

Weakening portfolio effect strength in a hatchery-supplemented Chinook salmon population complex

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Abstract: Biocomplexity contributes to asynchronous population dynamics, buffering stock complexes in temporally variable environments, a phenomenon referred to as a “portfolio effect”. We previously revealed a weakened but persistent portfolio effect in California’s Central Valley fall-run Chinook salmon (*Oncorhynchus tshawytscha*), despite considerable degradation and loss of habitat. Here, we further explore the timing of changes in variability and synchrony and relate these changes to factors hypothesized to influence variability in adult abundance, including hatchery release practices and environmental variables. We found evidence for increasing synchrony among fall-run populations that coincided temporally with increased off-site hatchery releases into the estuary but not with increased North Pacific environmental variability (measured by North Pacific Gyre Oscillation), nor were common trends well explained by a suite of environmental covariates. Moreover, we did not observe a simultaneous increase in synchrony in the nearby Klamath–Trinity system, where nearly all hatchery releases are on-site. Wavelet analysis revealed that variability in production was higher and at a longer time period later in the time series, consistent with increased environmental forcing and a shift away from dynamics driven by natural spawners.

Résumé : La biocomplexité participe à une dynamique asynchrone des populations, limitant les variations au sein des complexes de stocks dans les milieux variables dans le temps, un phénomène appelé « effet portefeuille ». Nous avons déjà fait état d’un effet portefeuille affaibli, mais persistant chez les saumons quinnats (*Oncorhynchus tshawytscha*), à montaison automnale de la vallée centrale de Californie, malgré la dégradation et la disparition considérables d’habitats. Nous examinons plus en profondeur le moment des modifications de la variabilité et de la synchronie et les relient à des facteurs présumés influencer la variabilité de l’abondance des adultes, dont les pratiques de lâcher des écloséries et des variables environnementales. Nous observons des indices d’une synchronie croissante dans les populations à montaison automnale qui coïncide dans le temps avec une augmentation des lâchers d’écloséries hors site dans l’estuaire, mais non avec une variabilité accrue du milieu nord-pacifique (mesurée par l’oscillation du tourbillon nord-pacifique); en outre, un ensemble de covariables environnementales n’explique pas bien des tendances répandues. De plus, nous n’observons pas une augmentation simultanée de la synchronie dans le système voisin de Klamath–Trinity, où presque tous les lâchers d’écloséries se font sur place. L’analyse des ondelettes révèle que la variabilité de la production est plus grande et présente une plus longue période plus tard dans la série chronologique, ce qui concorde avec un forçage environnemental accru et une dynamique de moins en moins contrôlée par les géniteurs naturels. [Traduit par la Rédaction]

Introduction

Environmental stochasticity drives variation in ecological dynamics within natural systems (May 1972). In coupled human–natural systems such as fisheries, decoupling this natural environmental variation from human-induced changes to populations is central to resource management. Diversity and heterogeneity comprise key characteristics that determine the resilience of ecological systems to environmental variation and change (Luck et al. 2003; Levin and Lubchenco 2008). In addition, biodiversity across multiple ecological scales, from genes to ecosystems, plays a critical role in the sustainable delivery of ecosystem services (e.g., Tilman and Downing 1994; Luck et al. 2003; Worm et al. 2006).

One often overlooked component of biodiversity is the phenotypic diversity found within and between populations of a given species, or biocomplexity (sensu Hilborn et al. 2003). Recent research has revealed that biocomplexity — particularly a diversity of life histories among populations — contributes to asynchronous populations dynamics, which buffers the complex in a tem-

porally heterogeneous environment (Hutchinson 2008; Rogers and Schindler 2008; Schindler et al. 2010; Yates et al. 2012). Such variance buffering of complex ecological systems has been described as a portfolio effect (PE; Doak et al. 1998; Schindler et al. 2010), borrowing on concepts from financial portfolio theory (Markowitz 1952; Koellner and Schmitz 2006).

The quintessential work on the biocomplexity in fisheries is that done on the sockeye salmon (*Oncorhynchus nerka*) stocks in Bristol Bay, Alaska (Schindler et al. 2010). This fishery is considered sustainable, and recent research has revealed evidence of biocomplexity among (Hilborn et al. 2003) and within (Rogers and Schindler 2008) the major fishing stocks. In stark contrast with Bristol Bay’s diverse and productive salmon fishery and other high latitude stocks with limited anthropogenic impact to freshwater habitat is California’s Central Valley fall-run Chinook (CVC) salmon (*Oncorhynchus tshawytscha*) stock complex (Griffiths et al. 2014). The Central Valley freshwater habitat is highly regulated and modified, and recent work suggests that the fall-run populations breeding in the different river systems are now genetically

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indistinguishable (Williamson and May 2005), in contrast with other studied salmon complexes that exhibit geographic structuring (e.g., Habicht et al. 2007), and that hatchery-produced fish contribute the majority of total production (Barnett-Johnson et al. 2007; Kormos et al. 2012; Mohr and Satterthwaite 2013; Palmer-Zwahlen and Kormos 2013).

California's CVC salmon populations, which support much of the ocean Chinook salmon fishery in California and Oregon (Lindley et al. 2009; Satterthwaite et al. 2015), have been impacted by various anthropogenic activities (e.g., habitat loss, hatcheries, harvest, water diversions), all of which have likely contributed to the erosion of biocomplexity. For example, hatcheries might dampen buffering effects by either synchronizing dynamics or homogenizing traits. In the Central Valley, a large-scale trucking program transports a variable proportion of fish from the five hatcheries to the San Francisco Estuary or directly to the ocean (California HSRG 2012; Huber and Carlson 2015). This program is designed to increase survival of the hatchery fish by bypassing mortality during the smolt outmigration (California HSRG 2012). An unintended consequence of this release practice is an increase in straying of adult hatchery fish to other rivers (Kormos et al. 2012; California HSRG 2012), likely due to disruption in imprinting during outmigration, important for successful return navigation to their birthplace. Natural stray rates are typically 3%–5% (Quinn 2005), whereas straying rates of transported fish can be as high as 80% and tend to increase with distance transported (CDFG–NOAA 2001). We hypothesize that transport-induced straying may be synchronizing dynamics among populations with and without hatcheries.

Such synchronization would be expected to reduce the strength of PE-induced buffering in the Central Valley. When Carlson and Satterthwaite (2011) analyzed a 52-year time series of CVC production for evidence of PEs, they noted that PE-induced buffering did remain in the system but that variability (as measured by coefficient of variation, CV, in aggregate production) was greater in the second half of the dataset (years 1983 to 2007), noting that synchrony (measured as mean pairwise correlation among rivers) was greater in the second half of the dataset while evenness was comparable in both halves. They did not explore the precise timing of these changes nor did they test evidence of the underlying mechanisms. Although it has been suggested that the CV may not always be a good metric of PE strength because of the allometric scaling of population variance with mean population size (Anderson et al. 2013), the same study found that salmon variance typically scaled with the square of population size, making the CV an appropriate metric for salmon systems.

Here we further the analyses of Carlson and Satterthwaite (2011) by (i) exploring the timing of the previously documented weakening of the PE in CVC and (ii) evaluating evidence for hatchery release practices and environmental factors that might contribute to portfolio weakening, by combining newly compiled data on hatchery production and release practices as well as additional statistical approaches. We hypothesize that increasing off-site releases of hatchery production into the estuary (or rarely directly into the ocean, hereinafter “estuary releases”) could increase variability and synchrony both through increasing demographic connectedness through straying (CDFG–NOAA 2001) and through increased sensitivity to temporal matches or mismatches with food availability due to constrained ocean entry timing (Satterthwaite et al. 2014a). We use wavelet analyses (Cazelles et al. 2008) and rolling windows (Moore et al. 2010; Krkosek and Drake 2014) to identify the timing of changes in the variability of Central Valley production and the synchrony of its component rivers. We compare this with the timing of changes in total hatchery production and the proportions of fish released into the estuary based on recently compiled data available in Huber and Carlson (2015). Additionally, we use maximum autocorrelation factor analysis (MAFA; Fujiwara 2008) to identify common trends among rivers

and explore relationships with hatchery practices and (or) environmental covariates, including sea surface temperature, March coastal upwelling, wind stress curl in spring (Wells et al. 2008), and the winter and spring North Pacific Gyre Oscillation (NPGO). We compare the timing changes in Central Valley fall-run synchrony with the timing of changes in ocean environmental variability as measured by the NPGO, the increased variability of which has been implicated in increased variability of the ocean ecosystem off California (Sydeman et al. 2013) and increased synchrony in the survival of Chinook and coho (*Oncorhynchus kisutch*) salmon released from hatcheries (Kilduff et al. 2015). We also explore temporal changes in evenness and the proportion of Central Valley production accounted for by each river to account for the possibility that major changes in productivity of individual rivers could change system evenness and thus the strength of the PE (Doak et al. 1998). Several lines of evidence suggest a role of estuary releases in weakening PE strength in this system. Finally, as a quasi-control, we test whether a simultaneous increase in synchrony occurred in the nearby Klamath–Trinity fall-run Chinook stock complex, where nearly all hatchery production is released upstream (California HSRG 2012).

Methods

Study system

Chinook salmon are semelparous, anadromous fish breeding in rivers of the northern Pacific Ocean, primarily distributed in the eastern Pacific from Alaska in the north through central California in the south. Historically, Chinook salmon breeding in California's Central Valley displayed extraordinary life history diversity (e.g., Fisher 1994; Yoshiyama et al. 2000; Williams 2006). While this stock complex includes four distinct breeding migrations or “runs” (fall, late fall, winter, and spring), it is currently dominated by the fall run. Moreover, each run was historically composed of several distinct subpopulations, each breeding in specific geographic locations in the Central Valley and exhibiting differences in life history characteristics such as juvenile rearing strategies and spawn timing (Yoshiyama et al. 2000; Lindley et al. 2007). Dam construction contributed to a rapid loss of Central Valley winter-run and spring-run Chinook (now federally endangered and threatened, respectively), because of a lack of access to historical spawning areas and habitat modifications. To mitigate for these effects, five hatcheries were established to propagate fall-run Chinook salmon, which naturally breed in low-elevation reaches of large rivers (Moyle 2002). Recent work suggests that the fall-run populations breeding in the different river systems are now genetically indistinguishable (e.g., Williamson and May 2005), likely due to a long history of movement of individuals (gametes) among hatcheries as well as considerable and ongoing straying of hatchery-produced fish as adults (CDFG–NOAA 2001). Chinook salmon mature at a range of ages, with CVC most often returning to spawn at age-3, with lesser contributions of age-2 and age-4 spawners and negligible contributions from older age classes (O'Farrell et al. 2013). By convention, California fall-run Chinook have an assumed 1 September birthday (O'Farrell et al. 2010), which corresponds to the return of adult spawners rather than juvenile emergence. For months earlier than September in the calendar year, and for returning spawners, ages are calculated as the calendar year minus the brood year (the year in which the parents spawned in the fall). Hatchery releases and natural outmigrations of juvenile fall-run Chinook in this system typically occur in the spring of the calendar year following the brood year; thus, age-3 fish return to spawn 2 years after their release or outmigration year.

The Klamath–Trinity basin in northern California is the second largest Chinook salmon population complex in California and the only other major contributor to California ocean salmon fisheries (Satterthwaite et al. 2015). There are two hatcheries in the system,

both of which release all of their production on-site, with minor exceptions in the 1980s (California HSRG 2012).

Data sources

We obtained estimates of river-specific production (spawning escapement and in-river harvest plus estimated harvest of fish that would have returned to each river, assuming ocean harvest of CVC is proportionately distributed among fish from each river relative to their returns) of fall-run Chinook from the CHINOOKPROD dataset, maintained by the US Fish and Wildlife Service's Anadromous Fish Restoration Program (<http://www.fws.gov/stockton/afnp>). This dataset reflects combined natural area and hatchery production and sums production for both natural spawning areas and hatcheries (see Carlson and Satterthwaite 2011 for discussion of the details of this dataset, the potential sources of measurement error, and their potential effects on measurements of PE). We restricted our analysis to nine rivers, representing both the Sacramento River and San Joaquin River basins, for which data were available for at least 53 of the 54 years from 1957 to 2010, the most recent year for which data were available online at the time of manuscript preparation. From the Sacramento River basin, we included the mainstem Sacramento River (Princeton Ferry to Keswick Dam), Battle Creek, the Feather River, the Yuba River, and the American River. From the San Joaquin River basin, we included the Mokelumne River, the Stanislaus River (missing data for 1982), the Tuolumne River, and the Merced River (Fig. 1). Five of these populations are supported by hatchery production: American, Battle, Feather, Merced, and Mokelumne. For wavelet analyses requiring time series without gaps, we interpolated the 1982 production for the Stanislaus River on the basis of the ratio among 1981, 1982, and 1983 production on the Tuolumne River, which was most correlated with the Stanislaus River ($r = 0.551$; Carlson and Satterthwaite 2011).

We obtained information on total releases from each hatchery as well as the number of fish released upstream (defined as releases upstream of Chippis Island, 38°3'18"N, 121°54'42"W) versus into the estuary (defined as releases downstream of Chippis Island) each year from a compilation of annual reports produced by each hatchery (Huber and Carlson 2015).

To compare patterns in production with the quasi-control Klamath-Trinity basin, we obtained information on escapement and in-river harvest from the "Megatable" maintained by California Department of Fish and Wildlife (<https://nrm.dfg.ca.gov/FileHandler.ashx?DocumentID=17948>) and ocean harvest from stock-specific ocean harvest estimates maintained by the Pacific Fishery Management Council (PFMC 2015). Escapement data for this system are only available since 1978, in-river harvest data since 1980, and ocean harvest data since 1983. In-river harvest data in the Klamath-Trinity basin is reported at a variety of scales; thus, when reconstructing returns (escapement plus in-river harvest) we apportioned in-river harvest among all tributaries upstream of the downstream boundary of the unit for which harvest was reported in proportion to their escapement and then apportioned ocean harvest among all tributaries in proportion to their returns. Production and returns show highly similar but not identical dynamics, since a varying proportion of harvest is assigned back to minor tributaries not tracked separately or included in synchrony calculations.

Trends in overall strength of PEs

We measured overall PE strength based on the comparison between CV for the stock complex as a whole compared with CVs for the component rivers and used 10-year moving windows to examine temporal patterns in overall PE strength. We calculated rolling 10-year CVs for each component river as well as the Central Valley stock complex as a whole. For each 10-year subset of the data, we also calculated the two major determinants of PE strength identified by Thibaut and Connolly (2013) — an index of

system synchrony (ϕ ; see eq. 1) and weighted mean of the CVs of individual river's production, with weights based on the mean proportion of production accounted for by each river during the time period under consideration. To compare synchrony with the Klamath-Trinity system, we used 8-year rolling windows because of the shorter time period available and made the comparison based on both returns (escapement plus in-river harvest) and production (returns plus ocean harvest) to maximize the length of the Klamath-Trinity time series and, thus, the number of years available for comparison.

We further investigated trends in variability, and the dominant periods of such variability, for each river and for basins and the stock complex as a whole using wavelet power spectrum analyses (Cazelles et al. 2008). We performed these analyses using the R (R Core Team 2014) package WaveletCo (Tian and Cazelles 2012), which uses a Morlet mother wavelet. The Morlet mother wavelet is widely used in ecological studies, offering high robustness to noise and high frequency resolution compared with common alternatives (Mi et al. 2005; Cazelles et al. 2008).

Trends in factors contributing to PE strength

We used 10-year moving windows to calculate Loreau and de Mazancourt's (2008) index of synchrony (ϕ):

$$(1) \quad \phi = \frac{\sum_{ij} v_n^r(i, j)}{\left[\sum_i \sqrt{v_n^r(i, i)} \right]^2} = \frac{v_n^c}{\left[\sum_i \sqrt{v_n^r(i, i)} \right]^2}$$

In this formulation, i and j index individual rivers, v_n^r is the covariance in production between rivers i and j (which is the variance in river i production if $i = j$), and the scalar v_n^c indicates the variance of total community abundance for a complex of n rivers, which, by definition, is the sum of all elements of the river production variance-covariance matrix (the summed variances plus the summed covariances). The denominator is the variance of a hypothetical complex with the same river-level variances, but in the presence of perfect synchrony. Additionally, we calculated pairwise correlation coefficients among all possible pairings of rivers.

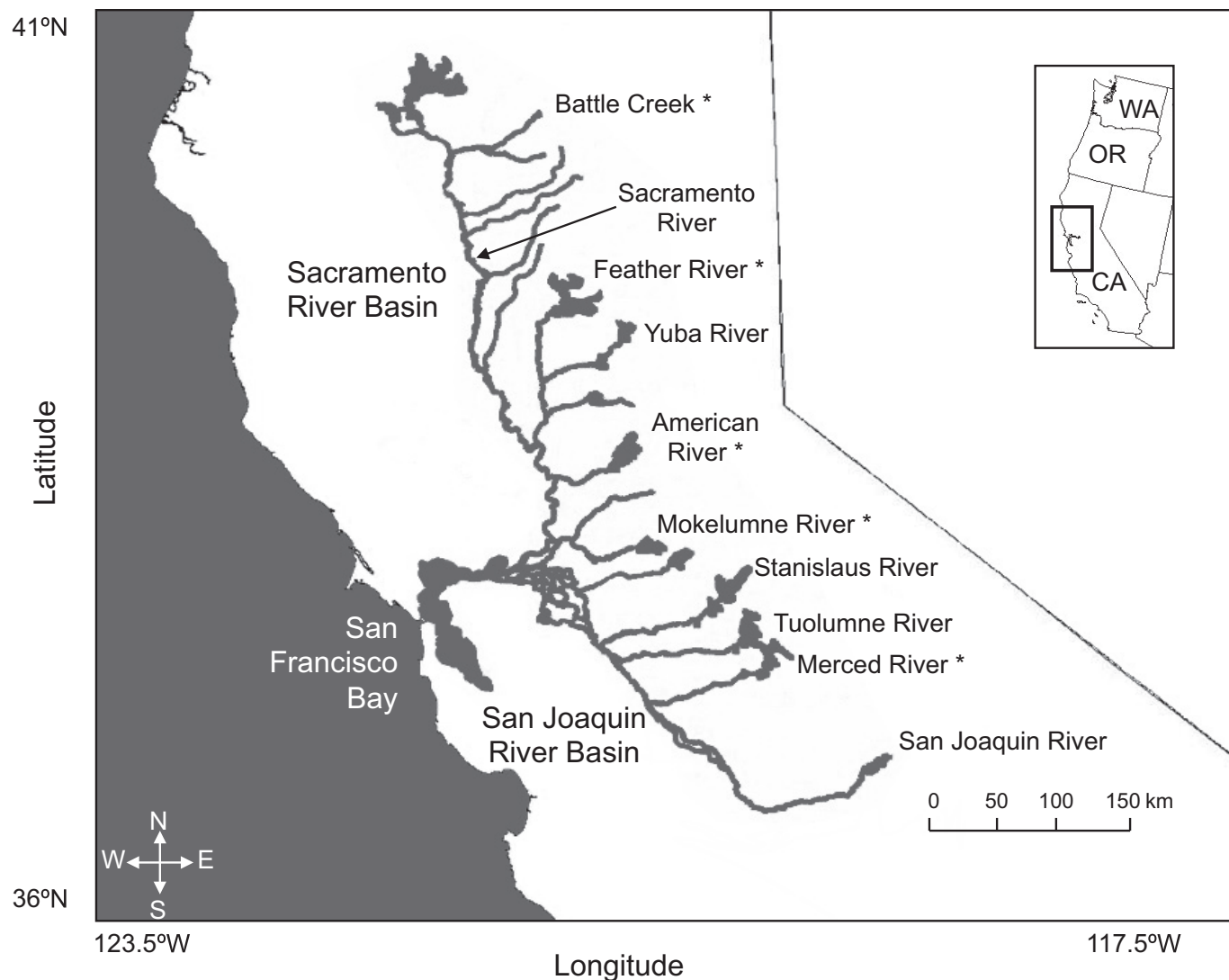
We also calculated the Shannon Equitability Index as a measure of evenness each year. This is similar to the more familiar Shannon Diversity Index (Shannon and Weaver 1948; Krebs 1989), but the latter index also depends on the total number of "species", which is constant in this case. The Diversity Index can be converted into the Equitability Index by dividing by the natural log of the number of species. In addition, we tracked the proportion of total production returning to each river to identify changes in the identities of the rivers contributing most to total production regardless of overall system evenness and tracked the total proportion of production on rivers with hatcheries versus those without hatcheries. For the purposes of this analysis only, all rivers that now have hatcheries on them were considered as rivers with hatcheries for the entire duration of the study, so that the number of rivers contributing to this total did not increase through time.

Finally, synchrony would be expected to increase — and so the PE weaken — during periods of overall growth or decline in total population complex size (Thibaut and Connolly 2013), since the common trend would be present in all rivers. Therefore, we fit trends (linear regression of abundance versus year and log abundance versus year) to total production over the entire time series.

Linking variability and PE components onto hypothesized hatchery management and environmental drivers

We first compared temporal trends in total hatchery releases and total estuary releases with trends in variability, the synchrony index, and mean pairwise correlations among rivers. To further

Fig. 1. Map of the Central Valley study system and major fall Chinook salmon-bearing rivers. Rivers marked with asterisks have hatcheries.



explore covariation in the dynamics of production returning to the different rivers and identify potential mutual drivers, we used maximum autocorrelation factor analysis (MAFA; Solow 1994), which has previously been employed to identify common trends among multiple salmon populations (Fujiwara 2008) and to explore the relationship between hypothesized environmental drivers and the common trends (Fujiwara and Mohr 2009). MAFA is conceptually similar to the more familiar multivariate techniques such as PCA, but is well suited to time series data because it explicitly considers the order in which data are collected and maximizes the signal-to-noise ratio in noisy population data (Solow 1994; Fujiwara 2008).

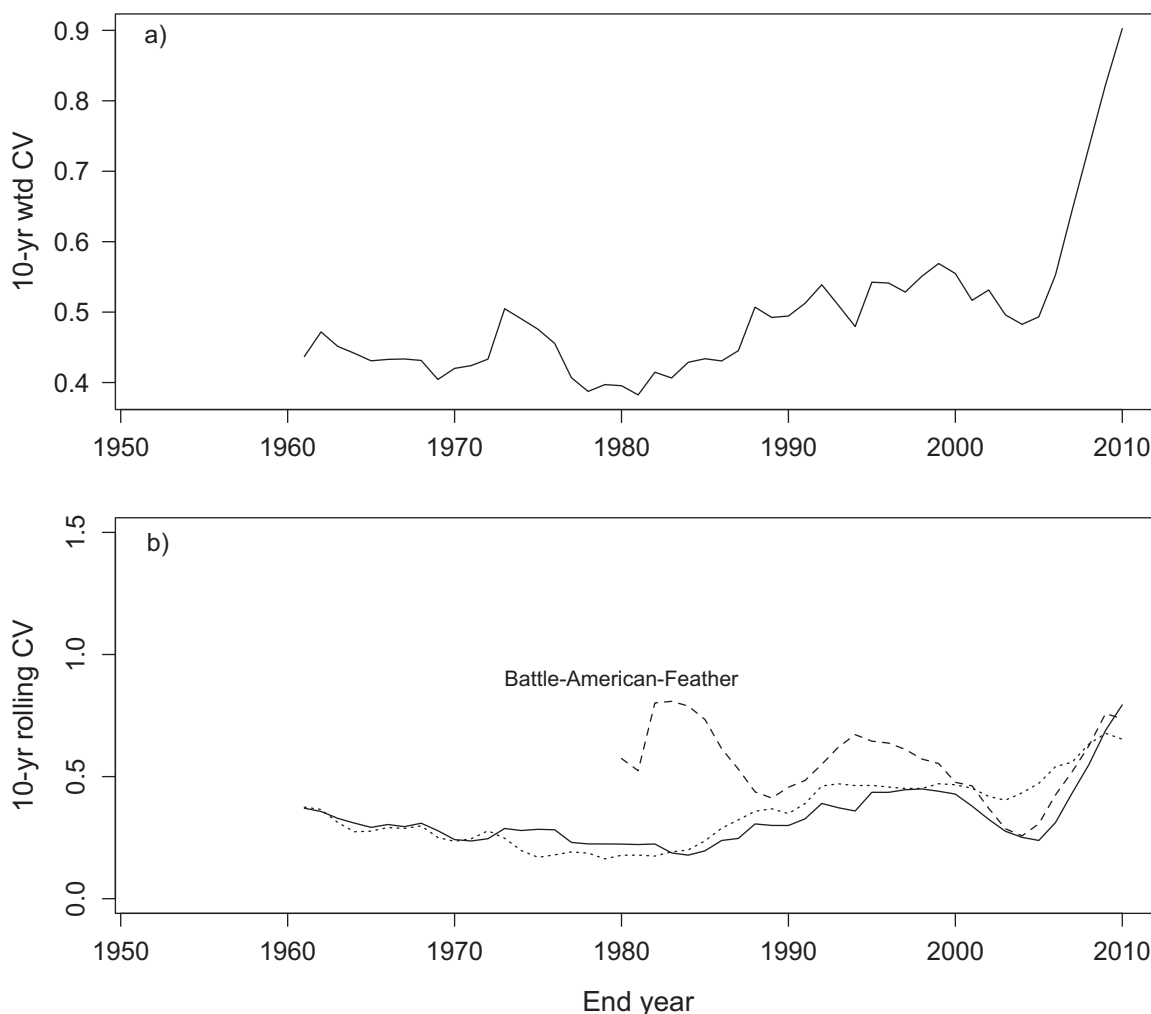
Based on an observed increase in estuary releases in 1981, we performed separate analyses on both the full time series of production and production from 1983 to present to see if shared dynamics became more prominent or more clearly linked to oceanic conditions after the shift to increased estuary releases.

Specifically, we first used MAFA to identify common smooth trends (the maximum autocorrelation factors (MAFs)) among the nine rivers and determine the loading of each trend onto each river's production. Loadings indicate how much variability in each subpopulation is explained by each scaled MAF, and following

Fujiwara (2008), we consider loadings with magnitudes greater than 0.32 to be related to that subpopulation's dynamics, with a loading greater than 0.71 considered "strong". These values correspond to explaining approximately 10% and 50%, respectively, of the variability in subpopulation variability.

Among those MAFs "relating" ($|\text{loading}| > 0.32$) to at least one river's production, we examined the correlation (Fujiwara and Mohr 2009) with total hatchery releases, total estuary releases, the proportion of releases downstream of Chippis Island, total releases from each hatchery, and five environmental covariates for the year of release previously demonstrated to be important to California Current productivity: (i) sea surface temperature (SST) outside of the Golden Gate (38°N, 123°W, obtained from <http://coastwatch.pfeg.noaa.gov/erddap/griddap/erdHadISST.html>) in March, April, and May (Schroeder et al. 2014); (ii) March coastal upwelling (Schroeder et al. 2014) along the Pacific coast at 39°N, obtained from <http://www.pfeg.noaa.gov/products/PFEL/modeled/indices/transport/transport.html>; (iii) wind stress curl at 39°N in March, April, and May (Wells et al. 2008), obtained from <http://www.pfeg.noaa.gov/products/PFEL/modeled/indices/upwelling/upwelling.html>; and (iv) winter (December–February) and (v) spring (March–May) NPGO (Sydeman et al. 2013), obtained from <http://http://npg.o3d.org>.

Fig. 2. Variability in Central Valley fall-run Chinook salmon production through time, measured using the coefficient of variation (CV) calculated over moving 10-year windows and then summarized as the abundance-weighted mean CV across rivers (a) or for individual rivers and the complex as a whole (b). In panel b, the solid line shows CV for the stock complex as a whole, the dotted line shows CV for all rivers without hatcheries (combined), and the dashed line shows individual rivers with hatcheries. The plots for rivers with hatcheries start 13 years after the respective hatcheries were established, such that the first 10-year window starts when the first brood of hatchery fish would be returning as age-3 adults, the most common age at spawning of Central Valley fall-run Chinook salmon. The abundance-weighting causes the difference between the line in panel a compared with the solid line in panel b.



Results

Increasing variability through time

Variability in production (escapement plus estimated harvest) for the entire Central Valley increased through time (10-year rolling CV increased by 0.004 year^{-1} on average for both the weighted mean CV (Fig. 2a) and the CV of the system as a whole; Fig. 2b). Linear regression indicated that the increase of CV with year was significant ($p \leq 0.01$, degrees of freedom (df) = 47), although the annual increase was not constant and most of the increase seemingly occurred since the mid-1980s. Variability in production on those rivers that never had hatcheries (main stem, Yuba, Stanislaus, Tuolumne) showed a similar trend through time. Variability in production on rivers on which hatcheries were established typically also increased during this period, although in many cases variability was higher on such rivers to begin with. By the end of the time series, the CV for the entire Central Valley and CV for rivers with hatcheries were similar, since most Central Valley production was on rivers with hatcheries (Fig. 2b).

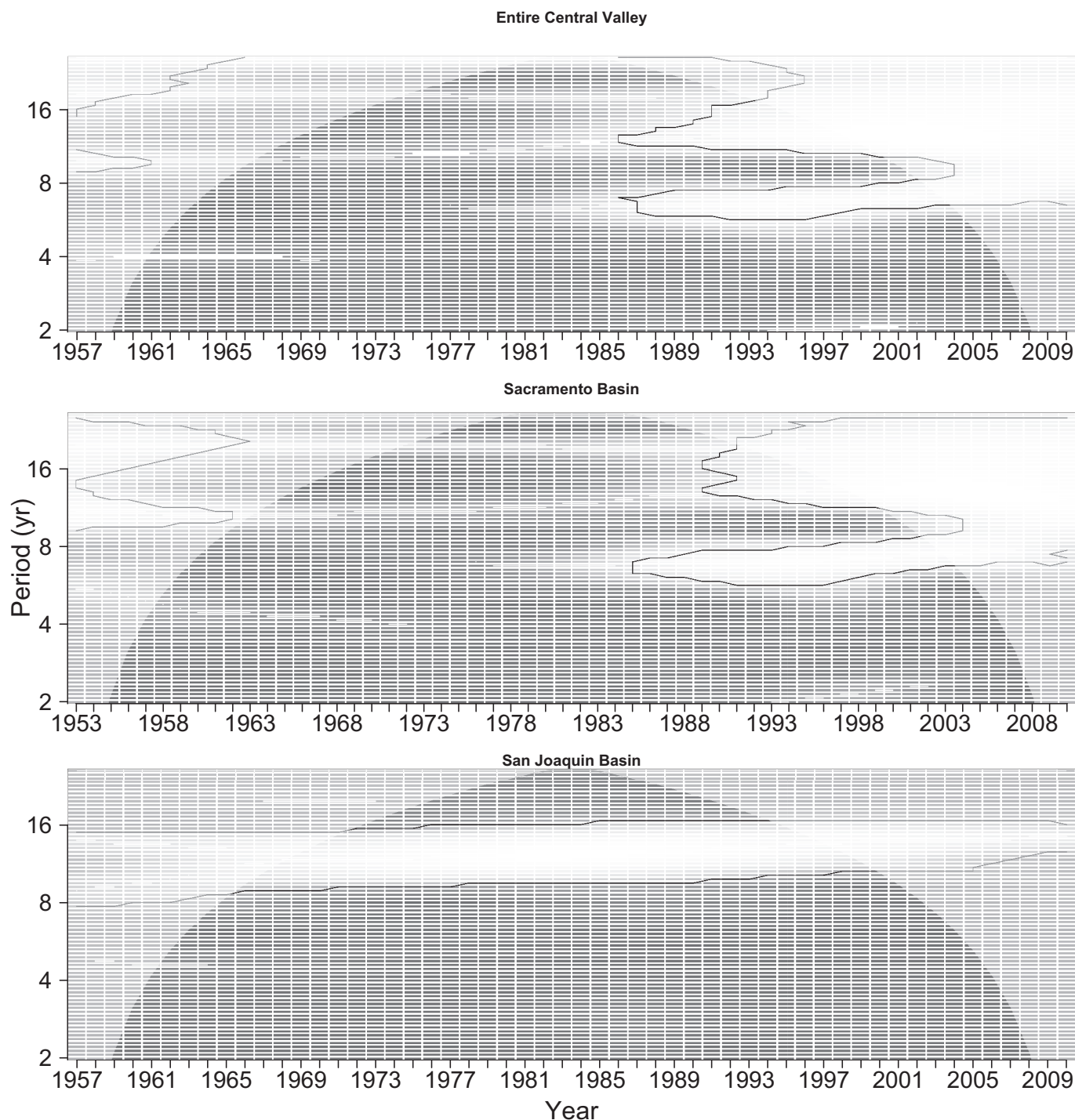
Wavelet analysis of Central Valley production showed an increase in variability along with a change in the dominant period

of variability (Fig. 3). Early on, moderate variability was evident at a period of 3–4 years as well as at periods longer than 8 years. The short-period variability became less evident through time, while high variability at longer periods became apparent through time. When analyzing production of each basin separately, the Sacramento basin showed patterns that were similar to the Central Valley as a whole. However, for the San Joaquin basin, the spectral character of variability was largely consistent through time, dominated by long (8+ years) periods of variation.

Trends in factors contributing to PE strength

Evenness in production on the different rivers (Fig. 4a) displayed a slow ($-0.0019 \text{ year}^{-1}$) but statistically significant decline (linear regression, $p = 0.003$, df = 52, adjusted $R^2 = 0.15$; Fig. 4b) for a total decrease of 0.10 compared with a mean of 0.71 over the time period of this study. The specific rivers with the highest production also changed through time, with generally higher production on rivers with hatcheries. As a result, the proportion of total Central Valley adult production on rivers that ever had hatcheries

Fig. 3. Wavelet analysis of production of the Central Valley fall-run Chinook salmon stock complex as well as production separated into the Sacramento versus San Joaquin basins. Lighter shading represents higher variability during a particular time at a particular period. The shaded outer region reflects areas outside the “cone of inference”, where boundary effects make results less reliable. Solid lines enclose areas with variation significantly greater than zero.

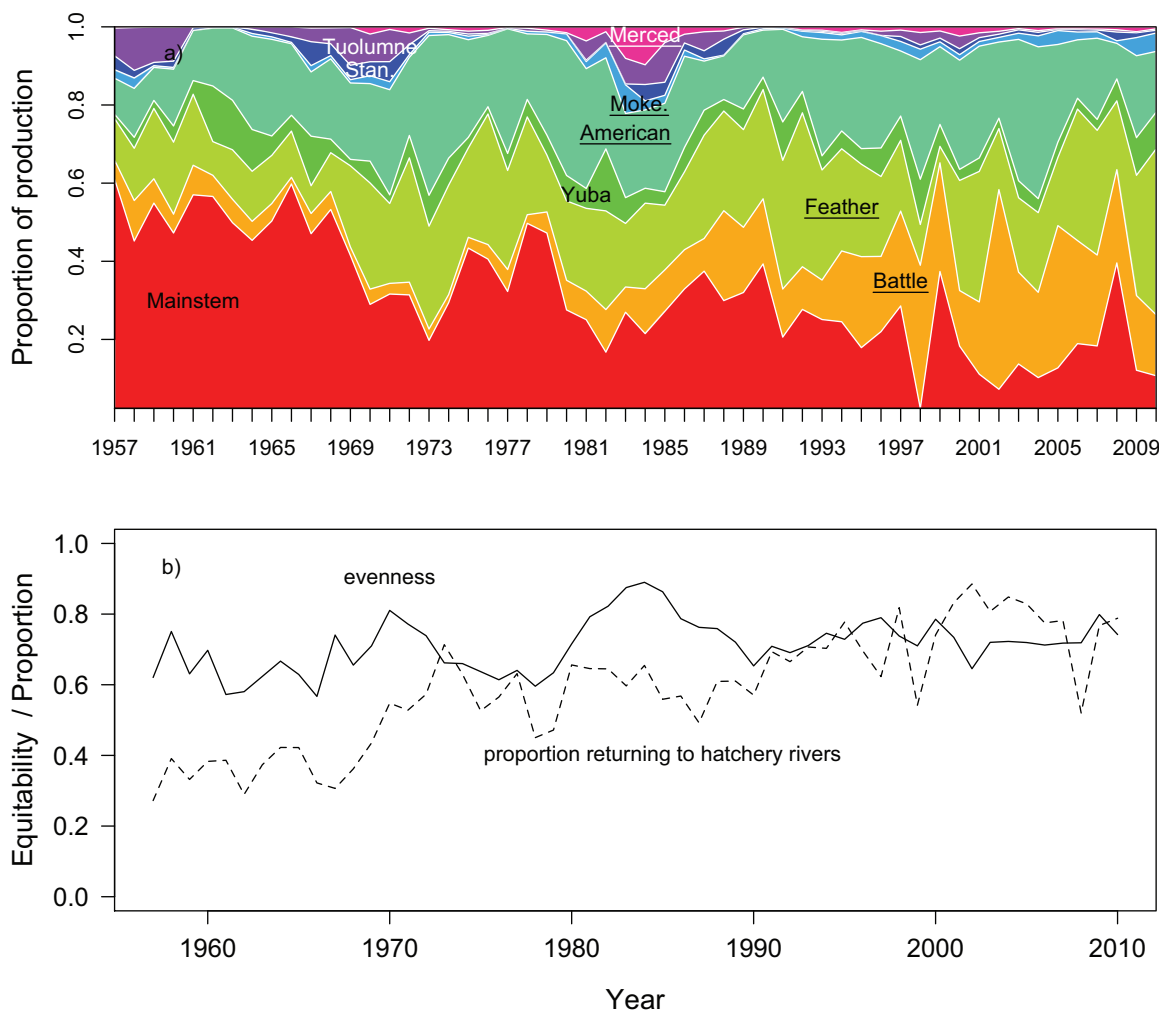


showed a significant ($p < 0.001$, $df = 52$, adjusted $R^2 = 0.71$) increase at a mean rate of $0.9\% \cdot \text{year}^{-1}$ (Fig. 4b).

After declining following an initial period of moderately high synchrony, system-wide synchrony (ϕ) increased from the mid-1980s on (Fig. 5a), and mean pairwise correlations among all rivers in their production increased from a mean near 0.2 at the start of the time series to a mean near 0.7 at the end (Fig. 5b). Until the

mid-1980s, mean pairwise correlations in production were consistently higher among rivers with hatcheries than those without. During this same time period, there were even periods where rivers without hatcheries were negatively correlated in production, suggesting strong buffering. Later, rolling 10-year mean pairwise correlations increased rapidly for rivers without hatcheries until they nearly matched those for rivers with hatcheries (Fig. 5b).

Fig. 4. Proportion of total production annually on each river (a), Shannon Equitability Index (evenness) of production each year (b, solid line), and proportion of production on rivers that ever had hatcheries (b, dashed line). Names of rivers with hatcheries are underlined in panel a. For the coloured version of this figure, refer to the Web site at <http://www.nrcresearchpress.com/doi/full/10.1139/cjfas-2015-0169>.



Thus, the increases in mean correlation among all rivers (linear regression, $p < 0.001$, $df = 48$) and among rivers without hatcheries ($p < 0.001$, $df = 48$) were statistically significant, while the increases in correlation between rivers with the two longest-operating hatcheries (Battle Creek and American River; $p = 0.962$, $df = 41$) and among the rivers with the three largest hatcheries (adding Feather River; $p = 0.187$, $df = 29$) were not significant.

Hatchery practices

Total hatchery releases peaked in the 1960s, declined to lower levels in the 1970s, and then increased to relatively steady levels from the mid-1980s through the end of the time series (Fig. 6a). Initially, all releases were in the upstream watershed, with only occasional releases into the San Francisco Bay Estuary between 1964 and 1976. Fish were released into the estuary every year since 1978, with the largest percent increase (over 500%) coming in 1981, corresponding to age-3 fish returning in 1983. At least 24% of hatchery fall-run Chinook were released into the estuary every year after that, with typical estuary release rates around 40% of total production. There was a coincident increase in the synchrony index of Central Valley returns and production, but not for the Klamath-Trinity system, where all hatchery fish are released in the upstream watershed (Fig. 6b).

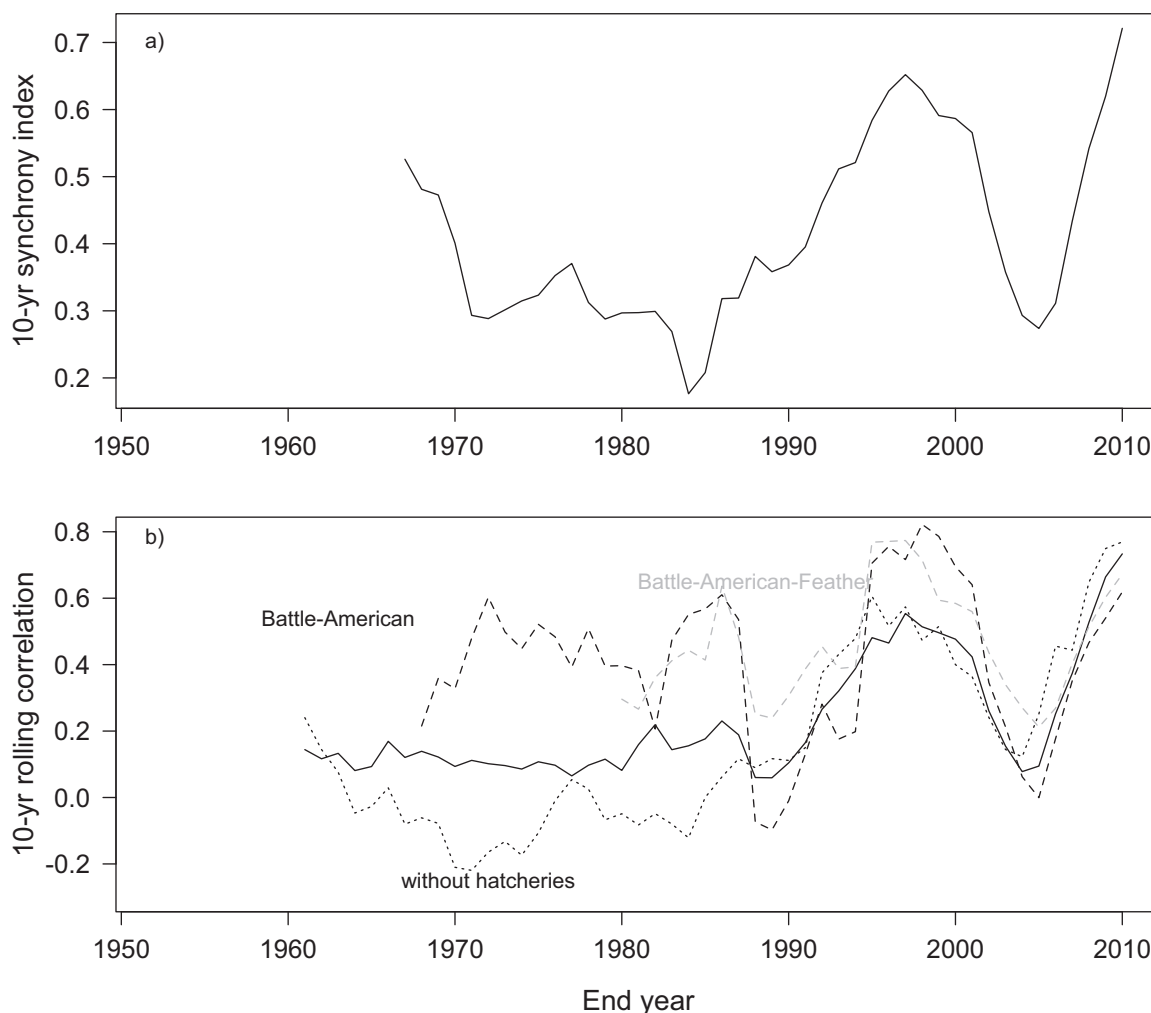
Hatchery contributions to production relative to river stability

Based on the clear increase in estuary releases in 1981 (corresponding to returns in 1983), we separated the production time series into a period of minimal estuary releases (1957–1982) and a period more heavily influenced by estuary releases (1984–2010). This break appeared visually to correspond approximately with the beginning of the increase in correlations among non-hatchery rivers (Fig. 5), and indeed the mean pairwise correlation among rivers without hatcheries was significantly higher (Welch t test, $p \ll 0.01$, $df = 26.721$) for the set of 10-year rolling windows starting in 1984 (mean $r = 0.45$) than the set of 10-year rolling windows ending in 1982 (mean $r = -0.04$).

Overall abundance

There was no evidence for a long-term trend in total production (linear regression $p = 0.57$, $df = 53$, estimated slope is positive, with SE approximately twice as large as the estimated value) or in the natural logarithm of total production ($p = 0.30$, estimated slope is negative, with SE approximately twice the estimate). However, mean total production is somewhat higher (approximately 716 000) for 1984–2010 than during 1957–1983 (approximately 521 000; $p = 0.0549$ in Welch t test with 34.6 adjusted degrees of freedom), and the natural logarithm of total production does show a significant ($p = 0.017$, $df = 25$) decreasing trend over the second half of the time series but not the first half.

Fig. 5. Synchrony index (ϕ) for the Central Valley fall-run Chinook complex calculated for 10-year rolling windows (a) and means of rolling 10-year correlations among production (b) on all rivers (solid line), rivers that never had hatcheries (dotted line), the two longest-operating hatcheries (Coleman Hatchery on Battle Creek and Nimbus Hatchery on the American River, dashed black line), and the three largest hatcheries (adding Feather River, dashed grey line).



Common trends and environmental effects

MAFA revealed common trends among production on the different rivers. For the full time series, we identified six MAFs (Fig. A1) loading onto at least one river's production (Fig. A2). Interestingly, MAF2 loaded positively onto the main stem and negatively onto nearly every other river (Fig. A2). MAF2 shows an overall downward trend (Fig. A2), and thus these loadings may represent a shift of production away from the main stem and toward other rivers (as reflected in Fig. 4a). MAF2 was not clearly correlated with any of the environmental variables explored nor with hatchery release practices, with the strongest correlation of -0.653 with total Feather River hatchery releases (Table A1) and with MAF2 showing a downward trend while total Feather River hatchery releases increased.

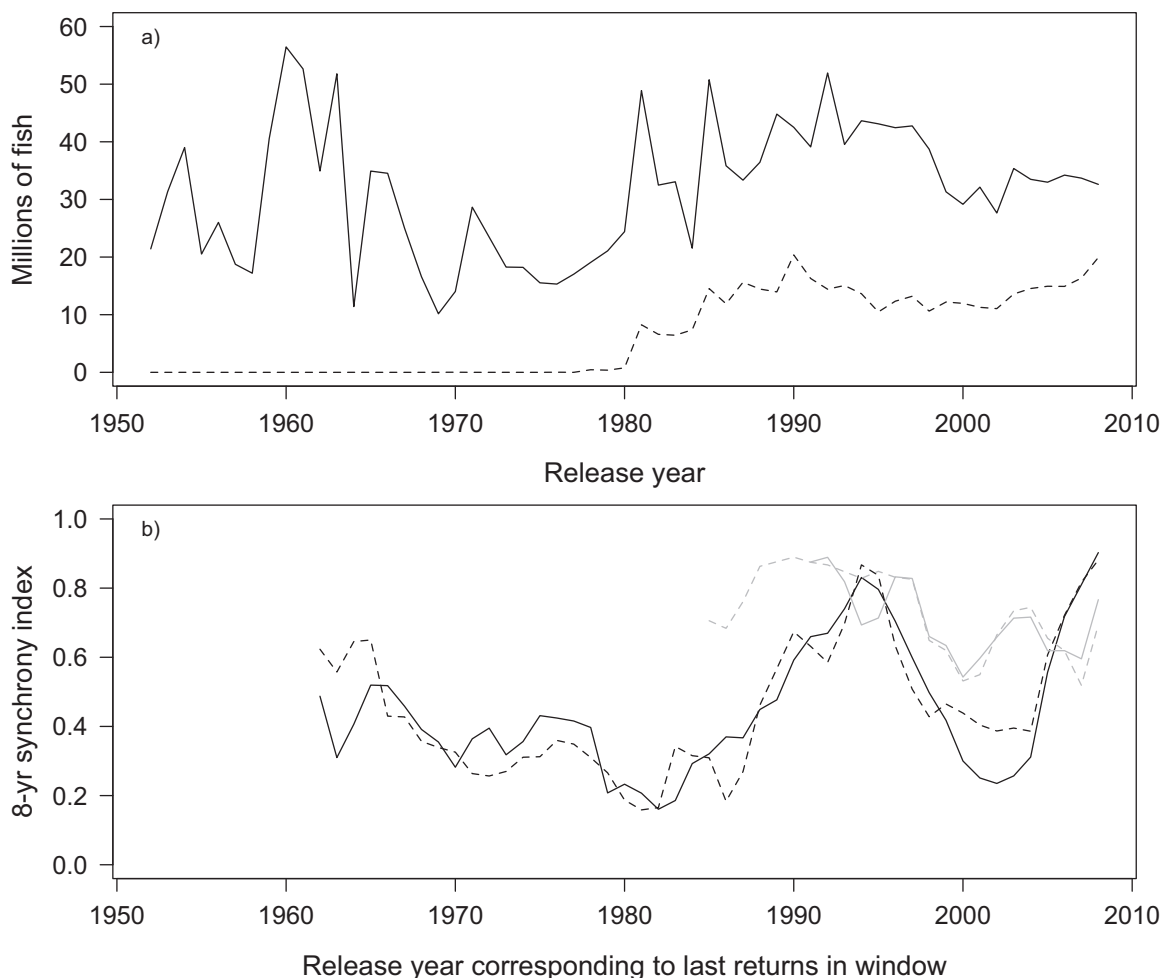
For production since 1983, six MAFs were again identified (Fig. A3) with all but MAF4 loading (if at all) with the same sign onto each river (Fig. A4; Table A2). MAF1 for the recent series represents a sharp decline in the late 1980s and early 1990s (Fig. A3) and loaded positively onto all of the rivers without hatcheries, as well as the Mokelumne and Merced rivers, which have small hatchery programs, but not onto the three rivers with the largest hatcheries. Recent MAF1 appeared to have relatively strong negative correlations with hatchery releases into the estuary (showing a downward trend as estuary releases in-

creased), a positive correlation with Nimbus (American River) releases, and no apparent link with any environmental covariates explored.

Discussion

The overall variability of Central Valley fall-run Chinook (CVC) production has increased through time, particularly since the mid-1980s. In addition, for the system as a whole and for the Sacramento basin, there has been a distinct shift in the dominant period of the variability. Early on, modes of variability were apparent with periods of both 3–4 years (i.e., the approximate mean spawning age in this system) and at longer periods, with comparable amounts of variation at both time scales. Recently, there is less variability at the generation time scale and considerably more variability with periods of 8+ years, which may reflect environmental variability with a longer characteristic period (Zhang et al. 1998; Giese and Carton 1999) becoming increasingly important compared with the strength of the previous cohort, since hatchery production from a small number of spawners can swamp the production of spawners returning to natural areas. Alternatively, the environment itself may have become more variable, and indeed Sydemann et al. (2013) tied increased variability in the North

Fig. 6. Central Valley fall-run Chinook salmon hatchery releases in calendar years 1952–2008 (a), based on Huber and Carlson (2015), and patterns in synchrony of Central Valley and Klamath–Trinity production (b). In panel a, the solid line represents total releases, and the dashed line represents releases into the San Francisco Bay Estuary or ocean (defined here as releases downstream of Chipps Island). Almost all fall-run hatchery fish are released in the calendar year following spawning, and most return at age-3, two calendar years after the release years; thus, the range of release years depicted in this figure matches the range of return years shown in other figures. For 8-year rolling synchrony indices (b), black lines are Central Valley and grey lines are Klamath–Trinity. Solid lines are production (escapement scaled up by both river and ocean harvest), and dashed lines are returns (escapement scaled up by in-river harvest only).



Pacific to numerous attributes of the ocean ecosystem off California.

Role of hatchery practices

An observational study such as ours cannot conclusively identify the underlying mechanisms driving the increased variability observed in this system, and a designed experiment at this scale would be prohibitively expensive and require several decades to generate sufficient data. Despite these weaknesses, we believe our analyses provide several lines of evidence suggesting that hatchery practices have played a role in weakening PE strength in this system, which we discuss below.

PE theory suggests that increased variability could be driven by reduced evenness among subpopulations and (or) by increasing synchrony (Doak et al. 1998). While evenness has remained fairly stable among fall-run subpopulations (though statistically significant because of a large number of years and relatively little year-to-year variation, the decline in evenness was quite small), the identity of the rivers contributing the most to the system as a whole has changed and has shifted toward larger contributions from rivers with hatcheries. The variability on rivers making only small contributions to the total production is relatively unimportant.

For example, despite high CVs on the Merced and Mokelumne rivers in the 1980s–1990s (Fig. 2b), there was little increase in the overall or weighted CV (Fig. 2a), whereas CVs were relatively high on rivers making up a substantial proportion of total production later in the time series.

In contrast with evenness, synchrony clearly increased over the course of the time series examined in this study. This increasing synchrony is concomitant with increasing hatchery production and increased estuary releases (Fig. 6), both of which are expected to increase straying rates (CDFG–NOAA 2001) and thus synchronize subpopulations within the stock complex. Straying could increase synchronicity both owing to direct demographic coupling as well as genotypic homogenization over time. Thus, the temporal coincidence of increased estuary releases with the increase synchrony of the Central Valley strongly supports a role of estuary releases and straying in increasing synchrony, especially since a simultaneous increase in synchrony was not observed on the nearby Klamath–Trinity basin where essentially all hatchery releases are made on-site.

It is important to note that hatchery practices may have stabilizing effects as well. Variability at the time scale of generations

has decreased, possibly because a fairly constant level of hatchery production has largely decoupled natural-area juvenile production from the number of fish recruiting to adulthood. This may have reduced the potential for variability arising from a “cohort resonance” mechanism (Worden et al. 2010; Botsford et al. 2014). In contrast with the Sacramento basin, the San Joaquin basin consistently displayed high variability and that variability was consistently at a longer time period. The lack of higher-frequency variation earlier on may reflect an observation by Hallock (1978) that escapement to the San Joaquin has long been uncorrelated to the number of spawners in the previous generation, but was correlated to flow when juveniles of the dominant age class were emigrating. Additionally, hatchery strays in the Central Valley may be subsidizing rivers without hatcheries and masking declining production in natural areas (Johnson et al. 2012). This subsidy could serve to increase system evenness, potentially contributing to a stronger PE. However, if rivers without hatcheries are now dominated by hatchery fish, hatchery subsidies could be homogenizing trait variability among populations that gives rise to variation in the very traits that underlie the PE.

Role of the environment and other factors

Despite the temporal concordance between increased hatchery releases into the estuary and increased synchrony, it is unlikely that any single factor fully explains all the changes we observed, and we cannot rule out alternate explanations such as increased variability in the environment, especially at longer time scales. For example, Kilduff et al. (2014) noted increased synchrony in survival among Chinook salmon populations at a broad geographic scale starting in the early 1990s, somewhat later than we observed in this study within a single basin. Sydeman et al. (2013) noted that the North Pacific climate has become increasingly variable and linked this to increasing variability in numerous attributes of the ocean ecosystem off the coast of California, most clearly the NPGO. However, the NPGO appears to have started increasing its variability in the 1970s and only reached even higher levels of variability in the late 1990s (Sydeman et al. 2013, their figure 4), timing that does not coincide well with the increased synchrony and variability observed in Central Valley fall-run production. We also used MAFA to explore the relationship between hypothesized drivers and the common trends in fall-run populations. None of the environmental variables appeared to clearly explain shared trends on the different rivers, and there were no clearer effects of oceanic conditions in the latter part of the time series when synchrony was higher — results that we interpret as further indirect support for the importance of estuary releases.

The fact that synchrony did not increase simultaneously for fall-run Chinook salmon in the nearby Klamath–Trinity basin also suggests that the increasing synchrony observed for CVC is unlikely to be the result of broad-scale changes in the ocean environment, since the ocean distribution of subadults from the two stocks has similar latitudinal extent (Weitkamp 2010), with most recoveries of tagged fish ranging from central California to northern Oregon. However, the two stocks experience different environmental conditions immediately upon ocean entry, since their respective river mouths are separated by 3.7 degrees of latitude, and fishery recoveries of Klamath-origin fish are more concentrated in the northern portion of their range than are Central Valley fish (Satterthwaite et al. 2014b versus 2013). There are also differences in the freshwater environment, in-river fisheries, and life history diversity that could confound a comparison between the two systems. Nevertheless, the Klamath–Trinity basin has the only other large Chinook salmon population in California and is thus the best available control. The contrasting patterns observed for the two basins suggest that something local to the CVC complex must have driven much of its increase in synchrony.

It is not entirely clear why synchrony (as measured by ϕ) was relatively high early in the Central Valley time series whereas the

mean pairwise correlation among rivers was not (Figs. 5a versus 5b), except that the mean pairwise correlation approach treats all river pairings as equally informative about overall system synchrony regardless of their size or intrinsic variability. Still, the presence of high synchrony early in the time series and large fluctuations in both synchrony and mean pairwise correlation late in the time series suggest a complicated interplay of factors influencing synchrony and the potential for further fluctuations or quasi-cyclic behavior. Although there was no evidence for long-term abundance trends in the dataset, short-term shared spikes or “collapses” could lead to temporary increases in synchrony, whereas a short-term deviation in a single river’s production would decrease synchrony (e.g., the decreased synchrony in the 2000s reflects a single year of anomalously high Battle Creek production; see Carlson and Satterthwaite 2011, their figure 3a). The increase in synchrony over the later part of the time series likely reflects the combined effect of increasing contribution by rivers with hatcheries (Fig. 4b), which have typically been highly correlated (Fig. 5b), along with a recent increase in synchrony among non-hatchery rivers as well (Fig. 5b). The recent shared “collapse” of subpopulations in 2008–2009 (Lindley et al. 2009) would also contribute to an increased statistical measure of synchrony, although it is unclear the extent to which increasing synchrony contributed to the collapse versus the collapse driving the increase in synchrony. The “collapse” was largely attributed to poor ocean conditions at the time of ocean entry (Lindley et al. 2009), but this environmental effect may not be entirely independent of hatchery practices. Because hatchery releases into the estuary mask the effects of river conditions and decrease the variance in ocean entry timing (Satterthwaite et al. 2014a), estuary releases may have increased the stock complex’s sensitivity to ocean conditions.

Implications

Despite the lack of a designed experiment, and acknowledging the potential contribution of multiple factors to a weakened PE in this system, it is clear that hatchery strays make up a nontrivial proportion of the total escapement even in most “natural” spawning areas (Johnson et al. 2012; Kormos et al. 2012), and it is clear that increased connectivity should tend to synchronize dynamics of subcomponents of a stock complex (Harrison 1994). Correlations among rivers in their production have increased through time, which is predicted to weaken the PE (Doak et al. 1998), and the PE does indeed appear to have weakened in this system. This increase in synchrony was concurrent with the rise of estuary releases, but not with a major change in the variability of the NPGO, nor was a simultaneous increase in synchrony observed in the nearby Klamath–Trinity system where hatchery releases are not trucked downstream. Thus, it seems that altering hatchery practices to reduce straying could strengthen the PE in this system, at a possible cost to overall abundance. Increased on-site releases would likely decrease straying, and also increase the importance of (potentially decorrelated) river survival in determining production. Both of these factors would be expected to reduce correlations and thus strengthen the PE in this system. At the same time, more closely mimicking natural processes could allow variation due to cohort resonance to increase.

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Appendix A. Results of multivariate analyses

Tables A1–A2 and Figs. A1–A4 appear on the following pages.

Table A1. Correlation of each maximum autocorrelation factor (MAF) with environmental covariates and hatchery release practices, for the full production time series 1957–2010.

Covariate	MAF1	MAF2	MAF3	MAF4	MAF5	MAF6
SST.38N.mar.apr.may	−0.324	−0.025	−0.152	0.085	0.108	0.118
Upwelling.39N.mar	0.283	0.058	0.028	−0.263	0.065	−0.124
Curl.39N.mar.apr.may	0.048	−0.514	0.159	−0.131	0.177	−0.147
NPGO.winter	0.189	−0.215	−0.175	−0.106	−0.062	−0.077
NPGO.spring	0.280	−0.253	−0.227	−0.123	0.016	−0.056
Total.releases	−0.181	−0.111	−0.197	−0.260	0.004	−0.036
Estuary.releases	0.261	−0.527	0.065	0.014	0.179	−0.027
Prop.estuary.releases	0.294	−0.556	0.076	0.036	0.135	−0.068
Feather.estuary.releases	0.273	−0.511	0.054	−0.007	0.159	0.002
Nimbus.estuary	0.061	−0.543	0.107	0.106	0.155	−0.105
Coleman.total	−0.152	0.268	−0.243	−0.147	−0.043	0.125
Nimbus.total	−0.378	0.197	−0.111	−0.252	−0.119	−0.235
Feather.total	0.072	−0.653	0.028	−0.133	0.297	0.002

Table A2. Correlation of each MAF with environmental covariates and hatchery release practices, for the recent production time series corresponding to increased Bay releases, return years 1983–2010.

Covariate	MAF1	MAF2	MAF3	MAF4	MAF8	MAF9
SST.38N.mar.apr.may	0.291	−0.153	−0.086	−0.026	0.125	0.120
Upwelling.39N.mar	−0.337	0.140	−0.048	−0.274	−0.307	−0.274
Curl.39N.mar.apr.may	0.061	0.036	0.014	−0.062	−0.076	−0.151
NPGO.winter	−0.207	0.055	0.363	−0.109	−0.204	0.064
NPGO.spring	−0.336	−0.055	0.294	−0.180	−0.097	0.069
Total.releases	0.204	−0.128	−0.243	0.117	−0.060	0.185
Estuary.releases	−0.779	−0.014	−0.240	0.047	−0.042	0.065
Prop.estuary.releases	−0.853	0.100	−0.060	0.003	0.010	−0.038
Feather.estuary.releases	−0.644	0.004	−0.147	0.012	0.057	0.104
Nimbus.estuary	−0.184	−0.002	−0.406	0.263	−0.179	0.193
Coleman.total	0.078	−0.314	−0.314	−0.030	−0.175	0.271
Nimbus.total	0.638	0.010	−0.255	0.044	0.061	−0.026
Feather.total	0.033	0.111	−0.066	0.113	0.057	0.088

Fig. A1. Maximum autocorrelation factors (MAFs, common smooth trends) for production returning to each Central Valley river for the full time series, 1957–2010.

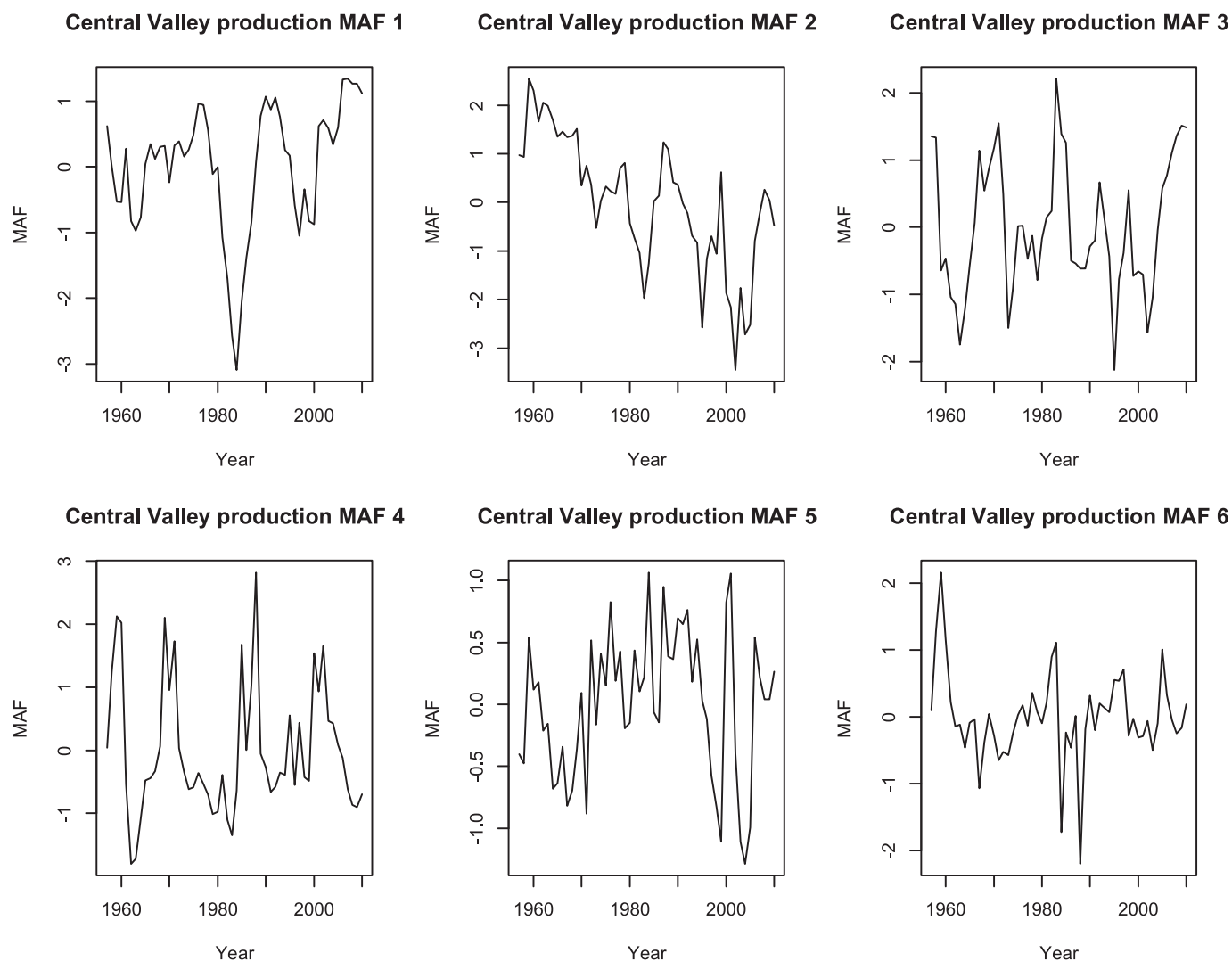


Fig. A2. Maximum autocorrelation factor (MAF) loadings for production returning to each Central Valley river for the full time series, 1957–2010.

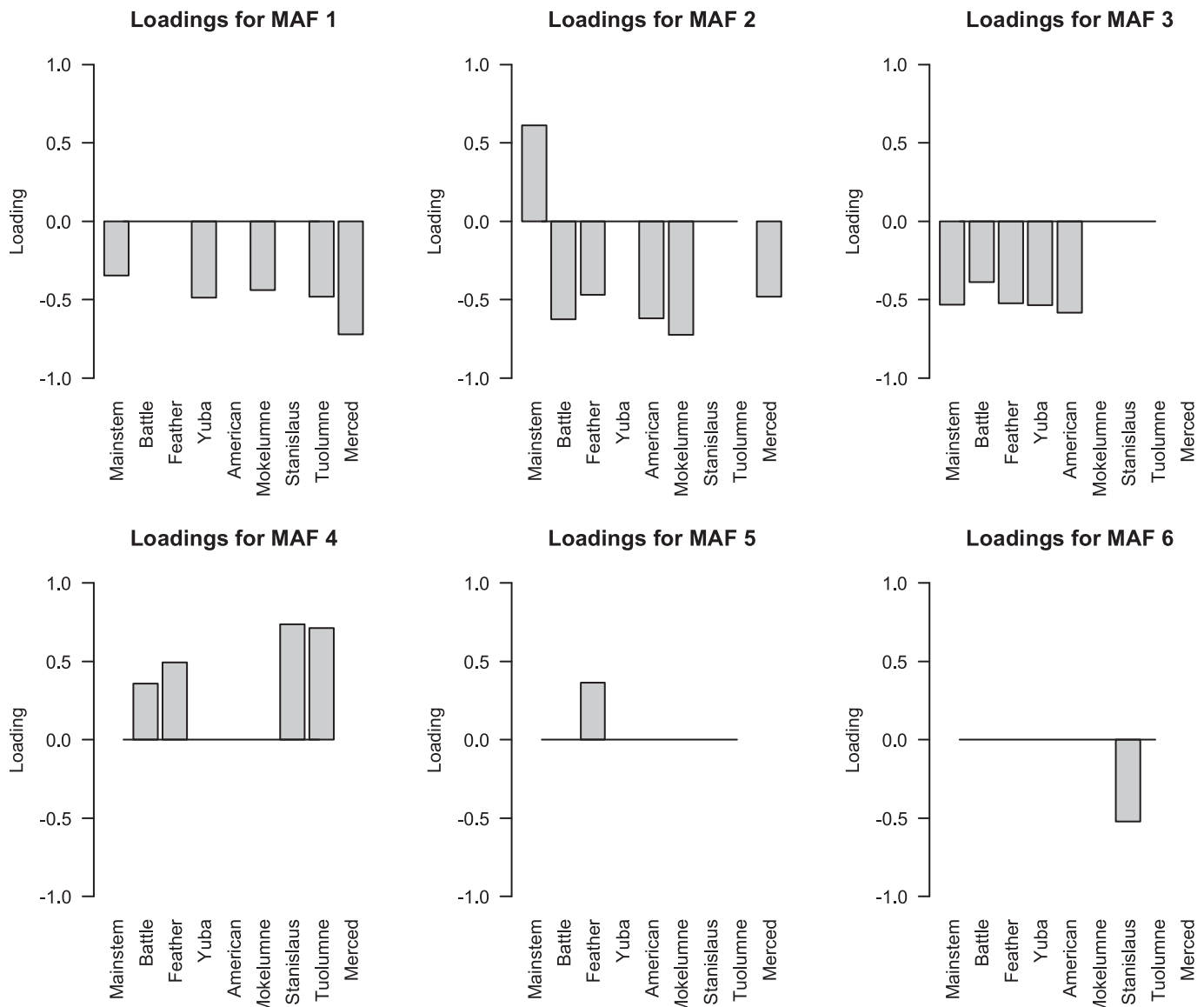


Fig. A3. Maximum autocorrelation factors (MAFs, common smooth trends) for production returning to each Central Valley river for the recent time series reflecting increased Bay releases, return years 1983–2010.

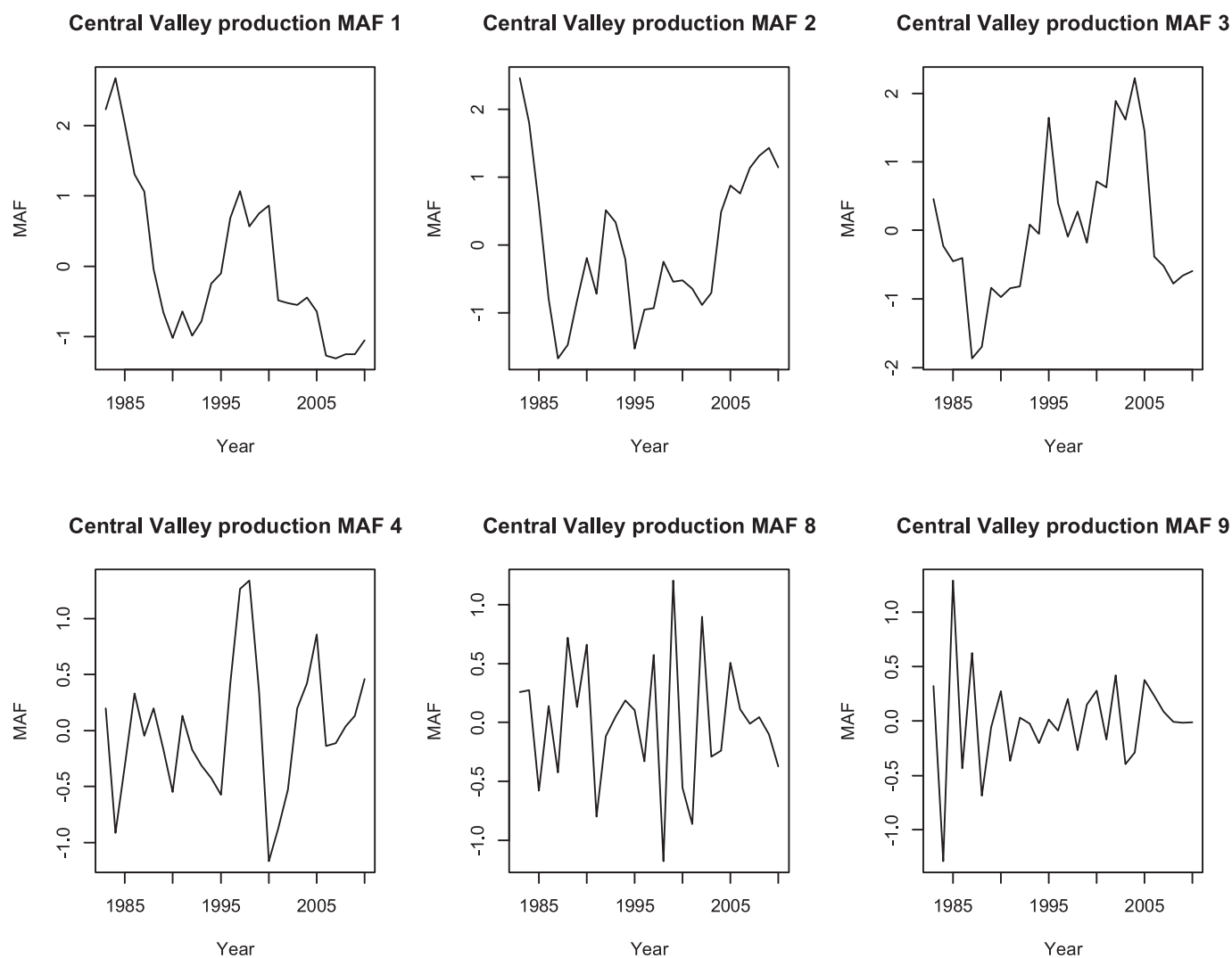


Fig. A4. Maximum autocorrelation factor (MAF) loadings for production returning to each Central Valley river for the recent time series reflecting increased Bay releases, return years 1983–2010.

