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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, 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 NPGO), 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 timeseries, consistent with increased environmental forcing and a shift away from dynamics driven by natural spawners.

Keywords: *Oncorhynchus*, population diversity, buffering, stability, ecosystem services, straying, hatchery practices

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 temporally heterogeneous environment (Olsen et al. 2008; Hutchinson et al. 2008; Rogers et al. 2008; Secor et al. 2009; 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 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 to Bristol Bay’s diverse and productive salmon fishery and other high

PE strength in a hatchery-supplemented salmon complex

latitude stocks with limited anthropogenic impact to freshwater habitat is California's Central Valley fall-run Chinook (CVC) salmon 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 indistinguishable (Williamson and May 2005), in contrast to other studied salmon complexes which 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

PE strength in a hatchery-supplemented salmon complex

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 Central Valley fall-run Chinook production for evidence of portfolio effects, 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 portfolio effect strength due to the allometric scaling of population variance with mean population size (Anderson et al. 2013), the same study found that for 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 (a) exploring the timing of the previously documented weakening of the portfolio effect in Central Valley fall Chinook, (b) 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, hereafter “estuary releases”) could increase variability and

PE strength in a hatchery-supplemented salmon complex

107 synchrony both through increasing demographic connectedness through straying
108 (CDFG/NOAA 2001) and through increased sensitivity to temporal matches or mismatches
109 with food availability due to constrained ocean entry timing (Satterthwaite et al. 2014a), so
110 we use wavelet analyses (Cazelles et al. 2008) and rolling windows (Moore et al. 2010;
111 Krkosek and Drake 2014) to identify the timing of changes in the variability of Central
112 Valley production and the synchrony of its component rivers. We compare this to the
113 timing of changes in total hatchery production and the proportions of fish released into the
114 estuary based on recently compiled data available (Huber and Carlson 2015). Additionally,
115 we use Maximum Autocorrelation Factor Analysis (MAFA, Fujiwara 2008) to identify
116 common trends among rivers and explore relationships with hatchery practices and/or
117 environmental covariates including sea surface temperature, March coastal upwelling,
118 wind stress curl in spring (Wells et al. 2008), and the winter and spring North Pacific Gyre
119 Oscillation (NPGO). We compare the timing changes in Central Valley fall-run synchrony to
120 the timing of changes in ocean environmental variability as measured by the NPGO, the
121 increased variability of which has been implicated in increased variability of the ocean
122 ecosystem off California (Sydeman et al. 2013) and increased synchrony in the survival of
123 Chinook and coho salmon released from hatcheries (Kilduff et al. in press). We also explore
124 temporal changes in evenness and the proportion of Central Valley production accounted
125 for by each river, to account for the possibility that major changes in productivity of
126 individual rivers could change system evenness and thus the strength of the portfolio effect
127 (Doak et al. 1998). Several lines of evidence suggest a role of estuary releases in weakening
128 PE strength in this system. Finally, as a quasi-control, we test whether a simultaneous
129 increase in synchrony occurred in the nearby Klamath-Trinity fall-run Chinook stock

PE strength in a hatchery-supplemented salmon complex

complex, where nearly all hatchery production is released upstream (California HSRG 2012).

Methods

Study system

Chinook salmon (*Oncorhynchus tshawytscha*) 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

PE strength in a hatchery-supplemented salmon complex

hatchery-produced fish as adults (CDFG/NOAA 2001). Chinook salmon mature at a range of ages, with Central Valley fall Chinook 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 September 1 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 two 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 Central Valley fall-run Chinook is proportionately distributed among fish from each river relative to their returns) of fall-run Chinook from the CHINOOKPROD data set, maintained by the US Fish and Wildlife Service's Anadromous Fish

PE strength in a hatchery-supplemented salmon complex

Restoration Program (<http://www.fws.gov/stockton/afpr>). This data set 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 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 between 1981, 1982, and 1983 production on the Tuolumne River, which was most correlated with the Stanislaus ($r=0.551$, 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 Chipps Island, latitude 38.055198; longitude -121.911904) versus into the estuary (defined as releases downstream of Chipps 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 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 portfolio effects

We measured overall portfolio effect strength based on the comparison between CV for the stock complex as a whole compared to 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 portfolio effect strength identified by Thibaut and Connolly (2013) - an index of system synchrony (ϕ , see equation 1), and weighted average of the CVs of

PE strength in a hatchery-supplemented salmon complex

individual rivers' 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 due to the shorter time period available, and made the comparison based on both returns (escapement plus in-river harvest) as well as production (returns plus ocean harvest) to maximize the length of the Klamath-Trinity timeseries 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 to common alternatives (Mi et al. 2005; Cazelles et al. 2008).

Trends in factors contributing to portfolio effect 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 which 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 portfolio effect 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.

PE strength in a hatchery-supplemented salmon complex

Therefore we fit trends (linear regression of abundance versus year and log abundance versus year) to total production over the entire timeseries.

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 to trends in variability, the synchrony index, and mean pairwise correlations among rivers. To further 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 timeseries 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 Factor [MAF]s) among the 9 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 Chipps Island, total releases from each hatchery, and five environmental covariates for the year of release previously demonstrated to be important to California Current productivity: 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); 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>; 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 winter (December-February) and spring (March-May) North Pacific Gyre Oscillation (NPGO, Sydeman et al. 2013), obtained from <http://npgo.o3d.org>.

Results

Increasing variability through time

Variability in production (escapement plus estimated harvest) for the entire Central Valley increased through time (10-yr rolling CV increased by 0.004/yr on average for both the weighted average 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 ($p < 0.01$, $df = 47$), 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 (mainstem, 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+ year) period variation.

Trends in factors contributing to portfolio effect strength

Evenness in production on the different rivers (Fig. 4a) displayed a slow ($-0.0019/\text{year}$) 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 to 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 showed a significant ($p<0.001$, $df=52$, adjusted $R^2=0.71$) increase at a mean rate of 0.9%/yr (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-yr mean pairwise correlations increased rapidly for rivers without hatcheries until they nearly matched those for rivers with hatcheries (Fig. 5b). 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.

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Hatchery practices

Total hatchery releases peaked in the 1960's, declined to lower levels in the 1970's, and then increased to relatively steady levels from the mid-1980's 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 timeseries 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 (Welch t-test, $p < 0.01$, $df = 26.721$) higher 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 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 716000) 1984-2010 than during 1957-1983 (approximately 521000, $p=0.0549$ 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.

Common trends and environmental effects

MAFA revealed common trends among production on the different rivers. For the full time series, we identified 6 MAFs (Fig. A1) loading onto at least one river's production (Fig. A2). Interestingly, MAF2 loaded positively onto the mainstem 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 mainstem 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), 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 1980's and early 1990's (Fig. A3)

PE strength in a hatchery-supplemented salmon complex

and loaded positively onto all of the rivers without hatcheries, as well as the Mokelumne and Merced 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 increased), 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 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 to 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 Sydeman et al. (2013) tied increased variability in the North 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 due to 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 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 timeseries.

In contrast with evenness, synchrony clearly increased over the course of the timeseries 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/NMFS 2001) and thus synchronize subpopulations within the stock complex. Straying could increase synchronicity both due to

PE strength in a hatchery-supplemented salmon complex

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 to 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 portfolio effect. 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 1970's and only reached even higher levels of variability in the late 1990's (Sydeman et al. 2013, their Fig. 4), timing which 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 timeseries 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 Central Valley fall-run Chinook 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

PE strength in a hatchery-supplemented salmon complex

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 vs. Satterthwaite et al. 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 Central Valley fall-run Chinook 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 timeseries whereas the mean pairwise correlation among rivers was not (Fig. 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 timeseries, and large fluctuations in both synchrony and mean pairwise correlation late in the timeseries, 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 2000's reflects

a single year of anomalously high Battle Creek production, see Carlson and Satterthwaite's (2011) Fig. 3a). The increase in synchrony over the later part of the timeseries likely reflects 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 drove 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 non-trivial 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

PE strength in a hatchery-supplemented salmon complex

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.

Appendix Detailed results of Maximum Autocorrelation Factor Analyses, including two tables (A1-A2) and four figures (A1-A4).

Acknowledgments

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References

- Anderson, S.C., Cooper, A.B., and Dulvey, N.K. 2013. Ecological prophets: quantifying metapopulation portfolio effects. *Meth. Ecol. Evol.* **4**: 971–981. doi:10.1111/2041-210X.12093
- Barnett-Johnson, R., Grimes, C.B., Royer, C.F., and Donohoe, C.J. 2007. Identifying the contribution of wild and hatchery Chinook salmon (*Oncorhynchus tshawytscha*) to the ocean fishery using otolith microstructure as natural tags. *Can. J. Fish. Aquat. Sci.* **64**(12): 1683–1692. doi:10.1139/F07-129
- Bjørnstad, O.N., Nisbet, R.M., and Fromentin, J.-M. 2004. Trends and cohort resonant effects in age-structured populations. *J. Anim. Ecol.* **73**: 1157–1167.
- Botsford, L.W., Holland, M.D., Field, J.C., and Hastings, A. 2014. Cohort resonance: a significant component of fluctuations in recruitment, egg production, and catch of fished populations. *ICES J. Mar. Sci.* **71**(8): 2158–2170. doi:10.1093/icesjms/fsu063.
- California Hatchery Scientific Review Group (California HSRG). 2012. California Hatchery Review Report. Prepared for the US Fish and Wildlife Service and Pacific States Marine Fisheries Commission. June 2012. 100 pgs.
- Carlson, S.M. and Satterthwaite, W.H. 2011. Weakened portfolio effect in a collapsed salmon population complex. *Can. J. Fish. Aquat. Sci.* **68**(9): 1579–1589. doi:10.1139/F2011-084
- Cazelles, B., Chavez, M., Berteaux, D., Menard, F., Vik, J.O., Jenouvier, S., and Stenseth, N.C. 2008. Wavelet analysis of ecological time series. *Oecologia*, **156**: 287–304. doi:10.1007/s00442-008-0993-2

PE strength in a hatchery-supplemented salmon complex

- 584 CDFG/NOAA. 2001. Final report on anadromous salmonid fish hatcheries in California,
585 Sacramento, California, USA.
- 586 Doak, D.F., Bigger, D., Harding, E.K., Marvier, M.A., O'Malley, R.A.E., and Thomson, D. 1998.
587 The statistical inevitability of stability-diversity relationships in community ecology.
588 *Am. Nat.* **151**(3): 264–276. doi:10.1086/286117
- 589 Fisher, F.W. 1994. Past and present status of Central Valley Chinook salmon. *Conserv. Biol.*
590 **8**(3): 870–873.
- 591 Fujiwara, M. 2008. Identifying interactions among salmon populations from observed
592 dynamics. *Ecology*, **89**(1): 4–11. doi:10.1111/j.1600-0706.2009.17570.x
- 593 Fujiwara, M. and Mohr, M.S. 2009. Identifying environmental signals from population
594 abundance data using multivariate time-series analysis. *Oikos*, **118**: 1712–1720.
595 doi:10.1111/j.1600-0706.2009.17570.x
- 596 Giese, B.S., and Carton, J.A. 1999. Interannual and decadal variability in the tropical and
597 midlatitude Pacific Ocean. *Journal of Climate*, **12**: 3402–3418.
- 598 Griffiths, J.R., Schindler, D.E., Armstrong, J.B., Scheuerell, M.D., Whited, D.C., Clark, R.A.,
599 Hilborn, R., Holt, C.A., Lindley, S.T., Stanford, J.A., and Volk E.C. 2014. Performance of
600 salmon fishery portfolios across western North America. *J. Appl. Ecol.* **51**(6): 1554–
601 1563. doi:10.1111/1365-2664.12341
- 602 Habicht, C., Seeb, L.W., and Seeb, J.E. 2007. Genetic and ecological divergence defines
603 population structure of salmon populations returning to Bristol Bay, Alaska, and
604 provides a tool for admixture analysis. *Trans. Am. Fish. Soc.* **136**: 82–94.
605 doi:10.1577/T06-001.1

PE strength in a hatchery-supplemented salmon complex

- 606 Hallock, R.J. 1978. A description of the California department of fish and game management
607 program and goals for the Sacramento River system salmon resource. Technical
608 report, California Department of Fish and Game.
- 609 Harrison, S. 1994. Metapopulations and conservation. Pp. 111-128 in: Large-scale Ecology
610 and Conservation Biology (P.J. Edwards, Webb, N.R., and May, R.M. eds.). Blackwell,
611 Oxford, UK.
- 612 Hilborn, R., Quinn, T.P., Schindler, D.E., and Rogers, D.E. 2003. Biocomplexity and fisheries
613 sustainability. Proc. Natl. Acad. Sci. **100**(11): 6564–6568.
614 doi:10.1073/pnas.1037274100
- 615 Huber, E.R. and Carlson, S.M. 2015. Temporal trends in hatchery releases of fall-run
616 Chinook salmon in California's Central Valley. San Francisco Estuary and Watershed
617 Science, **13**(2): jmie_sfews_27913.
- 618 Hutchinson, W.F. 2008. The dangers of ignoring stock complexity in fishery management:
619 the case of the North Sea cod. Biol. Lett. **4**: 693-695. doi:10.1098/rsbl.2008.0443
- 620 Johnson, R.C., Weber, P.K., Wikert, J.D., Workman, M.L., MacFarlane, R.B., Grove, M.J., and
621 Schmitt, A.K. 2012. Managed metapopulations: Do salmon hatchery 'sources' lead to
622 in-river 'sinks' in conservation? PLOS ONE, **7**(2): e28880.
623 doi:10.1371/journal.pone.0028880
- 624 Kilduff, D.P., Botsford, L.W., and Teo, S.L.H. 2014. Spatial and temporal covariability in early
625 ocean survival of Chinook salmon (*Oncorhynchus tshawytscha*) along the west coast
626 of North America. ICES J. Mar. Sci. **71**(7): 1671–1682. doi:10.1093/icesjms/fsu031

PE strength in a hatchery-supplemented salmon complex

- 627 Kilduff, D.P., Di Lorenzo, E., Botsford, L.W., and Teo, S.L.H. In press. Changing central Pacific
 628 El Niños reduce stability of North American salmon survival rates. *Proc. Natl. Acad.*
 629 *Sci.* doi: 10.1073/pnas.1503190112
- 630 Koellner, T. and Schmitz, O. 2006. Biodiversity, ecosystem function, and investment risk.
 631 *BioScience*, 56(12): 977-985. doi:10.1641/0006-
 632 3568(2006)56[977:BEFAIR]2.0.CO;2
- 633 Kormos, B., Palmer-Zwahlen, M., and Low, A. 2012. Recovery of coded-wire tags from
 634 Chinook salmon in California's Central Valley escapement and ocean harvest in
 635 2010. Technical report, California Department of Fish and Game Fisheries Branch
 636 Administrative Report 2012-02.
- 637 Krebs 1989. *Ecological Methodology*. Harper & Row. 654 pages
- 638 Krkosek, M. and Drake, J.M. 2014. On signals of phase transitions in salmon population
 639 dynamics. *Proc. R. Soc. B* **281**: 20133221. doi:10.1098/rspb.2013.3221
- 640 Levin, S.A. and Lubchenco, J. 2008. Resilience, robustness and marine ecosystem-based
 641 management. *BioScience* **58**(1): 27–32. doi:10.1641/B580107
- 642 Lindley, S.T., Grimes, C.B., Mohr, M.S., Peterson, W., Stein, J., Anderson, J.T., Botsford, L.W.,
 643 Bottom, D.L., Busack, C.A., Collier, T.K., Ferguson, J., Garza, J.C., Grover, A.M., Hankin,
 644 D. G., Kope, R.G., Lawson, P.W., Low, A., MacFarlane, R.B., Moore, K., Palmer-Zwahlen,
 645 M., Schwing, F.B., Smith, J., Tracy, C., Webb, R., Wells, B.K., and Williams, T.H. 2009.
 646 What caused the Sacramento River fall Chinook stock collapse? NOAA Tech. Memo.
 647 NOAA-TM-NMFS-SWFSC-447.
- 648 Lindley, S.T., Schick, R.S., Mora, E., Adams, P.B., Anderson, J.J., Greene, S., Hanson, C., May,
 649 B.P., McEwan, D.R., MacFarlane, R.B., Swanson, C., and Williams, J.G. 2007.

PE strength in a hatchery-supplemented salmon complex

- 650 Framework for assessing viability of threatened and endangered Chinook salmon
651 and steelhead in the Sacramento–San Joaquin Basin. San Francisco Estuary and
652 Watershed Science, **5**(1): jmie_sfews_10986.
- 653 Loreau, M. & de Mazancourt, C. 2008. Species synchrony and its drivers: neutral and
654 nonneutral community dynamics in fluctuating environments. Am.
655 Nat. **172**: E48–E66. doi:10.1086/589746
- 656 Luck, G.W., Daily, G.C., and Ehrlich, P.R. 2003. Population diversity and ecosystem services.
657 Trends Ecol. Evol. **18**: 331–336. doi:10.1016/S0169-5347(03)00100-9
- 658 Markowitz, H. 1952. Portfolio selection. J. Finance, **7**: 77–91.
- 659 May, R.M. 1972. Will a large complex system be stable? Nature, **238**: 413–414
- 660 Mi, X., Ren, H., Ouyang, Z., Wei, W., and Ma, K. 2005. The use of the Mexican Hat and the
661 Morlet wavelets for detection of ecological patterns. Plant Ecol. 179:1–19.
662 doi:10.1007/s11258-004-5089-4
- 663 Mohr, M.S. and Satterthwaite, W.H. 2013. Coded wire tag expansion factors for Chinook
664 salmon carcass surveys in California: estimating the numbers and proportions of
665 hatchery-origin fish. San Francisco Estuary and Watershed Science **11**(4):
666 jmie_sfews_13364.
- 667 Moore, J.W., McClure, M., Rogers, L.A., and Schindler, D.E. 2010. Synchronization and
668 portfolio performance of threatened salmon. Conserv. Lett. **3**(5): 340–348.
669 doi:10.1111/j.1755-263X.2010.00119.x
- 670 Moyle, P.B. 2002. Inland Fishes of California. University of California Press, Berkeley,
671 California, USA.

PE strength in a hatchery-supplemented salmon complex

- 672 O'Farrell, M.R., Mohr, M.S., Palmer-Zwahlen, M.L., and Grover, A.M. 2013. The Sacramento
673 Index (SI). NOAA Tech. Memo. NOAA-TM-NMFS-SWFSC-512.
- 674 O'Farrell, M.R., Palmer-Zwahlen, M.L., and Simon, J. 2010. Is the September 1 river return
675 date approximation appropriate for Klamath River fall Chinook? NOAA Tech. Memo.,
676 NOAA-TM-NMFS-SWFSC-468.
- 677 Olsen, E.M., Knutsen, H., Gjosaeter, J., Jorde, P.E., Knutsen, J.A, and Stenseth, N.C. 2008.
678 Small-scale biocomplexity in a coastal Atlantic cod supporting a Darwinian
679 perspective on fisheries management. *Evol. Appl.* **3**(1) :425-533.
680 doi:10.1111/j.1752-4571.2008.00024.x
- 681 Pacific Fishery Management Council (PFMC) 2015. Preseason Report I: Stock Abundance
682 Analysis and Environmental Assessment Part 1 for 2015 Ocean Salmon Fishery
683 Regulations. [Document prepared for the Council and its advisory entities.] Pacific
684 Fishery Management Council, 7700 NE Ambassador Place, Suite 101, Portland, OR
685 97220-1384, USA.
- 686 Palmer-Zwahlen, M., and Kormos, B. 2013. Recovery of coded-wire tags from Chinook
687 salmon in California's Central Valley escapement and ocean harvest in 2011.
688 Technical report, California Department of Fish and Game Fisheries Branch
689 Administrative Report 2013-02.
- 690 Quinn, T.P. 2005. The behavior and ecology of Pacific salmon and trout. American Fisheries
691 Society, Bethesda, MD.
- 692 R Core Team. 2014. R: A language and environment for statistical computing. R Foundation
693 for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL [http://www.R-](http://www.R-project.org/)
694 [project.org/](http://www.R-project.org/).

PE strength in a hatchery-supplemented salmon complex

- 695 Rogers, L.A., and Schindler, D.E. 2008. Asynchrony in population dynamics of sockeye
696 salmon in southwest Alaska. *Oikos* **117**: 1578-1586. doi:10.1111/j.0030-
697 1299.2008.16758.x
- 698 Satterthwaite, W.H., Mohr, M.S., O'Farrell, M.R., and Wells, B.K. 2013. A comparison of
699 temporal patterns in the ocean spatial distribution of California's Central Valley
700 Chinook salmon runs. *Can. J. Fish. Aquat. Sci.* **70**(4): 574-584. doi:10.1139/cjfas-
701 2012-0395
- 702 Satterthwaite, W.H., Carlson, S.M., Allen-Moran, S.D., Vincenzi, S., Bograd, S.J., and Wells, B.K.
703 2014a. Match-mismatch dynamics and the relationship between ocean-entry timing
704 and relative ocean recoveries of Central Valley fall run Chinook salmon. *Mar. Ecol.*
705 *Prog. Ser.* **511**: 237-248. doi:10.3354/meps10934
- 706 Satterthwaite, W.H., Mohr, M.S., O'Farrell, M.R., Anderson, E.C., Banks, M.A., Bates, S.J.,
707 Bellinger, M.R., Borgerson, L.A., Crandall, E.D., Kormos, B.J., Lawson, P.W., and
708 Palmer-Zwahlen, M.L. 2014b. Use of genetic stock identification data for comparison
709 of the ocean spatial distribution, size-at-age, and fishery exposure of an untagged
710 stock and its indicator: California Coastal versus Klamath River Chinook salmon.
711 *Trans. Am. Fish. Soc.* **143**(1): 117-133. doi:10.1080/00028487.2013.837096
- 712 Satterthwaite, W.H., Ciancio, J., Crandall, E., Palmer-Zwahlen, M.L., Grover, A.M., O'Farrell,
713 M.R., Anderson, E.C., Mohr, M.S., and Garza, J.C. 2015. Stock composition and ocean
714 spatial distribution inference from California recreational Chinook salmon fisheries
715 using genetic stock identification. *Fish. Res.* **170**: 166-178.
716 doi:10.1016/j.fishres.2015.06.001

PE strength in a hatchery-supplemented salmon complex

- 717 Schindler, D.E., Hilborn, R., Chasco, B., Boatright, C.P., Quinn, T.P., Rogers, L.A., and Webster,
 718 M.S. 2010. Population diversity and the portfolio effect in an exploited species.
 719 Nature, **465**: 609–612. doi:10.1038/nature09060
- 720 Schroeder, I.D., Santora, J.A., Moore, A.M., Edwards, C.A., Fietchter, J., Hazen, E.L., Bograd,
 721 S.J., Field, J.C., and Wells, B.K. 2014. Application of a data-assimilative regional ocean
 722 modeling system for assessing California Current System ocean conditions, krill, and
 723 juvenile rockfish interannual variability. Geophys. Res. Lett. **41**: 5942–5950.
 724 doi:10.1002/2014GL061045
- 725 Secor, D.H., Kerr, L.A., and Cadrin, S.X. 2009. Connectivity effects on productivity, stability,
 726 and persistence in a herring metapopulation model. ICES J. Mar. Sci. **66**(8): 1726-
 727 1732. doi:10.1093/icesjms/fsp154
- 728 Shannon, C.E. and Weaver, W. (1948) A mathematical theory of communication. The Bell
 729 Syst. Tech. J. **27**: 379–423 and 623–656.
- 730 Solow, A.R. 1994. Detecting change in the composition of a multispecies community.
 731 Biometrics **50**(2): 556–565. doi:10.2307/2533401
- 732 Sydeman, W.J., Santora, J.A., Thompson, S.A., Marinovic, B., and Di Lorenzo, E. 2013.
 733 Increasing variance in North Pacific climate relates to unprecedented ecosystem
 734 variability off California. Global Change Biol. **19**: 1662-1675. doi:10.1111/gcb.12165
- 735 Thibaut, L.M. and Connolly, S.R. 2013. Understanding diversity-stability relationships:
 736 towards a unified model of portfolio effects. Ecol. Lett. **16**: 140-150.
 737 doi:10.1111/ele.12019
- 738 Tian, H. and B. Cazelles (2012). WaveletCo: Wavelet Coherence Analysis. R package version
 739 1.0. <http://CRAN.R-project.org/package=WaveletCo>

PE strength in a hatchery-supplemented salmon complex

- 740 Tilman, D., and Downing, J.A. 1994. Biodiversity and stability in grasslands. *Nature*, **367**:
741 363–365.
- 742 Weitkamp, L.A. 2010. Marine distributions of Chinook salmon from the West Coast of North
743 America determined by Coded Wire Tag recoveries. *Trans. Am. Fish. Soc.* **139**(1):
744 147–170. doi:10.1577/T08-225.1.
- 745 Wells, B.K., Field, J.C., Thayer, J.A., Grimes, C.B., Bograd, S.J., Sydeman, W.J., Schwing, F.B.,
746 and Hewitt, R. 2008. Untangling the relationships among climate, prey and top
747 predators in an ocean ecosystem. *Mar. Ecol. Prog. Ser.* **364**: 15–29.
748 doi:10.3354/meps07486
- 749 Williams, J.G. 2006. Central Valley salmon: a perspective on Chinook and steelhead in the
750 Central Valley of California. *San Francisco Estuary and Watershed Science*, **4**(2):1–
751 398.
- 752 Williamson, K.C., and May, B. 2005. Homogenization of fall-run Chinook salmon gene pools
753 in the Central Valley of California, USA. *North Am. J. Fish. Manag.* **25**(3): 993–1009.
754 doi:10.1577/M04-136.1
- 755 Worden, L., Botsford, L.W., Hastings, A., and Holland, M.D. 2010. Frequency responses of
756 age-structured populations Pacific salmon as an example. *Theor. Popul. Biol.* **78**(4):
757 239–249. doi:10.1016/j.tpb.2010.07.004
- 758 Worm, B., E. Barbier, E.B., Beaumont, N., Duffy, J.E., Folke, C., Halpern, B.S., Jackson, J.B.C.,
759 Lotze, H.K., Micheli, F., Palumbi, S.R., Sala, E., Selkoe, K.A., Stachowicz, J.J., and
760 Watson, R. 2006. Impacts of biodiversity loss on ocean ecosystem services. *Science*,
761 **314**(5800): 787–790. doi:10.1126/science.1132294

PE strength in a hatchery-supplemented salmon complex

- 762 Yates, P.M., Heupel, M.R., Tobin, A.J., and Simpfendorfer, C.A. 2012. Diversity in young shark
763 habitats provides the potential for portfolio effects. *Mar. Ecol. Prog. Ser.* **458**: 269-
764 281. doi:10.3354/meps09759
- 765 Yoshiyama, R., E. Gerstung, F. Fisher, and Moyle, P. 2000. Chinook salmon in the California
766 Central Valley: an assessment. *Fisheries*, **25**(2): 6–20. doi:10.1577/1548-
767 8446(2000)025;0006:CSITCC;2.0.CO;2
- 768 Zhang, X., Sheng, J., and Shabbar, A. 1998. Modes of interannual and interdecadal variability
769 of Pacific SST. *Journal of Climate*, **11**: 2556-2569.

Draft

Figure captions

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

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 average 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 lightly dotted line shows CV for all rivers without hatcheries (combined), and the heavily dashed lines show 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 2a compared to the solid line in 2b.

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. Redder colors (or lighter shading in the greyscale printed version) represent 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.

PE strength in a hatchery-supplemented salmon complex

793

794 **Fig. 4.** Proportion of total production annually on each river (a), Shannon Equitability index

795 (evenness) of production each year (b, solid line), and proportion of production on rivers

796 that ever had hatcheries (b, dashed line). Names of rivers with hatcheries are underlined.

797

798 **Fig. 5.** Synchrony index (ϕ) for the Central Valley fall-run Chinook complex calculated for

799 10-year rolling windows (a) and means of rolling 10-year correlations among production

800 (b) on all rivers (solid black line), rivers that never had hatcheries (dotted line), the two

801 longest-operating hatcheries (Coleman Hatchery on Battle Creek and Nimbus Hatchery on

802 the American River, dotted black line), and the three largest hatcheries (adding Feather

803 River, dotted grey line).

804

805 **Fig. 6.** Central Valley fall-run Chinook salmon hatchery releases in calendar years 1952-

806 2008 (a), based on Huber and Carlson (2015), and patterns in synchrony of Central Valley

807 and Klamath-Trinity production (b). In (a), the solid line represents total releases and the

808 dashed line represents releases into the San Francisco Bay estuary or ocean (defined here

809 as releases downstream of Chipps Island). Almost all fall-run hatchery fish are released in

810 the calendar year following spawning, and most return at age-3, two calendar years after

811 the release years, thus the range of release years depicted in this figure matches the range

812 of return years shown in other figures. For 8-year rolling synchrony indices (b), black lines

813 are Central Valley and grey lines are Klamath-Trinity. Solid lines are production

814 (escapement scaled up by both river and ocean harvest) and dotted lines are returns

815 (escapement scaled up by in-river harvest only).

41°N

Latitude

36°N

123.5°W

Longitude

117.5°W

10-yr wtd CV

10-yr rolling CV

End year

Sacramento Basin

San Joaquin Basin

Millions of fish

Appendix Results of Multivariate Analyses

Table A1. Correlation of each MAF with environmental covariates and hatchery release practices, for the full production timeseries 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

PE strength in a hatchery-supplemented salmon complex - Supplementary material

Table A2. Correlation of each MAF with environmental covariates and hatchery release practices, for the recent production timeseries 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

PE strength in a hatchery-supplemented salmon complex - Supplementary material

Fig. A1. Maximum Autocorrelation Factors (common smooth trends) for production returning to each Central Valley river for the full timeseries, 1957-2010.

PE strength in a hatchery-supplemented salmon complex - Supplementary material

Fig. A2. Maximum Autocorrelation Factors loadings for production returning to each Central Valley river for the full timeseries, 1957-2010.

Fig. A3. Maximum Autocorrelation Factors (common smooth trends) for production returning to each Central Valley river for the recent timeseries reflecting increased Bay releases, return years 1983-2010.

PE strength in a hatchery-supplemented salmon complex - Supplementary material

Fig. A4. Maximum Autocorrelation Factor loadings for production returning to each Central Valley river for the recent timeseries reflecting increased Bay releases, return years 1983-2010.