





REVIEW


Eight Decades of Hatchery Salmon Releases in the California Central Valley: Factors Influencing Straying and Resilience


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Chinook Salmon *Oncorhynchus tshawytscha*.
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The California Central Valley contains the southernmost native populations of Chinook Salmon *Oncorhynchus tshawytscha*, which inhabit a highly variable, anthropogenically altered environment. To mitigate habitat loss and support fisheries, millions of fall-run hatchery salmon are released each year, often transported downstream to avoid in-river mortality, with consequences not fully understood. We synthesize historical trends in release location and timing (1941–2017), focusing on outcomes influencing stock resilience, adult straying, and ocean arrival timing. Over time, juveniles have been transported increasing distances from the source hatchery, particularly during droughts. Transport distance was strongly associated with straying rate (averaging 0–9% vs. 7–89% for salmon released on site vs. in the bay upstream of Golden Gate Bridge, respectively), increasing the effects of hatchery releases on natural spawners. Decreasing variation in release location and timing could reduce spatiotemporal buffering, narrowing ocean arrival timings and increasing risk of mismatch with peak prey production. Central Valley salmon epitomize the pervasive challenge of balancing short-term (e.g., abundance) against long-term (e.g., stability) goals.

INTRODUCTION

Hatcheries are often controversial given potential impacts on natural stocks (Ruckelshaus et al. 2002). Hatcheries in the western United States propagate around 2 billion Pacific Salmon *Oncorhynchus* spp. annually, and global production can exceed 5.3 billion (NPAFC 2018). Production rates are relatively stable and insensitive to freshwater carrying capacity (NPAFC 2018), leading to concerns about hatchery fish outcompeting and/or masking declines in natural populations (Johnson et al. 2012; Rand et al. 2012).

Transporting hatchery-produced juveniles to downstream release sites is increasingly used to improve freshwater survival, but often fosters straying in the returning adults (Quinn 1993; Keefer et al. 2008; Bond et al. 2017). Some degree of dispersal is natural, promoting gene flow and colonization of new habitats, but strays are essentially lost from donor populations and can reduce fitness in recipient populations via maladaptive gene flow and domestication selection (Keefer and Caudill 2014). Release location can also influence stock stability, as diversifying habitat use across a heterogeneous landscape can generate portfolio effects and broaden ocean arrival timings (Schindler et al. 2010; Satterthwaite et al. 2014).

Release timing also carries important tradeoffs. Later releases can reduce instream competition and produce larger individuals, but increase risk of natural-origin fish being displaced in the ocean (Zabel and Williams 2002) and could lead to early maturation (Vøllestad et al. 2004). Furthermore, extended hatchery rearing increases operating costs and disease risk (California HSRG 2012), while any practices constraining ocean arrival timing increase risk of temporal mismatch with peak prey production (Satterthwaite et al. 2014).

California Central Valley (CCV) Chinook Salmon *Oncorhynchus tshawytscha* spawn at the southernmost edge of the native species range. The region features a variable Mediterranean climate (Cid et al. 2017), and a rich mosaic of habitats and salmon life histories (Yoshiyama et al. 2001). Over the last 150 years, the landscape has been profoundly altered by gold mining, agriculture, and water development (SFEI-ASC 2014). Impassable dams block >70% of upstream Chinook Salmon spawning habitats, resulting in large declines in abundance (Yoshiyama et al. 2001). To mitigate habitat loss and maintain salmon fisheries, five production hatcheries were built, releasing more than 2 billion fall-run juveniles since 1941 (Huber and Carlson 2015). These hatcheries use an integrated design and focus on fall-run, although smaller programs with different goals exist for other runs (California HSRG 2012).

Fall-run hatcheries in the CCV have developed an extensive trucking program to reduce mortality during outmigration through an increasingly degraded system (Huber and Carlson 2015). While off-site releases also occur in other systems (e.g.,

Colombia River barging; Bond et al. 2017), CCV hatcheries often eliminate the entire migratory corridor by trucking smolts directly to the bay (specifically, the region between Chippis Island and Golden Gate Bridge, hereafter referred to as bay; Figure 1). An inadvertent consequence of trucking has been excessive straying rates (California HSRG 2012), implicated in the genetic homogenization of CCV stocks (Williamson and May 2005) and increasingly synchronized population dynamics (Satterthwaite and Carlson 2015).

Despite the effects of increased straying, the influence of hatchery release strategies and environmental factors on straying behavior remains poorly understood in the CCV. Past synthesis efforts were hampered by inconsistent marking rates and recovery efforts, inaccurate or inaccessible release records, and release patterns designed to maximize abundance rather than test hypotheses. The only systematic experiment in the CCV investigating the effect of transport distance on straying rate revealed a strong positive relationship between the two (Niemela 1996), but other covariates or populations were not examined.

In this paper, we (1) summarize hatchery release information, (2) document historical trends, and (3) quantify population responses (e.g. straying) to differing management actions and environmental conditions to understand the extent to which changing hatchery management practices may affect stock dynamics in a variable and changing climate. Specifically, we examine clustering of release sites across the landscape, and contraction of ocean arrival timings as a function of release date and location, given potential influence on the buffering capacity of the hatchery stock. For example, if all fish were released in a single location impacted by a toxic spill, the entire cohort could perish. The effect would be amplified if the release period were short and coincidental with peak toxicity. We also model straying rates of hatchery fish to assess the importance of release strategy (e.g., transport distance and timing), environmental conditions, and demographic factors on homing behavior, as elevated straying could homogenize the stock and reduce its adaptability. We conclude by synthesizing our results with other related studies, and discuss their implications for stock resilience in a changing climate.

METHODS

Data acquisition, visualization, and storage

The hatchery release database compiled by Huber and Carlson (2015) was updated to include detailed release information for CCV fall-run Chinook Salmon (brood years 1940 to 2016) produced by the federal Coleman National Fish Hatchery on Battle Creek (hereon in, Coleman or COL), and four State hatcheries: Feather River Hatchery (Feather or FEA), Nimbus Fish Hatchery on the American River (Nimbus or NIM), Mokelumne River Hatchery (Mokelumne

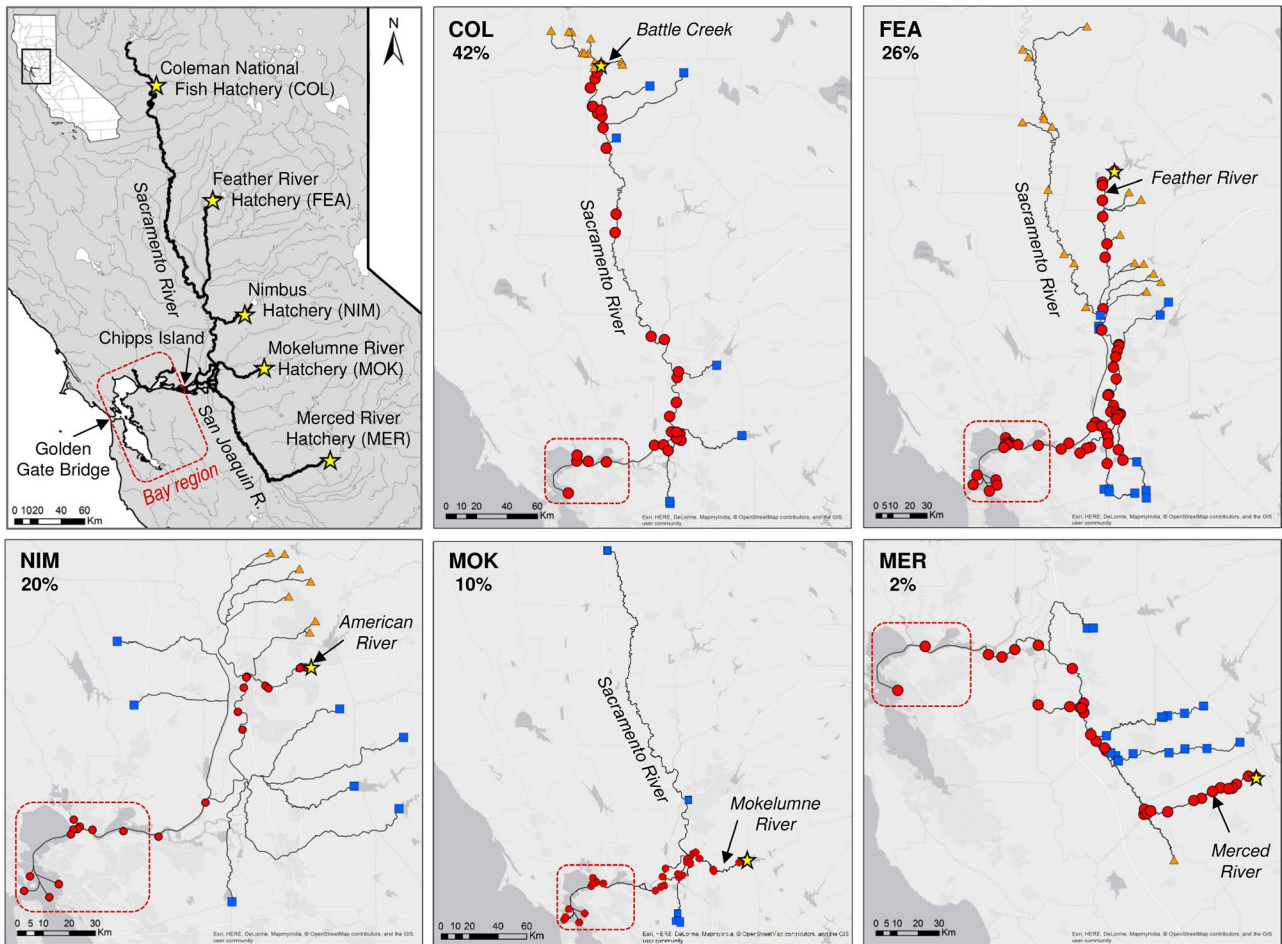


Figure 1. Locations of California Central Valley fall-run Chinook Salmon hatcheries (stars) and release sites, classified as being on likely outmigration routes (circles), on unlikely routes (squares), or upstream of the natal tributary (triangles). Black lines show routes used to measure transport distance (river distance from hatchery to release site). Each hatchery's mean contribution to annual production (for years when all five were in operation) are displayed.

or MOK), and Merced River Fish Hatchery (Merced or MER; Figure 1). Note that the releases in 1941 were from Coleman's precursor, Battle Creek Station. We identified or approximated coordinates using descriptions from annual reports, information stored at the hatcheries, electronic databases, and interviews with current and retired hatchery employees.

All releases are included in the database ($n = 8,088$ release groups, $n = 2,161,711,485$ individuals), but were excluded from further analysis if (1) outside the CCV or beyond the Golden Gate Bridge ($n = 122$ release groups, $n = 8,383,687$ individuals), or (2) terminal (e.g., above an impassable dam or used in laboratory research: $n = 163$ release groups, $n = 3,205,317$ individuals). Research releases that allowed most individuals to continue their seaward migration (e.g., trap efficiency studies) were retained.

Data visualization and storage

We built an interactive map (Available: <https://baydeltalive.com/fish/hatchery-releases>) to visualize historical patterns in release location and salmon abundance using “Shiny” and “Leaflet” packages in R 3.2.5 (R Development Core Team 2015). The database used to create this map and perform the analyses in this paper (including metadata, data sources,

assumptions, and annual summary statistics) can be downloaded from the About tab at the same URL, alongside folders containing hatchery release reports and the shape files used to estimate transport distances (see below).

Transport distance and release site clustering

To explore changes in trucking intensity, we measured transport distance (specifically, the river distance from source hatchery to release site along the most direct migratory route) for every hatchery release site combination using ArcGIS Editor function and National Hydrography Dataset streamlines (Figure 1). Routes were chosen for directness and likelihood of being used, using best scientific judgement and known pathways where possible (e.g., Perry et al. 2013). To explore environmental motives for trucking, we related transport distance to the Sacramento Valley Water Index (Available: <http://cdec.water.ca.gov/cgi-progs/ioidir/wsihist>; also displayed on the Interactive Map), which is based on unimpaired runoff during egg incubation and juvenile rearing (October–July).

To visualize the distribution of hatchery releases across the landscape at different time periods, we produced maps of kernel density estimates (a form of statistical smoothing) of log-transformed numbers of fish using R packages “Leaflet” and “spatstat.” To quantify the degree of clustering (a proxy for

potential vulnerability to patchy or spatially constrained stressors), we calculated the mean Euclidian distance between each pair of release sites each year, weighted by the number of fish released (effectively the mean annual among-fish distance). We fitted linear, cubic, and quadratic relationships between year and among-fish distance in JMP®, Version 13.0 (SAS Institute Inc., Cary, North Carolina, 1989–2019), and included the relationship exhibiting the highest r^2 value in the figure.

Ocean arrival timing

Ocean arrival dates were estimated as release date plus travel time. Travel times were estimated as outmigration distance (river distance from release site to the Golden Gate Bridge) divided by swimming speed. Different life stages exhibit different swimming capabilities, so we classified releases as fry (<70 mm), smolts (70–140 mm), or yearlings (>140 mm), based on fork length (or release timing when size data were unavailable; see Supplemental Methods). While such classifications are somewhat arbitrary, they are commonly used in this system and will be applied hereafter. As fry could undertake extensive freshwater rearing during outmigration, we excluded them from this particular analysis. We also only examined later years (1970–2017), because 1970 marked the point when all hatcheries were in operation and had also started to focus on larger, sea-ready juveniles. Smolt and yearling swimming speeds were estimated using acoustic tagged hatchery fish released across years and hydrologic conditions. See Supplemental Materials and Figure S1 for details and sensitivity analyses.

To explore the influence of trucking on ocean arrival timings, we compared the SD in our estimated ocean arrival dates (incorporating release date and travel time to Golden Gate Bridge) to the SD in release dates alone (effectively assuming that all fish had been released at Golden Gate Bridge, i.e., zero travel time).

Straying rates of hatchery fish

We estimated an index of straying rate (hereafter straying rate) using coded wire tag release and recovery data for the five focus hatcheries, queried from the Regional Mark Information System (Available: www.rmis.org). We limited the analysis to brood years 2006–2012 and escapement years 2008–2015. Brood year 2006 was the first year of the Constant Fractional Marking Program and associated improvements in sampling coverage (Kormos et al. 2012), and 2012 was the last brood year for which age 3 years (dominant return age, typically >60% of the escapement; e.g., Kormos et al. 2012) recoveries were available at the time of analysis. We calculated age at return (run year – brood year) and excluded ages 1 and 5 (0.04% and 0.05% of recoveries, respectively), then calculated a straying rate (S) for tag code i at age j as:

$$S_{i,j} = 1 - \left(\frac{\sum R_{i,j}}{\sum \bar{R}_{i,j}} \right)$$

R being the estimated number of recoveries in the source hatchery or natal river (expanded for the sampling rate in said recovery strata), and \bar{R} being expanded recoveries in any hatchery or spawning ground (note that <1% were recovered outside the CCV). We defined strays as adults recovered on spawning grounds or hatcheries outside their natal stream (i.e., permanent strays; Westley et al. 2013), and measured “donor” stray rates (*sensu* Keefer and Caudill 2014). By this definition, a fish released in a non-natal watershed that returns to the release location

would be considered a stray. See Supplemental Methods and Figure S2 for sensitivity analyses exploring the effect of alternative definitions and data treatments. The final dataset included 117,498 raw recoveries, equating to 296,361 expanded recoveries.

We modeled $S_{i,j}$ for all hatcheries combined, then each hatchery individually, using beta regression with a probit link (betareg R package; Cribari-Neto and Zeileis 2010), weighted to the log-transformed number of coded wire tag recoveries (sensitivity analyses indicated little effect of using alternative weights; Figure S3). Predictors were z-transformed and $S_{i,j}$ linearly transformed ($[S_{i,j} \cdot (n - 1) + 0.5]/n$ where n is the number of $S_{i,j}$ estimates; after Smithson and Verkuilen 2006) to meet model assumptions.

Model terms considered are described fully in Table S1, and the hypotheses governing term choice are largely summarized by Westley et al. (2015). Terms included source hatchery, release region (bay/upstream; Figure 1), transport distance (absolute and scaled between 0 and 1 by hatchery), release day and month, fish size and life stage at release, release group size, run size (combined escapement in natal spawning ground and hatchery for that return year), return age, run year, natal stream flows during release (April–May) and return (October–November) periods (absolute and normalized to each other within year), flow discrepancy (difference between release and return flows), regional temperature at return, Pacific Decadal Oscillation (PDO) during return year (a Pacific climate index associated with salmon demography [Mantua et al. 1997], and homing capabilities [Westley et al. 2015]) and PDO discrepancy (difference between release and return year indices), and number of days the Delta Cross Channel (a water conveyance structure that can facilitate straying between the Sacramento and San Joaquin River Basins [i.e. “interbasin” straying]; Marston et al. 2012) was open in October of the return year. We did not include “release type” because almost all releases were on a typical emigration pathway (i.e., “on-route;” Figure 1) during the experimental period. However, we hypothesize that upstream releases might stray at lower rates for a given transport distance given that these fish must enter or pass their natal stream in order to reach the ocean. Nor did we examine the effect of sex given frequent missing data.

To select the most parsimonious model(s), we used multi-model inference (MuMIn R package; Available: <https://CRAN.R-project.org/package=MuMIn>) and Akaike information criterion for small sample sizes (AIC_c ; Burnham and Anderson 2002). For highly correlated terms (e.g., release size, day, and month), we compared models with terms included in succession using likelihood ratio tests. If multiple models exhibited $\Delta AIC_c < 2$, a final model was selected if it included fewer (or more plausible) terms, and exhibited equal or better performance, as indicated by likelihood ratio tests, reduced collinearity, improved residual structure (homogeneous and normally distributed residuals), and higher pseudo r^2 values (Nakagawa and Schielzeth 2013).

RESULTS

Historical trends: Release location

Over the past 77 years, CCV fall-run hatcheries have shifted from on-site, natal releases to trucking their production increasing distances away from the hatchery (Figure 2; Figure 3; Interactive Map). In the 1960s–1990s, it was unpopular to cull fry that were in excess of the hatchery’s rearing capacity, so large numbers were planted in upstream reaches of non-natal tributaries that do not typically support self-sustaining salmon

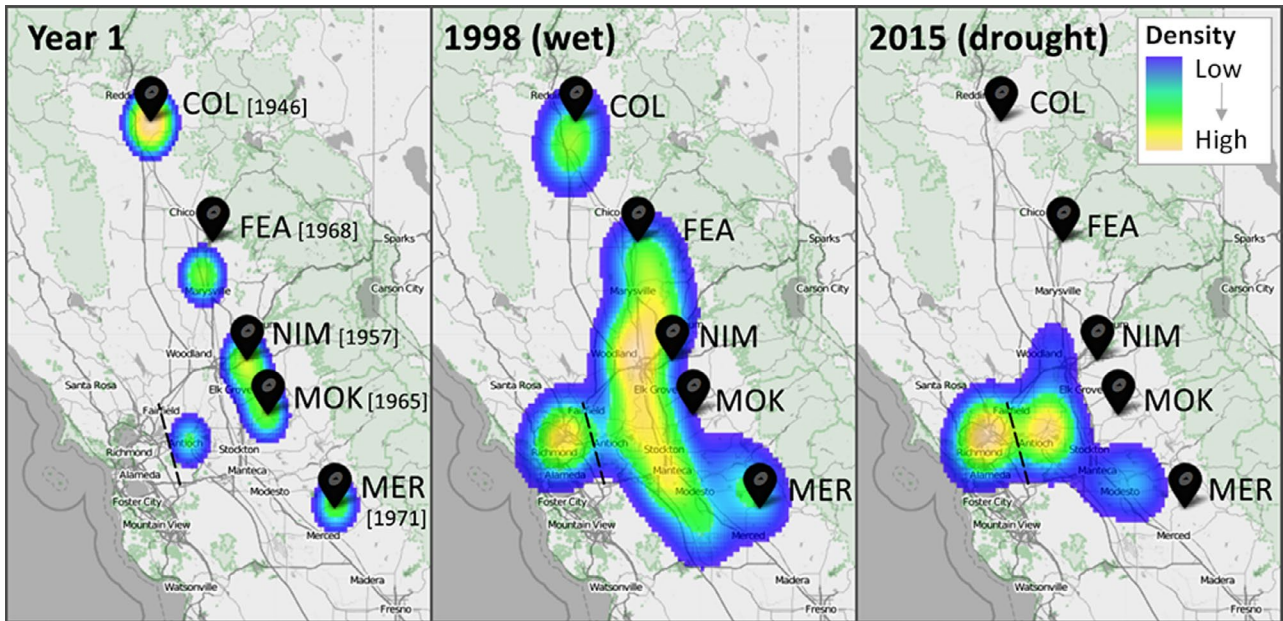


Figure 2. Distributions of hatchery salmon released during years characterized by (1) on-site or natal releases (represented by each hatchery's first release year). Note, Merced River Hatchery [MER] was the only hatchery to release any production outside the natal stream in its first year but did not do so again for another 10 years; (2) non-natal releases (e.g., wet year 1998); or (3) bay releases (e.g., drought year 2015). Bay delineation indicated by a dashed line. COL = Coleman National Fish Hatchery, FEA = Feather River Hatchery, NIM = Nimbus Hatchery, MOK = Mokelumne River Hatchery.

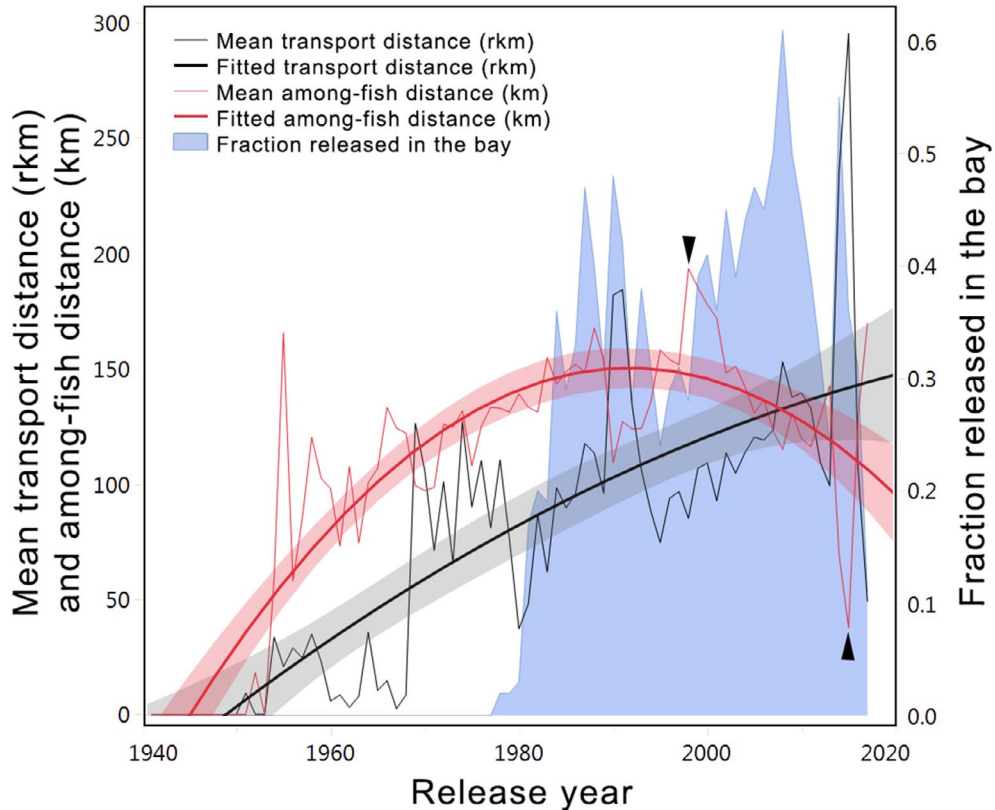


Figure 3. Historical changes in mean transport distance, among-fish distance, and the fraction of fish released in the bay (see inset key). All releases from 1941–1951 were from Coleman National Fish Hatchery (i.e., transport and among-fish distances = 0 km). Arrows indicate years highlighted in Figure 2. Fits \pm 95% CI (shaded area): Transport distance = $58.63(\text{year}) - 0.014(\text{year}^2) - 60,134$ ($r^2 = 0.62$); Among-fish distance = $274.7(\text{year}) - 0.069(\text{year}^2) - 273,438$ ($r^2 = 0.73$).

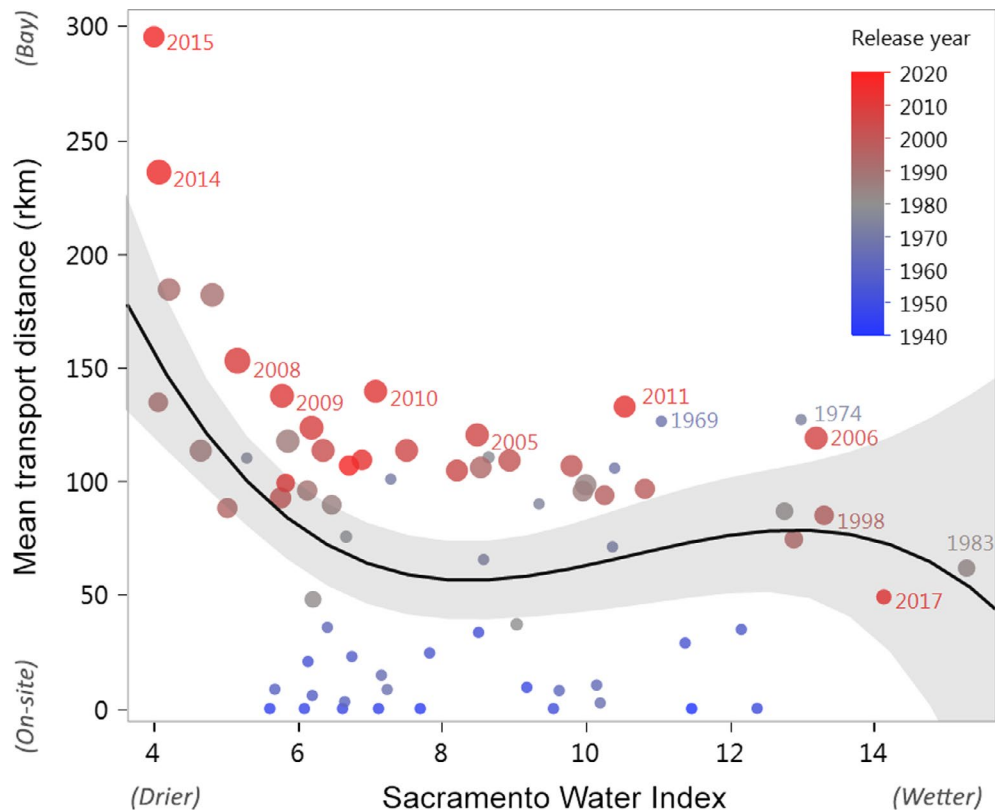


Figure 4. Transport distance (river distance between source hatchery and release site) as a function of environmental conditions (Sacramento Water Index [SWI] based on runoff during salmon incubation and rearing). Circles colored by release year (inset key) and sized according to the fraction released in the bay. Fit (thick line) \pm 95% CI (shaded area): Transport distance = $554 - 151.8(\text{SWI}) + 14.94(\text{SWI}^2) - 0.468(\text{SWI}^3)$ ($r^2 = 0.22$, or $r^2 = 0.55$ excluding years before 1980).

populations (R. Reynolds, retired California Department of Fish and Wildlife [CDFW], personal communication). Since 1980, trucking of hatchery smolts directly to the bay has become increasingly common (Figure 3), particularly for the larger state-operated hatcheries (>80% of Nimbus and Feather production in 2000–2015; Figure S4). This has resulted in mean transport distance generally increasing through time to its peak during the 2014–15 drought, although there was a large decrease in the historically wet year of 2017 ($\bar{X}_w = 236\text{--}295$ river kilometers [rkm] in 2014–2015 vs. 49 rkm in 2017; proportion released in the bay = 36–55% vs. 11%, respectively; Figure 3). These alternate release strategies (natal vs. non-natal vs. bay) resulted in increasing spatial diversity until the late 1990s, then increasing clustering, particularly during drought years (mean among-fish distance = 193 km in 1998 vs. 38 km in 2015 when >99% of production was released within ~20 km of the bay; Figure 2).

Coleman Hatchery typically releases on-site given known propensity for their trucked fish to stray (Niemela 1996), but as they account for approximately half of total fall-run production across all five hatcheries, their decisions have a large effect on overall trends. Sudden increases in transport distance occurred when Coleman (and other hatcheries) employed “emergency trucking” during recent droughts (1991–92, 2007–09, 2014–15). Emergency trucking was also employed following a precipitous decline in salmon returns in 2008–2009 (Carlson and Satterthwaite 2011), with 2008–2011 exhibiting higher transport distances and a higher fraction of bay releases than previous years featuring similar precipitation

levels (Figure 4). If releases pre-1980 (when bay releases began) are excluded, the relationship between transport distance and the Sacramento Water Index was more than twice as strong ($r^2 = 0.22$ vs. 0.55), with fish transported approximately 100 rkm further for a given set of flow conditions in the latter part of the time series.

Historical trends: Ocean arrival timing

Over the past 77 years, release timings have become increasingly restricted as fry and yearling releases have been gradually phased out. The SD in release dates and the fraction of fish released as smolts for three major periods (1941–69, 1970–99, 2000–17) were 91, 69, and 26 days (Figure S1), and 20, 54, and 96%, respectively. Since 1970, estimated ocean arrival timings have also narrowed (Figure 5). However, the exclusion of fry from this particular analysis (which were more prevalent during the first part of the analysis) means that the actual change in the spread of ocean arrival dates was almost certainly more extreme.

By incorporating release location into ocean arrival estimates, the spread in arrival timings was greater than the spread in release timings alone, suggesting that diversity in release locations can provide additional temporal buffering. However, the effect was marginal and only observed in the first decade of the analysis (Figure 5; note how the red envelope is only narrower than the gray envelope in the 1970s). Following onset of bay releases in 1980 (Figure 3), most years exhibited the opposite effect. We are confident that potential bias caused by using a static swimming speed was minimal, given that salmon >70 mm are likely to be

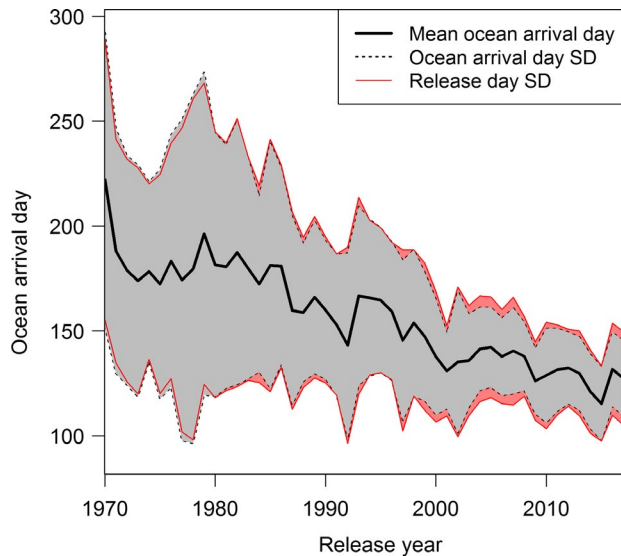


Figure 5. Annual mean (thick black line) \pm 1 SD (grey area/dashed lines) ocean arrival day, weighted by the number of fish released from all hatcheries between 1970 and 2017. Weighted SD in release day shown by red area/thin line. Fry (<70 mm) were excluded due to potential for extended freshwater rearing (i.e., uncertain travel times), but were included in release day plots (Figure S1).

sea-ready and can migrate the 518 rkm from Coleman to Golden Gate Bridge in a matter of weeks (mean \pm SD = 17.9 ± 5.5 days, $n = 17$), when release dates typically varied on the order of months (see also Supplementary Methods).

Straying rates of hatchery fish

Observed mean straying rates were highest for the southernmost hatcheries in the San Joaquin Basin (Mokelumne, Merced), intermediate for the northernmost hatcheries (Coleman, Feather), and lowest for Nimbus on the American River (Table 1). On-site releases (here defined as ≤ 5 rkm from the hatchery) yielded straying rates ranging from 0.3% (Nimbus) to 9.1% (Coleman; Table 1). Straying rates did not exhibit a simple relationship with return distance (river distance from the ocean to the hatchery), overall or for on-site releases, with Mokelumne exhibiting relatively high straying rates despite being closest to the bay (Table 1). Overall, most strays were recovered in the same basin as their source hatchery and/or the adjacent tributary (Mokelumne to the American River and vice versa; Table 1). Straying rates were 9 (Mokelumne) to 26 (Nimbus) times higher for bay releases than on-site releases (mean = 15; Table 1), but this appeared to relate to transport distance rather than a saltwater effect per se, with freshwater releases just upstream of the bay yielding similar straying rates (Figure 6).

Our final model explained 47% of the variance in straying rate for all hatcheries combined, with transport distance, run year, return age, flow discrepancy, and release group size exhibiting positive effects, and natal stream flow during the return period, return year PDO index, and release month exhibiting negative effects (Figure S5; Table S2). The model also included a significant interaction between hatchery and transport distance, with transport distance consistently positively related to straying rate (Table S2; Table S3), but more strongly for hatcheries on smaller watersheds (Merced, Mokelumne, Coleman; Figure 6). Most of the variance in straying was explained by transport distance, natal stream flow during the

Table 1. Mean straying rates with SD for all releases, bay releases, and on-site releases (defined as <5 river kilometers [rkm] from hatchery) for brood years 2006–2012 and return years 2008–2015. We calculated straying rates for each tag code then weighted summary statistics by the raw number of recoveries for each tag code. Note that the distance from Chipps Island to Golden Gate Bridge (“bay,” Figure 1) is 73 rkm. Typically, out of basin recoveries are represented by salmon reared in hatcheries in the Sacramento River Basin that were recovered in the San Joaquin River Basin, and vice versa, but they also include a small number (<1%) of fish recovered in Washington state. RBDD = Red Bluff Diversion Dam.

Source hatchery	Distance from hatchery to the bay (Chipps Island) (rkm)	Weighted mean straying rate (all releases) \pm SD	Weighted mean straying rate (on-site releases only) \pm SD	Weighted mean straying rate (bay releases only) \pm SD	Fraction of strays recovered out of basin (all releases)	Fraction of strays recovered out of basin (bay releases only)	Three most popular stray-into sites (proportion of strays)		
Coleman	445	13.2% \pm 18.3%	9.1% \pm 5.5%	88.8% \pm 4.1%	4%	8%	Sacramento River above RBDD (35%)	Feather River (13%)	Clear Creek (12%)
Feather	239	16.6% \pm 10.3%	N/A ^a	18.6% \pm 20.1%	4%	4%	Sacramento River above RBDD (44%)	Yuba River (16%)	Clear Creek (14%)
Nimbus	138	3.6% \pm 3.9%	0.3% \pm 0.3%	6.6% \pm 3.6%	57%	70%	Mokelumne River Fish Hatchery (33%)	Yuba River (18%)	Mokelumne River (8%)
Mokelumne	133	38.1% \pm 11.0%	5.8% \pm 1.2%	53.9% \pm 8.8%	53%	73%	American River (23%)	Stanislaus River (21%)	Nimbus Fish Hatchery (21%)
Merced	270	72.1% \pm 18.0%	6.4% \pm 6.2%	77.0% \pm 4.0% ^b	37%	37% ^b	Mokelumne River Fish Hatchery (25%)	Stanislaus River (20%)	Nimbus Fish Hatchery (14%)

^aFeather Hatchery did not release any tagged fish on-site (or anywhere in the natal watershed) during the study period, but their closest releases (123 rkm downstream) produced a weighted mean straying rate of 0.089 ± 0.144 SD.

^bMerced Hatchery performed no bay releases during this period so we report their stray rates for nearby releases at Jersey Point (approximately 20 rkm upstream of Chipps Island).

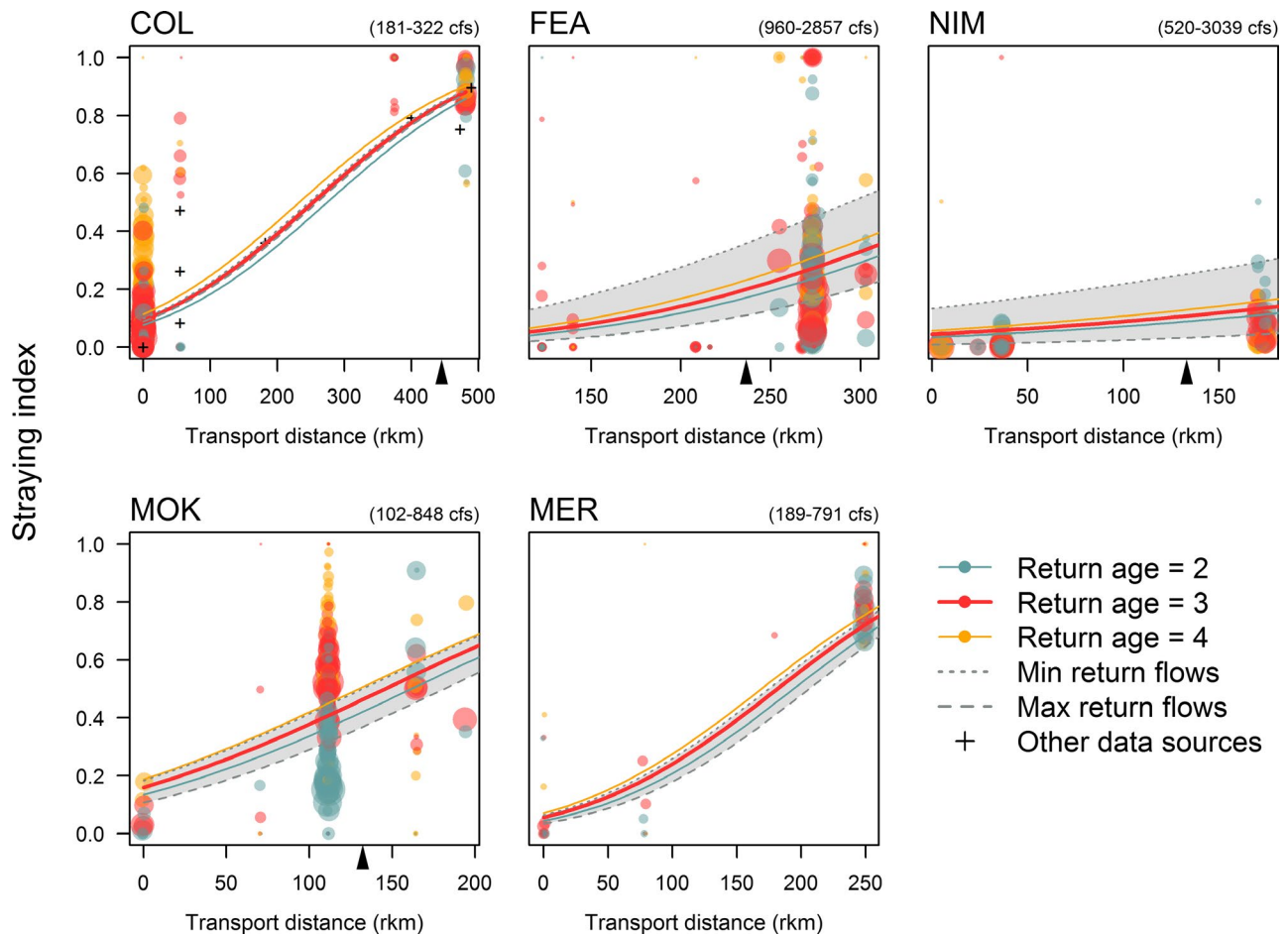


Figure 6. Observed (circles) and predicted (lines) straying indices of California Central Valley hatchery fish as a function of transport distance and return age (other covariates averaged; see Table S2). Indices based on coded wire tag recoveries from brood years 2006–2012 (this study; circles) and 1980–1991 (Niemela 1996; crosses). Circles sized by the logged number of tag recoveries (also used to weight model). Predicted straying rates for 3-year-old fish at minimum and maximum natal stream flows in return years 2008–2015, displayed above each plot. River distance from each hatchery to the bay indicated by an arrow (note, Merced River Hatchery [MER] did not perform bay releases during the years examined). COL = Coleman National Fish Hatchery, FEA = Feather River Hatchery, NIM = Nimbus Hatchery, MOK = Mokelumne River Hatchery.

return period, age, hatchery, and the hatchery by distance interaction. A simpler model using only these terms produced a similar fit ($r^2 = 46\%$), but substantially lower performance ($\Delta AIC_c = 84.6$). The effect of natal stream flows was strongest for off-site releases (Figure 6; Figure S6) and for the hatcheries closest to the bay (Mokelumne, Feather, Nimbus; Figure 1). Older fish were associated with larger differences between release and return flows (Figure S7), and both metrics were associated with increased straying (Figure 6; Table S2). Straying rates (weighted to the logged number of tag recoveries) averaged 18.7, 23.3 and 27.0% for 2-, 3- and 4-year-old fish, respectively, and 4.5, 7.2, and 13.6% for on-site releases only, respectively. Our model tended to overestimate straying rates for on-site releases, but corresponded well with previous estimates for Coleman based on different methods and brood years (Niemela 1996; Figure 6).

DISCUSSION

Fall-run Chinook Salmon in the CCV represent an acute example of the issues facing anadromous fishes worldwide, particularly those in fragmented river systems where active

transport of fish is increasingly being contemplated. Increased downstream transportation of CCV hatchery production reflects efforts to reduce mortality during outmigration through hot, degraded waterways inhabited with predatory fishes (SFEI-ASC 2014). The goals and spatial extent of the trucking program have shifted through time, with the 1970s–1990s dominated by fry releases spread broadly across the landscape, particularly in wet years accompanied by increased instream carrying capacity and passage connectivity, and the 2000–2010s dominated by smolt releases in and around the bay. Emergency trucking has been increasingly deployed as a tool to improve survival rates during droughts (e.g., 2014–2015), and aid recovery post-collapse (2008–2011). While rigorous comparisons of survival rates that isolate effects of trucking from other confounding factors are limited, the available data suggest that trucked releases tend to have higher recovery rates (Kormos et al. 2012), indicating some benefit of trucking for boosting mean abundance. However, our analyses suggest that since trucking to the bay began in the 1980s, the shorter outmigration distances have resulted in decreased temporal buffering. Upstream releases are also associated with greater opportunity

for differences in individual behavior (e.g. swimming ability and rearing propensity) to accumulate and broaden ocean arrival timings. Overall, today's CCV hatchery portfolio has been greatly simplified, exhibiting reduced variation in fish size, age, and stage at release (Huber and Carlson 2015), release location, and release dates. The main implications associated with these changes in hatchery practices are discussed below.

Implication 1 – Match–mismatch dynamics and volatile recruitment

Match–mismatch refers to the phenomenon of a population experiencing favorable (match) or unfavorable (mismatch) environmental conditions during critical life stages or habitat transitions, resulting in high or low recruitment rates, respectively (Satterthwaite et al. 2014). For example, cohort failure can occur if juvenile salmon enter the ocean over a narrow period of time that is mismatched with peak prey production. In recent years, CCV hatchery release dates and ocean arrival timings have become increasingly constricted, with most production now released in early May as rapidly grown smolts. California has a variable and increasingly unpredictable climate (Dettinger 2011; Swain et al. 2018), resulting in large spatiotemporal shifts in ocean upwelling dynamics and food availability for juvenile salmon once they reach the ocean (Satterthwaite et al. 2014). Thus, if the spread of ocean arrival dates remains constricted, match–mismatch theory predicts increasingly volatile recruitment of hatchery stocks.

We hypothesized that upstream releases would buffer recruitment variability by increasing the spread in travel times and ocean arrival dates. There was only marginal support for this hypothesis from smolt and yearlings released in the 1970s. Since the 1980s, variation in estimated ocean arrival dates tended to be lower than variation in release dates alone, suggesting increasing coordination of location and timing in hatchery release schedules. Indeed, in-river releases tend to be earlier than bay releases to try to avoid warmer upstream temperatures (J. Smith, U.S. Fish and Wildlife Service, personal communication).

We only included larger, sea-ready juveniles in this analysis, as smaller “fry” releases could exhibit significant differences in swimming speeds and rearing behaviors. Fry also tended to be released further upstream and across a broader array of habitats, diversifying growth opportunities (Sommer et al. 2001) and further increasing potential variation in their travel times. Given that fry represented 38% of the fish released in 1970–1999, but only 4% of the fish released in 2000–2017, their exclusion from Figure 5 means that the actual contraction in ocean arrival timings was almost certainly more substantial than implied, leaving CCV fall-run hatchery salmon vulnerable to match–mismatch events and swings in recruitment (Satterthwaite et al. 2014).

The economic and ecological implications of match–mismatch events are serious. While additional factors may have played a role, there is evidence that adult abundance has been less stable in recent years (Satterthwaite and Carlson 2015). Willmes et al. (2018) provide additional evidence that hatchery fish experienced lower survival than natural-origin fish (which emigrated over a broader window of time) when delayed upwelling led to the 2008–2009 stock collapse.

Implication 2 – Homogenization (and loss of hatchery broodstock) via elevated straying

Straying rates for on-site releases (hatchery means = 0.3–0.1%; Table 1) were fairly typical for this species (Quinn 1993;

Westley et al. 2013), but they exceeded 80% for many off-site releases. The fitness consequences of such high straying rates depend partly on the extent to which salmon exhibit assortative mating behavior (Quinn 1993), and partly on the relative abundance of natural- and hatchery-origin fish in a given year. However, they have almost certainly contributed to the genetic and demographic homogenization of today's fall-run stock (Williamson and May 2005; Dedrick and Baskett 2018). Elevated straying can impede the ability of populations to adapt to local stream conditions and reduce fitness (Araki et al. 2008). It can also contribute to hatcheries recovering insufficient broodstock to meet production goals, as observed at Coleman in 2017 (J. Smith, U.S. Fish and Wildlife Service, personal communication), 2 years after they trucked all their production downstream during the historic drought.

In our model, the terms that most strongly influenced straying rate were transport distance, natal stream flow during the return period, return age, and flow discrepancy. A positive effect of run year also suggests net increases in straying rates that are not explained by the other covariates, but individual models suggest this was driven by only two of the hatcheries (Table S3). Model outputs should be interpreted with caution, as we examined relatively few years, and release strategies were generally designed for production over hypothesis testing (e.g., >97% of Feather Hatchery production was released in the bay). We restricted our analysis to years following the implementation of constant fractional marking and the accompanying efforts to improve sampling coverage (Kormos et al. 2012). There are still potential inaccuracies in our straying estimates. However, it is reassuring that the indices we estimated for Coleman were nearly identical to those previously estimated using different methods and cohorts (Niemela 1996; Figure 6).

Higher transport distances were strongly associated with increased straying, presumably due to the elimination of olfactory waypoints (e.g., stream odors and junctions) that would have otherwise helped the individual navigate home (Pascual et al. 1995; Bond et al. 2017). The effect was positive and significant for all populations, reflecting studies across a range of systems and species (Solazzi et al. 1991; Pascual et al. 1995; Lasko et al. 2014). However, effect strength varied among hatcheries, and straying rates of on-site releases did not exhibit a simple relationship with return distance, suggesting the importance of untested factors such as route complexity, water chemistry, and the number and quality of alternative habitats along the migratory path (Quinn 1993).

The importance of natal stream flow is suggested by the large difference in straying rate for a given transport distance among watersheds of differing size, with higher flows during the return period associated with lower straying rates. Returning adults orientate using a combination of rheotaxis and olfaction (Keefer et al. 2006), and thus reduced flows could be associated with greater loss of olfactory cues. These patterns suggest that fall attraction flows could be a useful tool to reduce straying rates, already demonstrated in practice by Mokelumne (Del Real and Saldate 2014). However, for the two hatcheries furthest from the bay (Coleman and Merced), stream flows during the return period were slightly positively related to straying rate (Table S3), suggesting local effects of flow-related factors such as temperature. Coleman and Merced are also located on smaller watersheds with limited reservoir capacities, and due to water diversions and exports, little to none of the Merced River reaches the estuary in most years (Marston et al. 2012). Thus,

the success of attraction flows to improve salmon homing rates will likely vary by watershed and year.

Return age, flow discrepancy (difference between release and return natal stream flows), and straying rate were all correlated, although flow patterns varied among watersheds (Figure S7). As observed in other systems and species, older returns were more likely to stray, given diminished olfactory memories and/or larger environmental changes along their migratory path (Quinn 1993; Dittman and Quinn 1996). In the CCV, the combined effect of variable precipitation patterns and extensive water transfers (Grantham and Viers 2014; Cid et al. 2017) likely alter the location and strength of olfactory waypoints through time (Dittman and Quinn 1996), resulting in increased straying of older fish.

We also detected a weak effect of release month, suggesting that trucking salmon too early could disrupt natal imprinting. With few fry and yearling releases during the experimental period, we could not adequately test for differences in straying among life history types, but multiple studies have suggested that individuals that leave their natal tributary early stray at higher rates (Pascual et al. 1995; Hamann and Kennedy 2012). Thus, potential advantages (e.g., temporal buffering) of fry releases should be considered against potentially lower survival and homing rates. In case of non-linear responses to release timing (e.g., Pascual et al. 1995), we tried fitting generalized additive models, but many trends appeared implausibly multimodal, leading to concerns about overfitting the data. Release group size was also only weakly related to straying rate, suggesting potential density dependent and/or collective navigation effects (Westley et al. 2015; Berdahl et al. 2016). Similar to Westley et al. (2015), mean PDO during the return year was negatively associated with straying, but the effect was weak and not observed in individual models, suggesting that in this system, local processes may influence homing more than large-scale climate forcing.

Implication 3 - Influence of trucking on the imbalance between hatchery and natural stocks

Releasing large numbers of rapidly grown hatchery fish every year has created numeric and competitive imbalances between natural and hatchery stocks (Rand et al. 2012). The “hatchery advantage” is increased when freshwater conditions are warm and deteriorated, resulting in greater selection against natural populations during rearing. Trucking hatchery fish further augments this survival advantage by avoiding selection during outmigration. The net result is demonstrated by the dominance of hatchery fish in both fisheries and natural spawning grounds, even in rivers without hatcheries (Kormos et al. 2012). The movement of hatchery fish into natural spawning areas has likely helped to augment and sustain natural populations during periods of low recruitment (Johnson et al. 2012; Willmes et al. 2018), but may have also masked declines in natural stocks (Johnson et al. 2012). Furthermore, while the fitness consequences of such high exchange between hatchery and natural stocks have yet to be quantified in this system (Williamson and May 2005), studies from elsewhere suggest that they could be significant (Araki et al. 2008).

The future: Management tools and lessons learned

If current trends continue and climate change projections bare true (Cloern et al. 2011), CCV Chinook Salmon populations will become increasingly synchronous, unstable, and dominated by hatchery fish. Avoiding this relies on reducing

straying rates of hatchery salmon and increasing the numbers (or survival) of natural stocks. Releasing hatchery fish further upstream and increasing numbers of naturally out-migrating salmon could improve homing rates, as pheromones from conspecifics can provide navigational cues when olfactory imprinting has been impaired (Hierarchical and Collective Navigation Hypotheses; Bett and Hinch 2015; Berdahl et al. 2016). Other potential tools include allowing salmon to begin natural outmigration, then trucking them once they have passed critical olfactory waypoints (Bond et al. 2017), recirculating water during transport to improve sequential imprinting (e.g., barging; Keefer and Caudill 2014), and/or providing attraction flows via reservoir releases during return migration (Keefer et al. 2006). To improve the fitness and abundance of natural stocks, potential management actions include habitat restoration, physical exclusion of hatchery fish from natural spawning grounds (e.g., segregation weirs), and/or selective or terminal fisheries (California HSRG 2012). While regional coordination is important, given environmental and demographic differences among watersheds, actions should be designed and monitored on a population-specific basis.

Environmental stochasticity is the hallmark of California’s Mediterranean climate (Dettinger 2011; Cid et al. 2017), but with increasing volatility on the horizon (Cloern et al. 2011; Swain et al. 2018), and increasing dependence on hatchery supplementation (Kormos et al. 2012), questions clearly remain about how to balance short-term (e.g., abundance) vs. long-term (e.g., stability) goals. While trucking appears to be an effective tool for supplementing the fishery in a given year (Niemela 1996; Kormos et al. 2012), accompanying tradeoffs such as increased straying, competition, and sensitivity to match-mismatch dynamics should be scrutinized given lasting genetic, demographic, and economic consequences. Management actions that promote the genetic and demographic recovery of natural stocks, and increase trait diversity in both hatchery and natural stocks would be predicted to improve the long-term viability of these southernmost populations and help avoid future fishery closures (Schindler et al. 2010; Satterthwaite and Carlson 2015).

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SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article. 