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Temporal Trends in Hatchery Releases of Fall-Run Chinook Salmon in California's Central Valley

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ABSTRACT

The Central Valley fall-run Chinook salmon (*Oncorhynchus tshawytscha*) is the dominant population complex supporting the California and Southern Oregon commercial salmon fishery. The stock is largely dominated by hatchery production and has shown high variability in adult returns, suggesting that hatchery practices are critical to the long-term sustainability of the fishery. We compiled information from numerous sources to synthesize trends in the number, location, size, and timing of fall-run Chinook salmon released from the five Central Valley hatcheries between 1946 and 2012. Approximately 2 billion fish were released during this period, nearly half of which were released from the single federally operated hatchery. Juveniles have been planted off-site in the estuary with increasing frequency since the early 1980s, particularly by state-operated hatcheries. Approximately 78% of all releases occurred between January and June, including ~25% in April and ~20% in May. Release timing and size trends differed among hatcheries, and were correlated. For example, the Coleman and Nimbus hatcheries tended to release small fish (< 5 g, on average) early in the year, while the Feather, Mokelumne, and Merced hatcheries tended to release larger fish (> 10 g, on average) later in the year. Moreover, sizes-at-release (by month) have increased since the 1980s, leading to the emergence of a new life-history type that now comprises nearly all of the estuary releases: springtime releases of large ocean-ready "advanced smolts." We collapsed release timing and size data into a single index of life-history diversity and our results indicate a reduction in juvenile life-history diversity through time, with decreased variability in release number, timing, and size in recent years. Together, these results indicate a reduction in the diversity of life-history types represented in the fall-run Chinook salmon hatchery releases, which may be a factor that contributes to the decreased stability of the Central Valley fall-run Chinook salmon stock complex.

KEY WORDS

Oncorhynchus tshawytscha, San Francisco Estuary, Sacramento–San Joaquin Delta, artificial propagation, stocking, growth, life history, phenotypic diversity, portfolio effect

INTRODUCTION

Habitat loss and large-scale harvest of valuable animals and plants often requires extensive supplementation of artificially-propagated individuals in order to sustain the services they provide to humans (Laikre et al. 2010). An example is the post-World War II release of hundreds of billions of hatchery-reared Pacific salmonids across much of their Pacific Rim distribution (Mahnken et al. 1998). In the face of major habitat destruction and population declines (Lichatowich 2001), constraints on habitat restoration efforts (Bond and Lake 2003), and human nutritional preferences (FAO 2014), salmonid hatcheries satisfy important societal demands (NRC 1996) while providing a potentially valuable conservation tool (Naish et al. 2008).

Despite the benefits of fish hatcheries, the long-term sustainability of such technological fixes has been questioned (e.g., Fraser 2008). Reasons include overfishing of wild fish in mixed-stock fisheries (Nehlsen et al. 1991), negative behavioral and ecological interactions between hatchery and wild fish (Rand et al. 2012), and/or detrimental genetic effects (Reisenbichler and Rubin 1999; Araki et al. 2007). Indeed, the debate over the value of fish hatcheries for Pacific salmon is contentious (Ruckelshaus et al. 2002), with arguments in both their defense (e.g., Brannon et al. 2004) and opposition (e.g., Myers et al. 2004).

California's Central Valley Chinook salmon have received extensive attention because of their economic, environmental, and cultural importance (see reviews by Yoshiyama et al. 1998 and Williams 2006). The region represents the southern-most extent of the species' range, which spans approximately 40° latitude and 100° longitude across a diverse array of habitats including high- and low-elevation streams, floodplains, marshes, estuaries, bays, and nearshore and offshore oceanic habitats throughout the Northeast Pacific Ocean region (Augerot et al. 2005). The stock complex is characterized by an unprecedented degree of life-history diversity—it is the only Chinook salmon complex that contains four distinct runs named for the time of year when they return to freshwater as adults: winter, fall, late fall, and spring (reviewed by Williams 2006). The National Marine Fisheries Service (NMFS, now NOAA Fisheries) has classified these four runs into three Evolutionary Significant Units (ESUs) for purposes of management, based on genetic and life-history similarities. Abundances (Fisher 1994; Yoshiyama et al. 1998) and life-history diversity (Gustafson et al. 2007) of Central Valley Chinook salmon have been greatly reduced since Euro-American settlement due to interacting anthropogenic (Yoshiyama et al. 1998) and natural (Lindley et al. 2009) factors. The winter and spring run ESUs are considered endangered and threatened, respectively, under the federal Endangered Species Act and the fall/late-fall run ESU is classified as a federal and state Species of Concern (Myers et al. 1998).

Central Valley fall-run Chinook salmon breed and rear in low-elevation mainstem rivers (Moyle 2002). Adults migrate upstream from June to December, and spawn in gravel-bed streams from late September to December (Yoshiyama et al. 1998). Juveniles emerge from the gravel in the spring and spend a limited amount of time in their natal rivers before moving to downriver nursery habitats and then out to the ocean (Moyle 2002; Williams 2012). While they are regarded as ocean-type Chinook, Williams (2012) makes the distinction between fry migrants that travel directly to brackish water in the bays to rear and fry migrants that migrate to the Delta and rear there for an extended period (weeks to months) before continuing downriver to the bays, emphasizing that together these are the most common juvenile life-history patterns among Central Valley fall-run Chinook salmon. Emigration of fall-run juveniles from natal sites to downriver nursery grounds extends from December to July, with maximum activity occurring from February to June.

In addition to natural reproduction in Central Valley rivers, many fall-run Chinook salmon now breed in one of five production hatcheries in California's Central Valley. Like other salmon hatcheries, these hatcheries have several shared goals and practices, including collecting adult fish, selecting broodstock, spawning fish, rearing eggs through the juvenile life stage, and releasing these fish. The larger Central Valley fall-run population

complex receives significant hatchery contributions (Johnson et al. 2012; Kormos et al. 2012; Palmer–Zwahlen et al. 2013), and fishery catches are largely supported by hatchery production (Barnett–Johnson et al. 2007). The Central Valley fall-run Chinook salmon is the dominant stock that supports the California and southern Oregon coastal fishery (California HSRG 2012).

Recent research has revealed that the Central Valley fall-run Chinook stock complex is genetically homogenized (Williamson and May 2005), probably, in part, because of hatchery release practices (Garza et al. 2008). Specifically, hatchery fish released off-site are straying into basins with and without hatcheries, at rates approximately eight times greater (Sholes and Hallock 1979; Dettman et al. 1987; Cramer 1991; JHRC 2001; Kormos et al. 2012; Palmer–Zwahlen et al. 2013; Lasko et al. 2014) than background rates in this system of 5% to 10% for hatchery fish released on-site (Cramer 1991). Site infidelity is of interest to hatchery managers because of concerns about meeting broodstock quotas (JHRC 2001; California HSRG 2012) and for conservationists because it could be eroding local adaptations (Lindley et al. 2009) and masking population declines for wild fish (Johnson et al. 2012). Moreover, the constituent populations within the fall-run complex exhibit synchronous adult dynamics, which results in little buffering capacity and only a weak 'portfolio effect' (Carlson and Satterthwaite 2011). Similar to a portfolio of financial stocks, when individual fish populations exhibit diverse life histories and vary somewhat independently in their dynamics, the larger complex of populations is buffered against environmental variation (Hilborn et al. 2003; Schindler et al. 2010). While a weak portfolio effect remains in the Central Valley fall-run Chinook salmon stock complex, it has degraded through time (Carlson and Sattterthwaite 2011), probably, in part, from habitat loss and degradation as well as the influence of hatcheries.

In 2007–2008, the Central Valley fall-run Chinook salmon stock complex suffered a large-scale collapse that resulted in emergency commercial and recreational fishery closures (Lindley et al. 2009) and the provision of $170 million in federal disaster relief aid from 2008 to 2010 (Upton 2013) to mitigate the societal harm caused by this ecological shock. California state government records indicate that 5,000 to 23,000 jobs and a half billion to 2 billion dollars were lost to the state's economy in 2008–2009 as a result of the fishery collapse (Schwarzenegger 2008, 2009; State of California 2010). After fishery closures in 2008 and 2009, the U.S. Congress approved funds to form the California Hatchery Scientific Review Group in 2010 to synthesize information about hatchery operations and objectives following the model established by groups operating in Puget Sound and coastal Washington (HSRG 2004) and the Columbia River (HSRG 2009). The recently released review offered several key recommendations for improved management of California's anadromous fish hatcheries, which included the need to make full use of pre-existing data sets for more scientifically-informed management decisions (California HSRG 2012).

To improve transparency and contribute to more informed science and management efforts, we undertook a synthesis of 67 years of hatchery production and release data in California's Central Valley. Our first objective was to illuminate the temporal trends in fall Chinook releases, including a focus on (1) number released, (2) release location, (3) release size, and (4) release timing. A second objective was to explore patterns in life-history diversity of hatchery releases through time. By highlighting patterns and improving data access, our hope is that this effort will inform future research and management decisions.

MATERIALS AND METHODS

Study Site

Central Valley fall-run Chinook salmon all originate in the heavily modified foothill streams and valley floor rivers of the Sacramento and San Joaquin watersheds. To mitigate for lost breeding and rearing habitat resulting from dam construction, mitigation hatcheries were constructed. Five main production hatcheries propagate Central Valley fall-run Chinook salmon, including the Coleman National Fish Hatchery on Battle Creek, Nimbus Fish Hatchery

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on the American River, Feather River Hatchery, Mokelumne River Fish Hatchery, and the Merced River Fish Facility. The Coleman, Nimbus, and Feather hatcheries are in the Sacramento watershed whereas the Mokelumne and Merced hatcheries are in the San Joaquin watershed. The U.S. Fish and Wildlife Service (USFWS) operates the Coleman Hatchery; the California Department of Fish and Wildlife (CDFW; formerly named the California Department of Fish and Game or CDFG) operates the Nimbus, Feather, Mokelumne, and Merced hatcheries.

Release Data

We compiled information from 139 annual reports provided by the four state-operated hatcheries: Feather (34 reports, 1968 to 2001), Nimbus (47 reports, 1956 to 2002), Mokelumne (37 reports, 1964 to 2001), and Merced (21 reports, 1971 to 2001) hatcheries. From 2002 to 2012 for the Feather, Mokelumne, and Merced hatcheries and 2003 to 2012 for the Nimbus Hatchery, an electronic database compiled by CDFW and provided by David Krueger (*dave.krueger@wildlife.ca.gov*) was used instead of annual reports. At the time of writing, state hatchery data were considered in "draft" or non-finalized form from 2012 back to 1992 for the Feather, 1993 for the Nimbus and Mokelumne, and 1995 for the Merced hatcheries. According to one hatchery manager, any changes between the "draft" and "final" report stage are likely to be very minor (e.g., on the order of tens of fish, 2015 phone call between A, Kastner (California Department of Fish and Wildlife) and S.M. Carlson, unreferenced, see "Notes"). Zero releases occurred in 1975 (disease outbreak) and 1980 (low female escapement) for the Merced Hatchery. Additionally, no release data were available for the Merced Hatchery from 1991 to 1994 because the hatchery was closed for renovation. We obtained all data from 1946 to 2012 for the Coleman Hatchery from an electronic database provided by Kevin Niemela (*kevin_niemela@fws.gov*). We compiled release data from all five hatcheries into a single aggregate database. (Appendix A includes a description of the metadata; Appendix B includes the complete database, which will be updated periodically.)

Regardless of the source of data, the basic reporting unit was a cohort of fish released together at a given location over a specific period of time (hereafter referred to as a "release group"). Typically, each release group was associated with information about brood year, total number of fish released, location of release, mean weight-at-release, and release time of year. Annual state hatchery reports spanned two calendar years from July 1 in year t to June 30 in year $t+1$. When fish of a given cohort were released before and after the June 30 cutoff for reporting, data were pooled from multiple annual reports. For an extremely limited number of cases, the release time-range spanned more than 365 days. When this occurred, the release group was assigned to the year when the majority of releases occurred. In a small number of cases involving volitional releases from hatcheries, the number of fish released per release group was not reported. Instead, estimates of total egg production and egg-to-fry survival rates were reported. In these instances, we estimated total fish released per release group by multiplying total egg production by egg-to-fry survival rate estimates. This phenomenon only occurred during the early stages of hatchery operation and represents a very small proportion (0.37%) of the total releases of fall-run Chinook salmon from the Central Valley hatcheries.

The release locations were reported at different levels of detail using non-standardized nomenclature. Consequently, only a coarse-level release location analysis is provided in this investigation: those fish released in the San Francisco Estuary (defined here as releases downstream of Chipps Island: lat 38.055198; long −121.911904) and those released upstream of this point. Inland releases made upstream of impassable dams were not included in the analysis, nor those used for laboratory work (0.31% of total releases).

Fish weights were reported in most cases (90% of total releases) and expressed as a single mean fish mass for the release group. When a range of weights were reported, the range midpoint was calculated and applied to the release group. To improve the relevance of size data and facilitate comparisons with other studies, weights were converted to fork lengths (FL) by the following relationship generated by data

downloaded from the Regional Mark Processing Center (RMPC, *http://www.rmpc.org/*) for hatchery-produced fall-run Chinook salmon. Specifically, we included data from 1,578 release groups with lengths and weights reported from 1981 to 2013 (mean length: 79-mm FL; length range: 36 to 217 mm FL; $R^2 = 0.95$):

$$\ln(\text{FL, mm}) = 0.313 \bullet \ln(\text{WEIGHT, g}) + 3.840$$

The start month and end month for a given release group was usually the same but occasionally a range of months were reported (7.8% of total releases), and in other cases only the release year was reported (9.5% of total releases). Because of these irregularities, release timing data were restricted to cases when the release start and end months were the same (82.7% of total releases). We focused on release month because information about release day-of-month was limited through much of the early and middle parts of the data set.

To calculate the dispersion in release size and timing, we calculated the yearly population standard deviation (SD) for releases from each hatchery and all hatcheries combined as:

$$\text{Population } SD = sqrt(\Sigma\,(p_i \bullet (X_i - X_{avg})^2)$$

where p_i equals the number of fish in release group i divided by the total number of fish released per year with size or month-of-release reported, X_i equals the size or month-of-release of fish in release group i, and X_{avg} equals the average size or average month-of-release of fish per year (calculated as the weighted mean across all release groups).

To examine temporal trends in release variability, we then examined the coefficient of variation (CV) for release number, size, and timing. For release number, we calculated decadal CVs by dividing 10-year standard deviations by corresponding means for each hatchery and all hatcheries combined. The CV for release size and timing is the population SD divided by the average size or average month-of-release per year for all hatcheries combined.

Life-History Designations and Life-History Diversity

We classified the life histories of released fish according to size-classes determined from information provided by the state hatchery annual reports and by Williams (2012). "Fry" were defined as fish with estimated fork lengths < 55 mm; "fingerlings (or parr)": ≥ 55 to < 70 mm; "smolts": ≥ 70 to < 87.5 mm; "advanced (or ocean-ready) smolts": ≥ 87.5 to < 140 mm; and "yearlings": ≥ 140 mm. The 87.5-mm cutoff for the smolts and advanced smolts was based on two factors: (1) it approximates the average size of ocean entry for Central Valley fall-run Chinook salmon (Williams 2012, originally derived from Lindley et al. 2009), and (2) it represents the estimated fork length attributed to a fish weighing 7.56 g (60 fish per lb), which was emphasized in the annual reports as a distinct release type.

Timing and size data were collapsed into a single life-history diversity index developed for juvenile Chinook salmon ("Early Life-History Index [ELHD]," Johnson et al. 2014) that combines elements of fish abundance, trait richness (i.e., number of traits), and trait evenness (i.e., relative frequency of each trait). Johnson et al. (2014) developed the index to characterize the diversity of life histories observed among juvenile Chinook that originate from the Columbia River system, with a goal of developing a quantitative index that could be used to assess trends in life-history diversity through time (e.g., before and after a restoration effort) or to compare life-history diversity through space. The index incorporates both morphological (e.g., size class) and behavioral (e.g., release month) attributes, and offers a quantitative and standardized method to evaluate these often-measured and ecologically-relevant juvenile Chinook salmon life-history traits across broad spatial and temporal scales. Johnson et al. (2014) describe three different calculations for the ELHD index that place different emphases on time–size trait combinations. We used the first-order diversity estimator index (${}^1ELHD$) recommended by the authors because of its insensitivity to rare or abundant trait combinations. We presented the normalized index (${}^1ELHD_{norm}$) because it converts the index to an easily comprehendible range (0-1), with

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values that represent the proportion of total possible release time–size class combinations:

$$^{1}ELHD_{norm} = \left(\exp\left(-\Sigma p_i \bullet \ln(p_i)\right)\right) / T$$

where p_i is the proportion of the total abundance for the ith month-size class combination and T is the total number of month–size class combinations. Since there are 12 months in a year and 5 size classes investigated in this study, the total number of possible time–size combinations was 60. Since not all size classes are expected to be released each month (e.g., a fry 55 mm FL or smaller is not expected to migrate downstream in August), a more realistic value of $T = 17$ was chosen for this study (see "Results"), which reflects actual month-size combinations observed among the hatchery releases.

All statistical analyses were performed with JMP® software version 8.0 (SAS Institute Inc., Cary, NC, USA), and effects were considered significant at $\alpha = 0.05$.

RESULTS

Number Released

Using the data compiled from the CDFW annual reports and CDFW and USFWS databases, we calculated the number of fall-run Chinook produced in Central Valley hatcheries across the years 1946 to 2012. Just over two billion hatchery-reared fall-run Chinook salmon were released during this period, representing 253 hatchery–year combinations (Figure 1F). Approximately half (52.4%) of these fish ($n = 1.05 \times 10^6$) were released from the federal hatchery at Battle Creek (Coleman). Amongst the state hatcheries, the Nimbus Hatchery was numerically dominant in terms of total releases ($n = 455 \times 10^6$, representing 22.6% of total releases), followed by the Feather ($n = 352 \times 10^6$, 17.5%), Mokelumne ($n = 127 \times 10^6$, 6.3%), and Merced ($n = 22 \times 10^6$, 1.1%) hatcheries (Table 1).

The release number trends for the individual hatcheries showed different patterns (Figures 1A–E, Table 1). Coleman Hatchery releases (mean = 15.8×10^6; median = 13.4×10^6; CV = 0.53; Figure 1A) were highly variable from inception through the 1970s and have stabilized since then. Mokelumne releases increased over time and were highly variable (mean = 2.7×10^6; median = 2.2×10^6; CV = 0.91; Figure 1D) , in part, from facility remodeling in 2002. Releases from the Feather Hatchery were relatively consistent through time (mean = 7.9×10^6; median = 8.2×10^6; CV = 0.39; Figure 1B). Releases from the Nimbus and Merced hatcheries were somewhat bimodal, with peaks occurring in the mid-1960s and early 1980s for the Nimbus Hatchery (mean = 8.1×10^6; median = 5.8×10^6; CV = 0.67; Figure 1C) and in the mid-1990s and mid-2000s for the Merced Hatchery (mean = 0.6×10^6; median = 0.4×10^6; CV = 0.83; Figure 1E).

Release Location

Approximately 20.8% of all releases in the time series occurred downstream of Chipps Island in the San Francisco Estuary ($n = 418 \times 10^6$, Figure 1F), with breakdowns by hatchery presented in Table 1. The first planting in the estuary happened in 1964 but large scale planting in the estuary did not begin until 1981 when 16.9% of all releases were deposited in the estuary (previous yearly high was 3.2%). From 1981-2012; an average of 13.0×10^6 fish were released in the estuary per year (min = 6.4×10^6; max = 20.4×10^6; median = 13.3×10^6; CV = 0.25; Figure 1F). The Feather Hatchery released the most fish outside the freshwater environment ($n = 217.7 \times 10^6$, Figure 1B), followed by Nimbus ($n = 125.5 \times 10^6$, Figure 1C), Mokelumne ($n = 55.7 \times 10^6$, Figure 1D), Coleman ($n = 17.7 \times 10^6$, Figure 1A), and Merced ($n = 1.0 \times 10^6$, Figure 1E) hatcheries.

Size at Release

The average release size of all hatcheries combined was 5.9 g, equivalent to ~81 mm FL (see "Methods," Figure 2F). Release sizes were bimodal, with the Coleman (Figure 2A) and Nimbus (Figure 2C) hatcheries mainly releasing small fish (mean = 3.9 g or 71 mm FL and 4.9 g or 77 mm FL, respectively, Table 1). The Feather (mean = 10.7 g or 98 mm FL, Figure 2B), Mokelumne (mean = 13.4 g or 105 mm FL, Figure 2D), and Merced (mean = 12.7 g or 103 mm FL, Figure 2E) hatcheries released larger fish overall

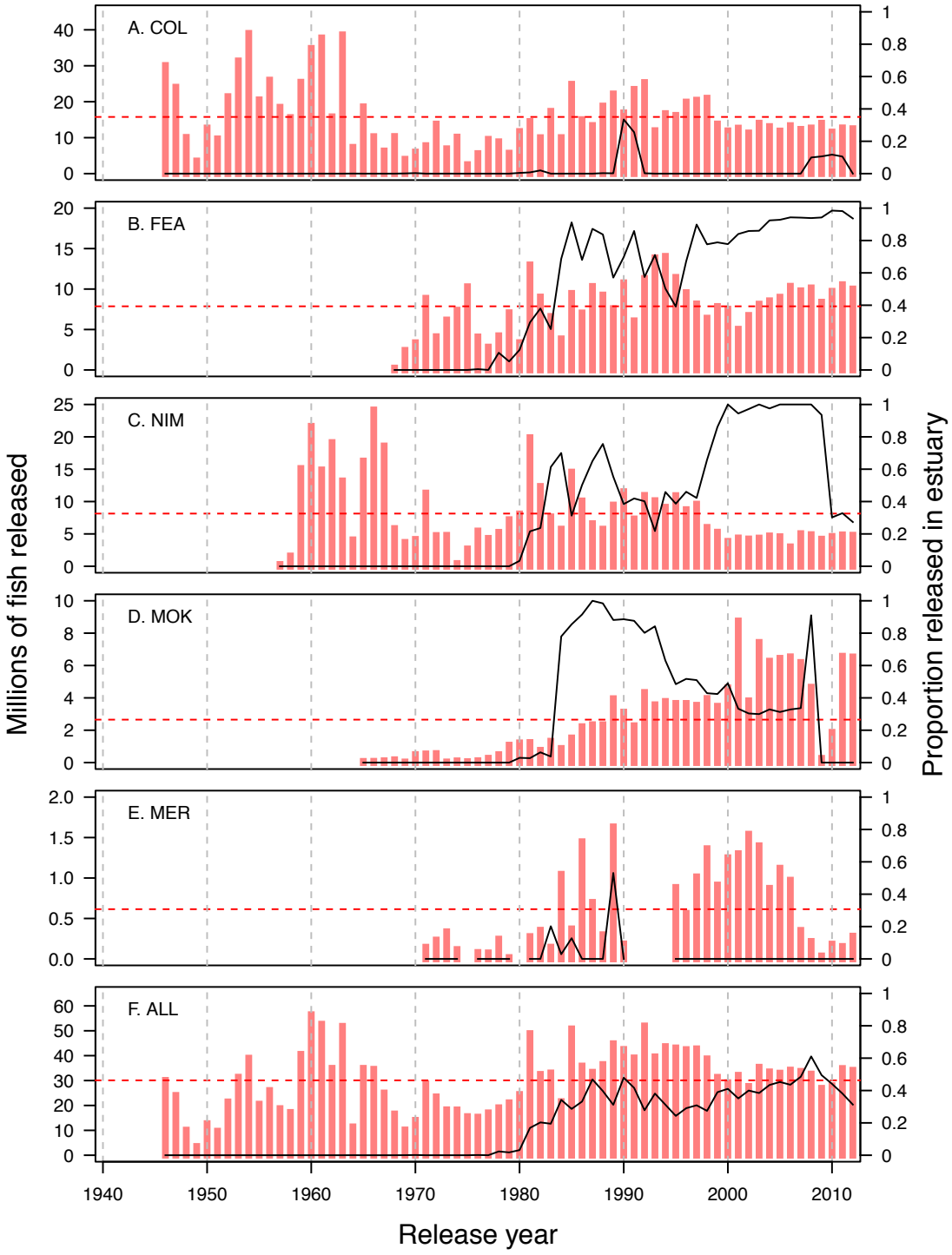

Figure 1 Annual fall-run Chinook salmon released from five of California's hatcheries that produce Central Valley fall-run Chinook salmon (**A**–**E**), including data for all five hatcheries (**F**) combined. Red bars are millions of fish released (left Y-axis) and the black line represents the proportion of the total number of releases that occur downstream of Chipps Island (right Y-axis). The dashed horizontal line on each panel indicates the mean number of releases over the entire release period. Panels show data from these five hatcheries: (**A**) Coleman, (**B**) Feather, (**C**) Nimbus, (**D**) Mokelumne, and (**E**) Merced. Panel (**F**) shows data for all five hatcheries combined.

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Table 1 Summary table with mean and calculated values for each hatchery

	Coleman	Feather	Nimbus	Mokelumne	Merced
Range of release years included in database	1946-2012	1968-2012	1956-2012	1964-2012	1971-2012
Number of release years	67	45	57	49	42
Total number of fish released (millions)	1,053	352	455	127	22
Mean number of fish released (millions)	15.8	7.9	8.1	2.7	0.6
Median number of fish released (millions)	13.4	8.2	5.8	2.2	0.4
Percentage of fish released (%)	52.4	17.5	22.6	6.3	1.1
CV in number released across years	0.53	0.39	0.67	0.91	0.83
Total number released to estuary (millions)	17.7	217.7	125.5	55.7	1.0
Mean size at release (g)	3.9	10.7	4.9	13.4	12.7
Mean time of release (date)	11-April	13-May	19-April	16-May	11-May
Mean proportion of each life stage released **(%)**					
Fry (< 55 mm FL)	42.9	13.4	41.8	1.2	1.2
Fingerlings (≥ 55 to < 70 mm FL)	8.4	4.3	2.6	0.8	4.3
Smolts (≥ 70 to < 87.5 mm)	39.0	21.3	24.6	14.5	61.4
Advanced smolts (≥ 87.5 to < 140 mm)	8.9	55.8	30.0	75.9	21.4
Yearlings (≥ 140 mm)	0.8	5.2	1.1	7.6	11.6

(Table 1). On average, Coleman (Figure 2A), Nimbus (Figure 2C), and Feather (Figure 2B) hatcheries released similarly-sized fish over time; the Mokelumne (Figure 2D) and Merced (Figure 2E) hatcheries released smaller fish over time.

Release Timing

The month with the greatest number of total released fish was April (24.7% of total releases), followed by May (20.4%), June (14.8%), March (11.6%), February (10.0%), January (4.5%), July (4.3%), October (3.1%), August (2.2%), September (2.1%), December (1.4%), and November (0.8%) (Figure 3). The average release month of all hatcheries combined was 4.7 which is equivalent to calendar day April 22 (Figure 3F). The Coleman (average month 4.4 or calendar day April 11, Figure 3A) and Nimbus (average month 4.6 or April 19, Figure 3C) hatcheries tended to release fish earlier in the year than the Feather (average month 5.4 or May 13, Figure 3B), Mokelumne (average month 5.5 or May 16, Figure 3D), and Merced (average month 5.3 or May 11, Figure 3E) hatcheries (Table 1). Overall, release timing was unimodal, with a skewed peak of later-year releases occurring during the 1960s and gradually trending towards earlier releases over time (Figure 3F). From 2000 to 2012 nearly all releases occurred in the months of April (51.2% of all fish released), May (30.4%), and June (18.4%) (Figure 3F).

Temporal Trends in Variability of Releases

To further evaluate release trends, we investigated the relationship between variability (measured as coefficient of variation, CV) versus year for release number (Figure 4A), release size (Figure 4B), and release timing (Figure 4B). In all cases, we found that variability has decreased (Figures 4A, 4B). For total releases over 10-year periods, the trends declined for all hatcheries (Figure 4A). Similarly, there have been reductions in release month variation ($R^2 = 0.30$, $P < 0.0001$) and release size variation ($R^2 = 0.38$, $P < 0.0001$) through time (Figure 4B), and these were correlated ($R^2 = 0.82$, $P < 0.0001$).

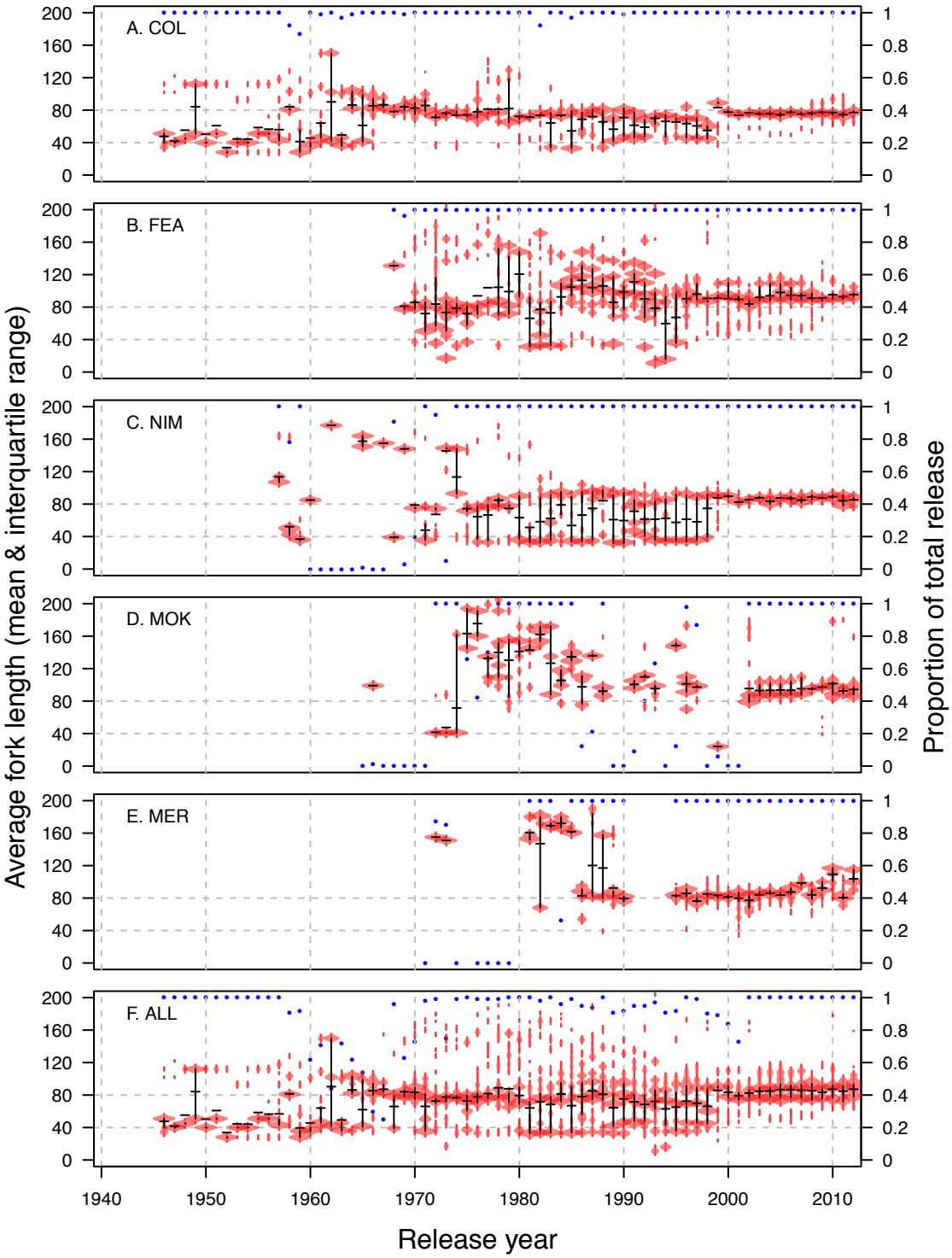

Figure 2 Annual fork length-at-release (left Y-axis) and interquartile range (black cross, dash represents the mean and whiskers represent the IQR)—with violin plot in red to show the associated density distribution—and the proportion of total yearly releases per year (right Y-axis) with size data reported (blue circle). Panels show data for five different hatcheries: (A) Coleman, (B) Feather, (C) Nimbus, (D) Mokelumne, and (E) Merced. Panel (F) shows data for all five hatcheries combined.

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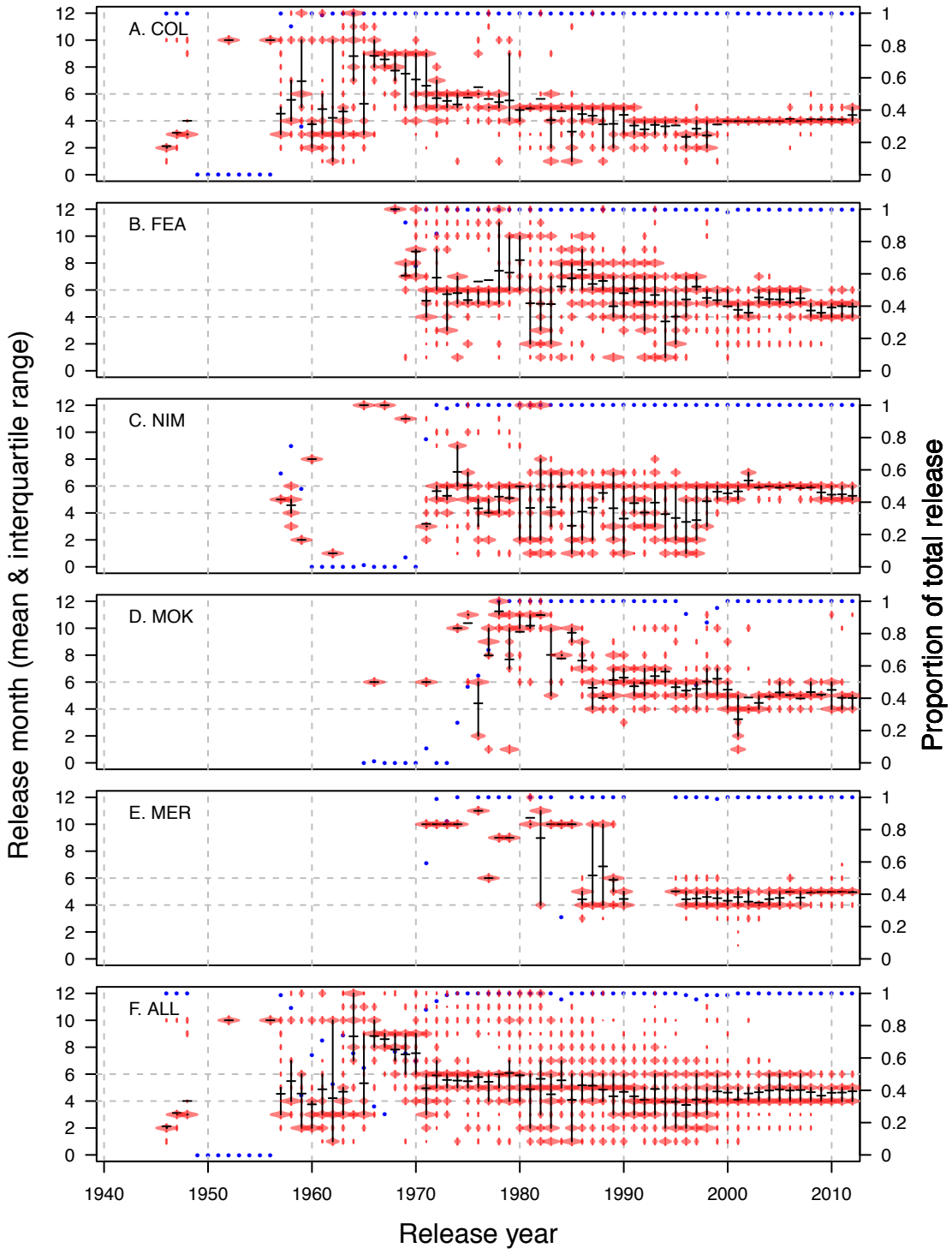

Figure 3 Annual release month (left Y-axis) including mean and interquartile range (black cross, dash represents the mean and whiskers represent the IQR)—with violin plot in red to show the associated density distribution—and the proportion of total release per year (right Y-axis), with data reported at the monthly scale (blue circle). Panels show data for five different hatcheries: (A) Coleman, (B) Feather, (C) Nimbus, (D) Mokelumne, and (E) Merced. Panel (F) shows data for all five hatcheries combined.

Life History at Release

Fry, smolts, and advanced smolts represented the dominant life-history types released by Central Valley fall-run Chinook salmon hatcheries (Figure 5, Table 1). Over time, the releases of smolts and advanced smolts have steadily increased whereas fry, fingerling, and yearling releases have largely ceased (Figure 5). The Coleman Hatchery released the majority of their fish as fry (42.9% of total releases for the hatchery) and smolts (39.0%). The Nimbus Hatchery has had a balanced release of fry (41.8%), advanced smolts (30.0%), and smolts (24.6%) over the entire time-series. The majority of Feather releases were advanced smolts (55.8%) followed by smolts (21.3%), whereas the majority of Merced releases were smolts (61.4%) followed by advanced smolts (21.4%). The Mokelumne Hatchery released most of their fish as advanced smolts (75.9%). From 2000 to 2012, smolts and advanced smolts averaged 16.1×10^6 (52%) and 14.0×10^6 (45%) fish released per year from all hatcheries combined, respectively, whereas fry (0.3×10^6 yr^{-1}, 0.9%), fingerling (0.5×10^6 yr^{-1}, 1.7%), and yearling (0.07×10^6 yr^{-1}, 0.2%) releases averaged far less during the same period.

Generally, fry were released from January to March (87% of total fry releases), fingerlings from March to May (89% of total fingerling releases), smolts from April to June (93% of total smolt releases), advanced smolts from April to July (80% of total advanced smolt releases), and yearlings from October to January (86% of total yearling releases) producing the 17 dominant size class–month combinations used for the life-history diversity index calculation (see "Materials and Methods").

The early life-history diversity of releases based on index values (i.e., ${}^1ELHD_{norm}$) was found to be unimodal and symmetrical and could be described by a second order polynomial fit ($y = -0.0003x^2 + 1.2823x - 1271.5$, $R^2 = 0.62$) with peak release diversity occurring in the 1980s (Figure 6). Values from 1949 to 1956 were excluded because of poor release timing information (only 0.03% of fish released during this period had the same start and end release months). Maximum diversity values occurred in 1983 and 1993 (${}^1ELHD_{norm} = 0.66$ for both years). Minimum diversity occurred in 1946 and 1947 (${}^1ELHD_{norm} = 0.08$ for both years) when most fish were released as fry from the Coleman Hatchery, approximately 300 km upstream of Chipps Island. Average annual ${}^1ELHD_{norm}$ values and CVs (in parentheses) for the 5 decades from 1960 to 2009 were 0.29 (0.25), 0.44 (0.24), 0.52 (0.12), 0.46 (0.19), and 0.27 (0.12), respectively.

DISCUSSION

Here we present an overview of the main trends in hatchery releases of Central Valley fall-run Chinook salmon from hatchery inception through 2012. Through compilation of a suite of datasets, we were able to ask questions about temporal patterns in hatchery releases, including juvenile release numbers, locations, sizes, timing, and life-history stages.

Our analysis revealed several patterns in release abundance over time, including differences both among and within hatcheries. For example, total releases from the two dominant producers, Coleman and Nimbus hatcheries, have declined over time, whereas those from the Feather, Mokelumne, and Merced have increased (Figure 1). Variation in the total release number has declined steadily over time for all hatcheries (Figure 4A), particularly as release strategies have stabilized in recent years. The vast majority of fish have been and continue to be released from three of the five hatcheries that propagate fall-run Chinook salmon—Coleman [~53%], Nimbus [~23%], and Feather [~18%]—and these hatcheries have different release strategies, which has implications for the larger fall-run stock complex.

Fish sizes-at-release were low from the 1940s to mid-1960s (Figure 2F), reflecting the popular practice of releasing fry directly from the Coleman (Figure 2A) and Nimbus (Figure 2C) hatcheries at the time. Average size-at-release has decreased since the 1960s at the Mokelumne (Figure 2D) and Merced (Figure 2E) hatcheries largely because yearlings are no longer being released at the San Joaquin hatcheries. In contrast, average size-at-release has remained relatively more consistent since the 1960s at the Coleman (Figure 2A), Nimbus (Figure 2C),

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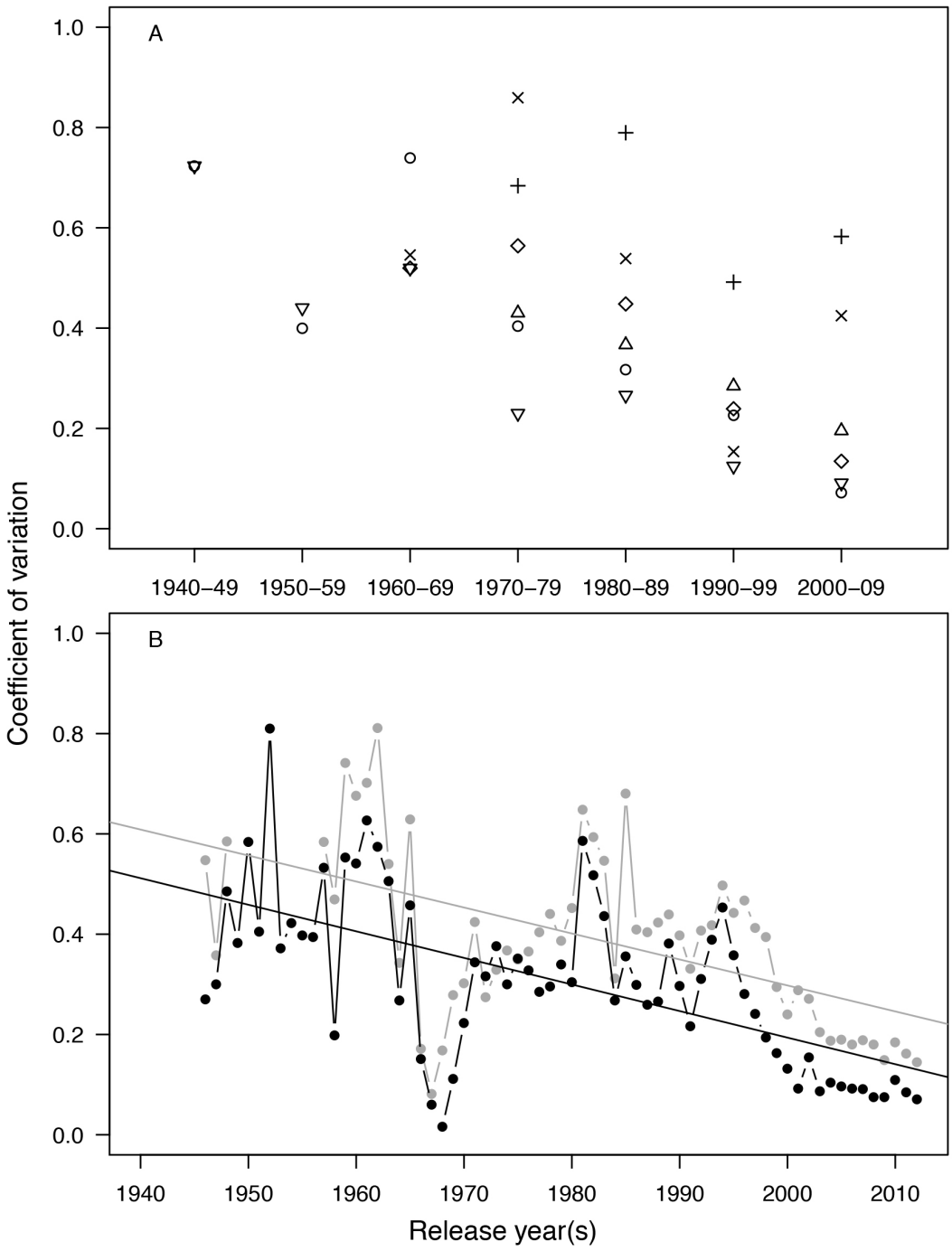

Figure 4 Portfolio reductions of key release traits, expressed as declining coefficient of variation (CV) trends for (**A**) decadal release number for the Coleman (○), Nimbus (◊), Feather (△), Mokelumne (×), Merced (+), and all (▽) hatcheries, and (**B**) fork length-at-release (black dots and black line) and month-at-release (grey dots and grey line) for all hatchery data combined. In panel **A**, data were included beginning for the first decade when release information was available for the majority of years within the decade.

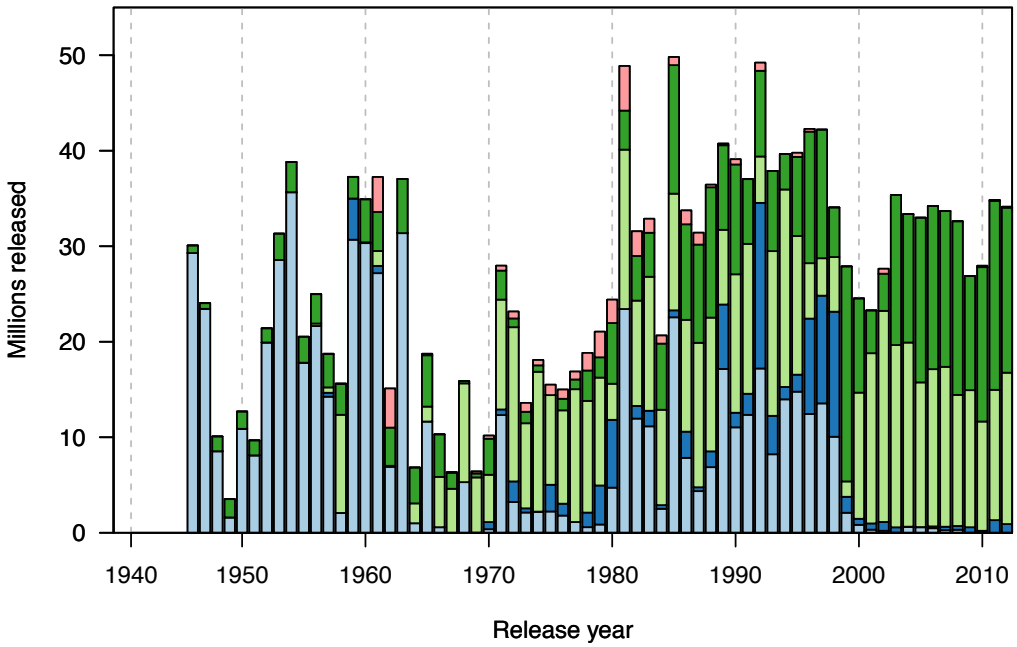

Figure 5 Release life-history types, presented as total released per type across all years and hatcheries. Life-history types are based on size (fry: <55 mm, light blue bar; fingerlings: ≥55 to <70 mm, dark blue bar; smolts: ≥70 to <87.5 mm, light green bar; advanced smolts: ≥87.5 to <140 mm, dark green bar; yearlings: ≥ 140 mm, pink bar). Note that the discrepancies between figure 1 and figure 5 are due to the decision rule to only include fish whose release begin and end months are the same for life history analyses presented in this plot.

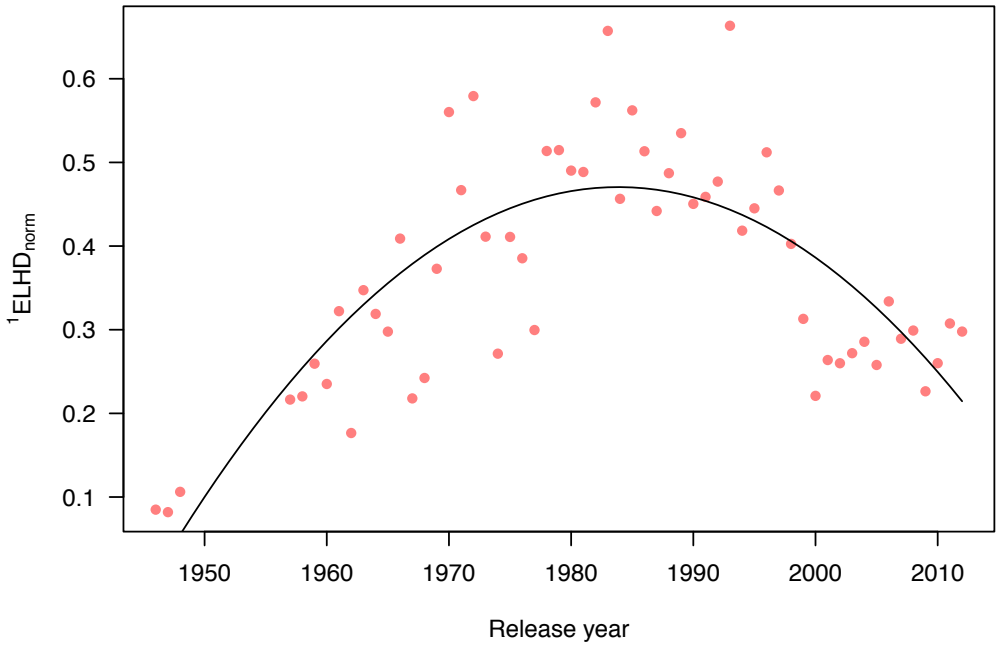

Figure 6 Release portfolio as expressed by a life-history diversity index ($^1ELHD_{norm}$, see "Materials and Methods") developed for juvenile Chinook salmon (pink circles). The first-order normalized diversity estimator incorporates release month and size data and expresses values as a proportion of total possible release month–fish size combinations. The overall trend is unimodal and symmetrical with release diversity peaking in the 1980s (best described as a second-order polynomial fit, $y = -0.0003x^2 + 1.2823x - 1271.5$, black line).

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and Feather (Figure 2B) hatcheries, although both the Coleman and Nimbus hatcheries show a recent uptick in release size and stabilization of release size beginning in the late 1990s. Similar to trends in release number, the variability in size-at-release has decreased over time for all five hatcheries combined (Figure 4B), particularly since 2000 (Figures 2A, 4B).

There is an apparent pattern of releases occurring later in the year from the 1940s to the 1960s (Figure 3F), but this may be partially biased by data reporting, which cannot account for fish out-migrating volitionally from spawning channels (a practice that largely ceased in the 1960s according to state annual reports). Data reporting has become more reliable since the 1970s, and there is an overall trend of earlier releases since then, with most releases occurring during the spring (Figure 3F). Among other factors, these patterns may reflect insufficient flows earlier in the year to allow out-migration of poor-swimming fry, and freshwater thermal barriers later in the year for older and larger fish. Some of the shifts in release timing are related to shifts in release size (e.g., cessation of yearling releases from the San Joaquin hatcheries is associated with shifts from fall to late-spring releases) as well as release location, which we discuss below.

While not an original objective, one observation regarding size-at-release was an increase in size-at-release for each release month over time (Figure 7A). This has led to an apparent "substitution of growth for time" effect, as fish released in April in recent years are approximately the same average size as those released in May in the late 1980s and early 1990s and in June in the late 1970s (Figure 7A). Ultimately, this resulted in a new life-history release type that emerged in the early 1980s and has steadily increased in frequency since then: April, May, and June releases of ocean-ready "advanced smolts" (Figure 7B). This phenotype comprised 16%, 24%, and 35% of total fish released from all hatcheries for the years 1980 to 1989, 1990 to 1999, and 2000 to 2009, respectively (Figure 7B). Furthermore, April, May, and June releases of advanced smolts between 87.5-mm and 100-mm FL comprised a steadily increasing proportion of total estuarine plants since 1980 (Figure 7C). Assuming that spawning and emergence schedules have remained largely unaltered, this trend may reflect improvements in hatchery practices (e.g., better feed, and improved immunology, density, and temperature controls) and/or efforts to target the largest and fastest-growing fish for earlier releases. There may also be domestication selection for rapidly growing fish, which has been shown to occur in other artificially propagated salmonids (Fleming et al. 2002). Regardless of the mechanism(s), variables related both to ecological *state* (e.g., variable release size and month patterns, Figures 2A–F, 3A–F) and *process* (i.e., increasing size-at-release for each release month, Figure 7A) have been changing for hatchery-produced Central Valley fall-run Chinook salmon over the course of 67 years (~20 salmon generations) of hatchery management. Through future research, we aim to better understand the consequences of these changes on adult demographic properties and the dynamics of the stock complex.

Causes of the Trends

A full exploration of changes in hatchery practices and policies that have influenced the production trends is beyond the scope of this paper, but are likely many, and include:

- shifting hatchery management strategies intended to boost juvenile survival rates and maximize the average contribution of a given program to ocean fisheries,
- aquacultural and economic constraints (Sholes and Hallock 1979), such as limited hatchery rearing capacity and the relatively high costs and risks associated with producing older and larger fish,
- environmental stochasticity (e.g., droughts), and
- technological advancements (e.g., disease and avian depredation controls) (see Lufkin 1991; Brown 2006, as well as detailed information in the annual hatchery reports).

Some of the more striking shifts in release patterns that we highlight in Figures 1 through 3 are fairly well understood, including shifts in production

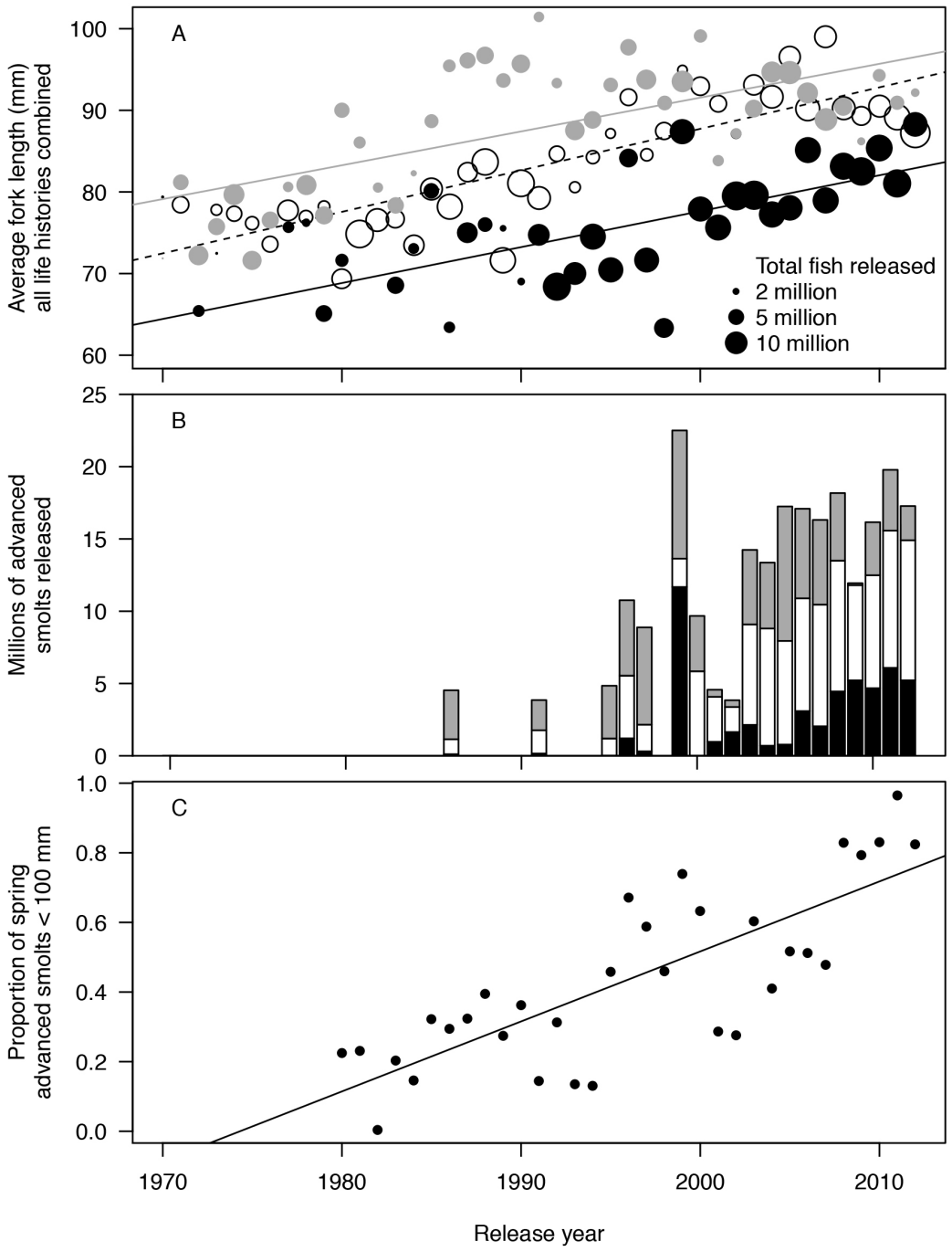

Figure 7 (**A**) Average fork lengths for April (black circles and trendline, y = 0.0811x + 2.7614, $R^2 = 0.43$, $P < 0.001$); May (white circles and dashed trendline, y = 0.1273x + 3.7744, $R^2 = 0.70$, $P < 0.001$); and June (grey circles and trendline, y = 0.1051x + 5.5073, $R^2 = 0.39$, $P < 0.001$) from 1970 to 2012. Circle sizes represent relative differences in monthly total release numbers. (**B**) Advanced (i.e., ocean-ready) smolt releases in April (black stacked bar), May (white stacked bar), and June (grey stacked bar) for all hatcheries combined across all years. (**C**) Increasing temporal trend of the proportion of total estuary plants comprised of spring (i.e., April, May, and June) releases of advanced smolts between 87.5 mm and 100 mm FL (with series year used instead of calendar year, y = 0.0206x + 0.0774, $R^2 = 0.64$, $P < 0.001$).

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goals and biomass allocations (e.g., many small vs. fewer larger fish). For example, the Coleman National Fish Hatchery production goals originally included ~40 million 1.5- to 2-inch fish (fry) and 2 million 5- to 7-inch fish (yearlings) (Cope and Slater 1957; 2013 email from S. Hamelberg (USFWS) to S.M. Carlson, unreferenced, see "Notes"). Studies conducted in the 1960s and 1970s revealed that smolts released in the spring survived at higher rates than fry released in the fall (USFWS 1982), which led to a shift away from fry releases over time towards a release of smolts, as presented in the 1987 Coleman National Fish Hatchery Station Development Plan (USFWS 1987; 2013 email from S. Hamelberg (USFWS) to S.M. Carlson, unreferenced, see "Notes"). This shift is readily apparent when considering the recent stabilization in numbers, size, and timing of releases from Coleman National Fish Hatchery (Figures 1A, 2A, and 3A). Kevin Niemela (USFWS) additionally emphasized that the shift toward smolt releases began earlier (in the mid 1960s) and that fry production in the 1980s and 1990s from Coleman could be considered 'added production,' that is, production on top of the established smolt production.

In another example from one of the state-operated hatcheries, release patterns from the Feather River Hatchery have stabilized since the mid-1990s. Around this time, new target numbers were made final (6 million mitigation fish + 1 to 2 million enhancement fish, 2015 phone conversation between A. Kastner, (CDFW) and S.M. Carlson, unreferenced, see "Notes"). This timing also coincides with a shift towards planting fish directly in the estuary, which was associated with shifts towards releasing fish at ~85 mm (i.e., 60 fish lb^{-1}, Figure 2B) a size that is typically reached by April to mid-May, hence releases concentrated during this time (Figures 3B, 7A) (2015 phone conversation between A. Kastner, (CDFW) and S.M. Carlson, unreferenced, see "Notes").

Generally, since the early 1980s there has been an increasing trend of planting fall-run Chinook directly into the San Francisco Estuary (Figure 1) to avoid exposing fish to undesirable conditions in the degraded freshwater environments (JHRC 2001; Newman and Rice 2002, Figure 1). Three state hatcheries—Nimbus (Figure 1B), Feather (Figure 1C), and Mokelumne (Figure 1D)—have released the most fish in the estuary. Such "off-site" releases present a conundrum for both hatchery and conservation managers. Recent improvements in marking strategies have indicated that smolts released in the estuary, especially advanced smolts from the Feather Hatchery acclimated to net pens, contribute disproportionately more to fishery catches and hatchery returns (Kormos et al. 2012; Palmer–Zwahlen et al. 2013). However, these same fish are straying at rates up to eight times greater (Kormos et al. 2012; Palmer–Zwahlen et al. 2013) than the background rates of 5% to 10% estimated for hatchery fish that were released "on-site" at the hatchery (Cramer 1991). Given that both Feather and Nimbus hatcheries are large producers that currently release a large fraction of fish off-site (Figure 1), these two hatcheries are likely generating a disproportionate number of strays, including strays to systems without hatcheries. Indeed, recent evidence from the constant fractional marking program suggests that these hatcheries do contribute a high number of strays to non-hatchery streams (Kormos et al. 2012; Palmer–Zwahlen et al. 2013). In contrast, the Coleman National Fish Hatchery, produces many more fish but tends to release these fish on-site, which leads to considerably lower out-of-basin straying (Kormos et al. 2012; Palmer–Zwahlen et al. 2013). Important exceptions were off-site releases from Coleman during the recent stock collapse (see the recent uptick in off-site releases in Figure 1A), which resulted in high rates of out-of-basin straying of fish from Coleman (Palmer–Zwahlen et al. 2013). In response to the current drought, we can expect the recent off-site releases of fish from Coleman will have the same effect. These patterns are all consistent with strong positive relationships observed between straying rate and distance trucked (Dettman et al. 1987; Cramer 1991; JHRC 2001; Lasko 2014), and our current understanding of salmon homing mechanisms in which salmon are thought to sequentially imprint on freshwater as they move downstream (Dittman and Quinn 1996). This matter deserves serious management attention because local adaptations (Utter 2004) and the ability to adapt to future environmental changes (Ghalambor et al. 2007)

can be rapidly altered by excessive immigration of individuals from different genetic stocks or from selective environments (Myers et al. 1998), or both, which could reduce the resiliency of this stock complex, a topic we discuss further in the next section.

Implications

Life-history diversity enhances stock stability via a portfolio effect that provides enhanced resiliency to fluctuating environmental conditions (Hilborn et al. 2003; Schindler et al. 2010; Carlson and Satterthwaite 2011). Based on the premise that life-history diversity improves resilience, salmon recovery plans often include restoration activities to increase life-history diversity (e.g., in the Columbia River system, NMFS 2011; Johnson et al. 2014). It is therefore reasonable to assume that life-history diversity of hatchery fish has implications for stock performance, particularly when the complex is dominated by hatchery fish such as the Central Valley fall-run Chinook salmon complex (Barnett–Johnson et al. 2007; Johnson et al. 2012; Kormos et al. 2012; Palmer-Zwahlen et al. 2013). Indeed, Hankin (1990) reported that the Chinook salmon population structure from Klamath River and southern Oregon hatcheries is strongly related to life histories of hatchery releases. More generally, size-at-release and month-of-release of juvenile fish eventually affects important adult demographic properties such as average age, size-at-age, and maturation schedules—all of which can influence the dynamics and stability of the stock complex.

Our analysis of size-class-based life-history types revealed distinct temporal patterns (Figure 5). Fry, smolts, and advanced smolts were the numerically dominant life-history stages released by all hatcheries, with recent shifts towards releases of smolts and advanced smolts (Figure 5). The practice of releasing fry, fingerlings, and yearlings largely ceased during the late 1980s and early 1990s (Figure 5). Using an index to characterize life-history diversity of the hatchery releases ($^{1}EHHD_{norm}$, Johnson et al. 2014), we found that the current life-history diversity at release is about half of the maximum measured in the 1980s and is similar to levels measured early in the time-series (Figure 6). It should be noted that, until the 1960s, only the Coleman and Nimbus hatcheries were operational, which limits direct comparisons between early and modern management schemes. Also noteworthy is that the early life-history index (ELHD) does not account for shifting release types over time, such as we have documented in this system (e.g., March releases of fry from hatcheries early in the time series was equivalent to June releases of advanced smolts in the estuary later on). Moreover, upstream releases of small-sized fish have more potential to diversify into different phenotypes before reaching the San Francisco Bay and Pacific Ocean than ocean-ready, larger fish deposited in the estuary (Myers et al. 1998; Healey 1991). Therefore, the *true* life-history diversity of ocean-arriving fish was likely higher for a given $^{1}EHHD_{norm}$ index value early in the time-series compared to more recent values (Figure 6) because of the increasing trend of downstream releases over time (Figure 1).

Beyond the changes in release practices and life-history diversity of fall-run Chinook salmon hatchery releases, the importance of the average contribution and variability in adult returns from each hatchery is also worth considering. Doak et al. (1998) emphasize that stock complexes are better buffered when abundances of constituent populations are more even, and releases are very uneven among the different hatcheries (Figure 1). Moreover, within hatchery populations, there is likely a positive relationship between average contribution rate and its variability. From a management perspective, high average contribution is desirable, but high variability is not—so there is a trade-off here that warrants closer attention by both hatchery and fishery managers. Ideally, hatchery releases from all five Central Valley hatcheries that produce fall-run Chinook salmon would be coordinated and managed in concert with other aspects of the fishery, such as harvest rates, to consciously balance the harvest level, variability, and sustainability of this system.

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CONCLUSIONS

We compiled and synthesized information on hatchery releases of fall-run Chinook salmon from California's Central Valley from various sources to create a single database of hatchery releases, representing 253 hatchery–year combinations (see Appendix B). These data are now available to the broader community interested in considering the role of hatchery practices in Central Valley fall-run Chinook salmon dynamics. As a first step towards exploring these patterns, we examined trends in hatchery release practices through time. We found that variation in release number, location, size, and timing of hatchery fall-run Chinook salmon releases has decreased over time in significant and consistent ways. In particular, the years of 1999 to 2012 were characterized by strong ecological homogenization of the fall-run hatchery release life-history portfolio (Figure 6). Coincident with the recent drop in early life-history diversity has been the multiple fishery closures and increasingly variable returns of adults to Central Valley hatcheries and non-hatchery spawning grounds (Lindley et al. 2009; Carlson and Satterthwaite 2011; PFMC 2014)—an apparent relationship that warrants closer inspection.

Another trend that deserves more attention is the observation that fish are attaining larger sizes at earlier times (Figure 7A). This has produced a phenotype (i.e., spring releases of advanced smolts) that was non-existent earlier in the time series (Figure 7B). The spring advanced smolt phenotype comprises a steadily increasing proportion of releases into the San Francisco Estuary (estuary). Early findings from the constant fractional marking program indicate that estuary releases of advanced smolts contribute the most to commercial fishing and hatchery escapement (Figure 7C). However, these fish are also straying from their natal hatchery at alarmingly high rates. If domestication selection for faster growing fish is a major reason for the observed trends in Figure 7A, then limiting introgression of hatchery genes into wild gene pools should be a top management priority.

Several management actions could allow for more complete expression of life-history diversity in this stock complex. For naturally produced fish, examples include the designation of salmon sanctuaries to protect wild populations where they still exist, and the continued restoration of freshwater and brackish water habitats, especially those that re-introduce habitat complexity that allows for a greater expression of juvenile phenotypes. For hatchery-produced fish, one possibility is to directly manipulate the phenotypes of hatchery releases to artificially generate diversity within hatchery releases (e.g., by staggering time-at-release). Another option is to release fish closer to the hatchery so that, like their natural counterparts, they are exposed to habitat complexity that generates phenotypic diversity during their out-migration. Indeed, when fish are released far downstream from natal sources, especially at crowded densities, they have less exposure to an array of energetically profitable nursery habitats, including intermittent (Limm and Marchetti 2009) and gravel-bed (Chapman and Bjornn 1969) streams, floodplains (Jeffres et al. 2008), and wetlands (Healey 1980; Roegner et al. 2010) that allow for a fuller range of genetic, phenotypic, and physiological expression within populations (Myers et al. 1998). Moreover, releasing high densities of ocean-ready fish may increase the vulnerability to match–mismatch dynamics when these fish enter the ocean (Satterthwaite et al. 2014). Consequently, population resilience and persistence is presumably under greater threat when fish are released in large numbers at restricted times, sizes, and locations, a common current practice at all of the Central Valley fall-run Chinook salmon hatcheries.

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