.01	<0.01	0	<0.01	<0.1
unknown	3.8	0.9	8.4	1.3	8.7
Release program goals:					
Annual total number released (millions)	–	0.62	0.43	0.45	0.25
Size-at-release (g)	–	113.4	113.4	113.4	113.4
Release month	–	Jan	Jan–Mar	Jan–Feb	Feb–Mar
Primary release location latitude (°N)	–	40.2635	38.5996	39.058	38.2285
Primary release location longitude (°W)	–	122.2245	121.5059	121.6106	121.4913
Primary release location distance from hatchery (rkm)	–	31.8	36.3	71.9	70.6

Note: Also shown are release program goals according to California Hatchery Scientific Review Group (CA HSRG) (2012, Appendix VIII).