Weakened portfolio effect in a collapsed salmon population complex

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Abstract: Recent research has highlighted the importance of interpopulation diversity in fostering the stability of population complexes. Here we focus on California's recently collapsed fall-run Chinook salmon (*Oncorhynchus tshawytscha*) and ask whether portfolio effect induced buffering is observed across the complexity hierarchy from individual populations to populations within a river basin (Sacramento, San Joaquin) to the entire Central Valley. Some buffering was observed when comparing the coefficient of variation in adult returns to a given river basin with its constituent populations but not when comparing returns to the entire Central Valley with its constituent basins because of disproportionately many fish returning to the Sacramento Basin. Moreover, we report that positive correlations in population dynamics between rivers were stronger in the last 25 years of the study compared with the first 25 years. Together, these results suggest evidence of only a weak portfolio effect that has deteriorated in recent years. Nonetheless, we also report that correlations between rivers decreased significantly with distance, suggesting that some biocomplexity remains. Our results suggest that the greatest potential for strengthening the portfolio effect would come through restoration of San Joaquin Basin populations, which at low abundance currently contribute little to the overall buffering capacity despite low cross-basin correlations.

Résumé : Des travaux récents ont souligné l'importance de la diversité entre les populations pour favoriser la stabilité des complexes de populations. Nous nous intéressons ici à la montaison d'automne de saumons chinook (*Oncorhynchus tshawytscha*) qui s'est récemment effondrée en Californie et nous cherchons à savoir s'il se produit un phénomène tampon causé par un effet portefeuille dans la hiérarchie de la complexité à partir des populations individuelles, aux populations d'un bassin versant (Sacramento, San Joaquin) et à l'ensemble de la Vallée centrale. On observe un certain effet tampon lorsqu'on compare le coefficient de variation des retours d'adultes dans un bassin versant donné à ses populations constituantes, mais non lorsqu'on compare les retours de l'ensemble de la Vallée centrale à ses bassins constituants, parce qu'un nombre disproportionnellement élevé de poissons retournent au bassin de Sacramento. De plus, nous signalons que les corrélations positives dans la dynamique des populations entre les rivières sont plus fortes durant les 25 dernières années de l'étude que durant les 25 premières. Dans leur ensemble, ces résultats fournissent des indications de l'existence de seulement un faible effet portefeuille qui s'est atténué ces dernières années. Néanmoins, nous signalons aussi que les corrélations entre les rivières décroissent significativement en fonction de la distance, ce qui laisse croire qu'il demeure de la biocomplexité. Nos résultats indiquent que la façon la plus prometteuse de renforcer l'effet portefeuille serait de restaurer les populations du bassin de San Joaquin qui, à faible abondance, contribuent actuellement peu à la capacité tampon globale, malgré les faibles corrélations entre les bassins versants.

[Traduit par la Rédaction]

Introduction

The potential importance of species diversity in fostering stability has been long appreciated in community ecology (MacArthur 1955; Elton 1958; Tilman and Downing 1994). Recently, there has been a growing appreciation for the importance of interpopulation diversity to the stability of population complexes. Much of this latter work has focused on fish stocks, which often display considerable phenotypic diversity and, consequently, decoupled population dynamics, resulting in greater stability in annual returns (e.g., Hilborn

et al. 2003; Hutchinson 2008; Schindler et al. 2010) or reduced recruitment variability (e.g., Rogers and Schindler 2008; Greene et al. 2010; Moore et al. 2010). Such biocomplexity (sensu Hilborn et al. 2003) has been shown to be important for long-term sustainability of the larger stock complex and the fisheries that exploit these stocks (Hilborn et al. 2003; Anderson et al. 2008) because of a stabilizing portfolio effect (PE), wherein the variability of the aggregate of stocks is considerably less than the variability of the constituent stocks (Greene et al. 2010; Schindler et al. 2010).

Perhaps the best example of this stabilizing PE comes

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from research on the Bristol Bay sockeye salmon (*Oncorhynchus nerka*) complex (e.g., Hilborn et al. 2003; Greene et al. 2010; Schindler et al. 2010). This research has revealed that spatially aggregated returns to Bristol Bay were 41%–77% more stable (as measured by reduction in coefficient of variation (CV) in production) than individual stocks (Schindler et al. 2010), because of the diverse life histories within this complex (Greene et al. 2010). This work highlights the importance of population diversity for stabilizing resource flows to industries and ecosystems and contributes to a growing body of research emphasizing the importance of biocomplexity among fish stocks in promoting stability (e.g., Hutchinson 2008; Olsen et al. 2008). Aggregated stocks are buffered to changing conditions by a diversity of responses made possible by behavioral (Kerr et al. 2010) and life history diversity (Greene et al. 2010), which reflects both genetic diversity and phenotypic plasticity in the constituent stocks, as well as habitat heterogeneity (Oliver et al. 2010). However, it is also important to realize that some degree of stabilization should be expected in any aggregate measure made by summing variable components unless those components are perfectly correlated. In fact, this is a statistical inevitability (Doak et al. 1998).

Here we ask, what happens when biocomplexity is lost? We address this question by focusing on California's recently collapsed Central Valley fall-run Chinook salmon (*Oncorhynchus tshawytscha*), which support the California and southern Oregon Chinook salmon fishery. In spring 2008, state and federal fishery managers imposed an emergency closure of this fishery because of anticipated poor returns (Lindley et al. 2009). The fishery closure represented the first in the fishery's 157 year history. California's Central Valley Chinook salmon have been impacted by various anthropogenic activities (e.g., dams, habitat loss, hatcheries), all of which have likely contributed to a loss of biocomplexity.

We use long-term time series data for multiple populations of fall-run Chinook salmon breeding in California's Central Valley to test for evidence of a weak PE in this collapsed stock complex. We expect much biocomplexity has been lost because of degradation of the system, but the potential for a PE remains because the Central Valley contains multiple rivers with remaining stocks. Here we quantify variation in returns across the complexity hierarchy from individual rivers to the aggregated stocks and quantify the degree of independence in dynamics between the different rivers. We hypothesize that there should be some buffering even in a degraded system because the component stocks will not be perfectly correlated. We thus predict that there will be a measurable PE in the Central Valley despite its degraded state and that the degree of buffering will increase with an increasing number of component stocks making up a stock complex. In addition, we hypothesize that degraded basins will contain populations exhibiting little biocomplexity, resulting in higher mean correlations between their constituent rivers and less buffering.

Materials and methods

The system

Pacific salmon are structured into discrete breeding populations because of their natal homing behavior (e.g., Dittman

and Quinn 1996). These reproductively isolated populations are then subject to local selection pressures, including a suite of local biotic and abiotic factors. Many fitness-related traits are heritable (Carlson and Seamons 2008), thus allowing for natural selection to drive adaptation to local conditions. The combination of natal homing and their use of a diversity of breeding and rearing habitats results in considerable intraspecific variation in phenotypic traits and population productivity. Historically, Chinook salmon breeding in the Central Valley rivers displayed extraordinary life history diversity (e.g., Fisher 1994; Yoshiyama et al. 2000; Williams 2006). Indeed, this is the only system across the entire range of the species known to contain four distinct breeding migrations or "runs" (fall, late fall, winter, and spring). Moreover, each of the four major Central Valley runs was historically composed of several distinct stocks, each breeding in distinct sites and, thus, encountering distinct local conditions and exhibiting distinct life histories (Lindley et al. 2007).

Construction of dams on nearly all of the major rivers in the Central Valley resulted in a selective loss of habitats, which disproportionately affected certain life history components (e.g., Lindley et al. 2007; McClure et al. 2008). Dam construction resulted in 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 historic breeding sites and modified flow and temperature regimes. To mitigate for lost breeding habitat, 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), presumably because of 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). Even more alarming is the recent finding that over 90% of the fish captured in the ocean fishery are of hatchery origin (Barnett-Johnson et al. 2007), suggesting that the fall-run stock is composed largely of hatchery-produced fish. An overall goal of ours is to understand the extent of buffering achieved in this system given the current state of the habitat and management activities, and consequently we focus our analyses on total adult returns, which includes both natural and hatchery production.

Adult production data

All of the analyses described herein are based on estimates of total (natural and hatchery production combined) adult returns for fall-run Chinook salmon to rivers in the Central Valley of California, USA (Fig. 1). These numbers were obtained from the CHINOOKPROD data set, maintained by the US Fish and Wildlife Service's Anadromous Fish Restoration Program (http://www.fws.gov/stockton/afrp). This data set is an attempt to estimate both natural production ("wild" fish) and total production (natural production + hatchery production), and we focused on the latter. These totals reflect escapement as well as ocean and in-river harvest. These data have been collected over a period of over five decades by multiple researchers using multiple methods. There are many caveats (e.g., different sampling methods in different time periods and sites) and many sim-

Fig. 1. Map of the Central Valley in California, USA, with our study rivers indicated. The five populations supported by hatchery production are denoted with an asterisk.
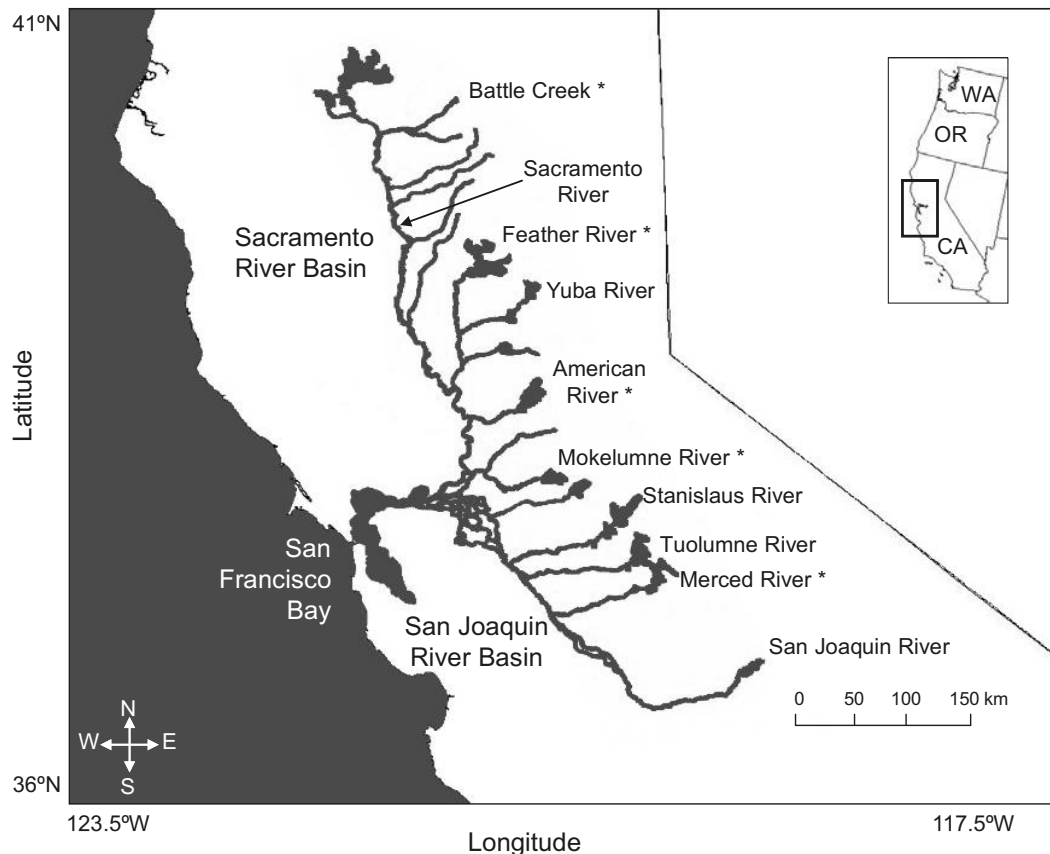
plifying assumptions (e.g., all stocks subject to the same ocean harvest rates) that clearly have the potential to influence the final estimates of adult returns to different sites. We relied on expert opinion to guide our choice of which data to use for analyses, for example, the underlying escapement data (i.e., GRANDTAB data, also available from http://www.fws.gov/stockton/afrp) are those used by management agencies, such as NOAA Fisheries (e.g., Lindley et al. 2007; Williams et al. 2007; NMFS 2010). Additionally, we performed simulations to explore the possible impacts of observation error on our analyses, which we found to be minimal (Appendix A).

We restricted our analysis to nine rivers, representing both river basins, for which data were available for at least 51 of the 52 years from 1957 to 2008. From the Sacramento River Basin (hereafter SAC 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 (hereafter SJ 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.

We were thus able to assess buffering across the full complexity hierarchy from individual rivers to the two river basins to the entire Central Valley. We note two special cases: the Mokelumne River (SJ Basin) and Battle Creek (SAC Basin). The Mokelumne River is a special case because although it naturally flows into the San Joaquin River, the

Delta Cross Channel carries water (and potentially fish) from the Sacramento River into it as well. Battle Creek also represents a special case because counts on this river show an obvious upward trend since the 1980s that may inflate our estimate of variation in that system. Thus, we repeated all analyses of the SJ Basin with and without the Mokelumne River and all analyses of the SAC Basin with and without Battle Creek.

Quantifying buffering induced by the PE

Pooling all years together, we calculated the CVs in adult returns for each river separately. We quantified potential buffering induced by the PE by comparing the mean CV for individual rivers with the CV calculated at larger scales, first pooling together all production within each basin and finally pooling together all rivers in our data set (see also Schindler et al. 2010). We used total adult returns rather than an index of productivity (e.g., recruits per spawner) because our data did not allow distinguishing among returning adults from different birth-year cohorts. Because we are missing data from the Stanislaus River in 1982, we excluded 1982 from all calculations of CV. We excluded 1982 regardless of whether the Stanislaus River was included in a calculation to avoid confounding effects of using different data sets for the other rivers for calculations including and excluding the Stanislaus.

To assess the importance of the number of substocks in buffering the total stock complex, within each basin we also compared the CV calculated for each river independently with that calculated for each possible grouping of two, three, four, and five rivers. We did not attempt to assess this rela-

Fig. 2. The absolute contributions of fall-run Chinook salmon from the two major river basins (black area: San Joaquin; grey area: Sacramento) within California's Central Valley to the total adult production (catch plus escapement). Note that this is a stacked plot so that the sum of the black plus grey areas represents the total returns to the Central Valley.
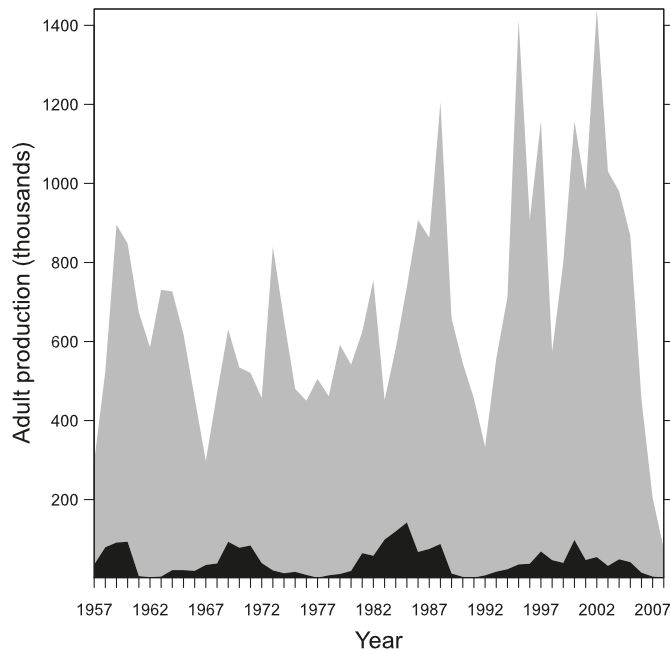

tionship statistically because the data violated several assumptions of regression and other common model-fitting tools: the variance is nonhomogeneous, the number of replicates varied across values of the independent variable, and there was non-independence among data points since the populations in each river contribute to multiple data points.

Quantifying degree of independence in dynamics between different rivers

To assess the degree of independence between dynamics in the different rivers, we calculated Pearson's correlation coefficients between all pairs of rivers. When testing the statistical significance of each correlation coefficient, we used one-tailed tests because we were specifically interested in positive correlations between rivers that would indicate synchronous dynamics. In testing for the significance of correlations, we adjusted the degrees of freedom to account for temporal autocorrelation in return numbers using the methods of Pyper and Peterman (1998).

We compared the mean level of correlation between basins and across basins using Wilcoxon rank sum tests because correlations were typically not normally distributed. We used one-tailed tests on the hypotheses that mean correlation would be higher within basins than across basins, and that mean correlation would be higher in the more degraded SJ Basin. We examined the relationship between the distance between rivers and correlations in their dynamics using Mantel tests (Legendre and Legendre 1998) on the entire Central Valley and within each basin separately. The distance between each river was calculated based on the river distances between the confluences of each river with the mainstem Sacramento or San Joaquin rivers, with three exceptions.

Fig. 3. Estimated number of fall-run Chinook adults produced each year on the focal rivers in the Sacramento River (*a*) or San Joaquin River (*b*) basins.
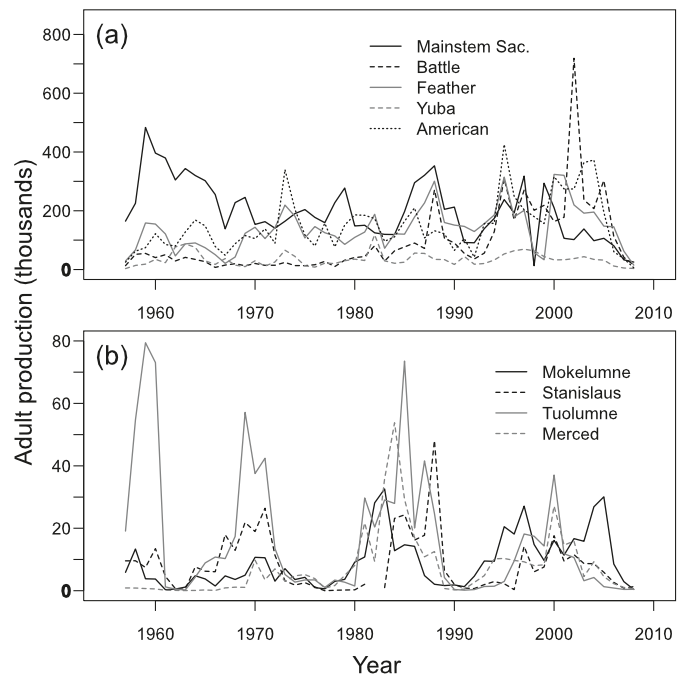
First, we defined the "confluence" for the mainstem Sacramento to be Princeton Ferry, the location above which censuses were taken for the mainstem Sacramento return numbers. Second, as Battle Creek flows into the mainstem Sacramento above this point, we considered Battle Creek and the mainstem Sacramento to be coincident in space. Finally, we considered the Feather and Yuba rivers coincident because the Feather flows into the Yuba upstream of its confluence with the mainstem Sacramento. We obtained these distances from the NHDPlus data set (http://www.horizon-systems.com/nhdplus/).

We performed an additional comparison between the first 25 years and last 25 years of our data set to explore whether there was evidence for a weakened PE over time. We calculated correlations among river returns and reductions in CV at various levels of aggregation as before. In addition, we checked for a temporal change in the evenness of the system by computing the Shannon diversity index (Shannon 1948; Krebs 1989) for mean returns to rivers in the various basins in both time periods.

All statistical analyses used R (R Development Core Team 2010). For Mantel tests, we used the "mantel" function in package "vegan" (Oksanen et al. 2011). Tests of the significance of correlation coefficients used R code modified from Rogers and Schindler 2008, available upon request.

Results

Buffering induced by the PE

The total return to the SAC Basin was typically an order of magnitude larger than that to the SJ Basin (Fig. 2). Estimated production for each river varied somewhat asynchronously through time (Fig. 3), with a range of means and variability (Table 1).

Table 1. Mean, standard deviation (SD), and coefficient of variation (CV) in the estimated number of fall-run Chinook adults produced each year on the focal streams in the Sacramento River (*i*) or San Joaquin River (*ii*) basins.

	Sacramento River Basin					San Joaquin River Basin			
	Mainstem	Battle	Feather	Yuba	American	Mokelumne	Stanislaus	Tuolumne	Merced
Mean	200 270	95 818	137 791	33 156	149 707	8 791	8 417	16 493	7 551
SD	100 309	123 449	75 013	20 201	93 604	8 060	9 223	20 868	10 369
CV	0.501	1.288	0.544	0.609	0.625	0.917	1.096	1.265	1.373

The mean CV for returning adult numbers for individual SAC Basin rivers was 0.714 ± 0.325 (mean ± standard deviation, SD) or 0.570 ± 0.058 when excluding Battle Creek. Pooling all rivers within the SAC Basin together reduced the CV to 0.440 (Fig. 4*a*), a 38% reduction compared with the individual river mean (or to 0.375 for a 34% reduction when excluding Battle Creek). The mean CV for returning adult numbers for individual SJ Basin rivers was 1.163 ± 0.200 (or 1.245 ± 0.140 when excluding the Mokelumne River). Pooling all rivers within the SJ Basin together reduced the CV to 0.850 (Fig. 4*a*), a 27% reduction compared with the individual mean (or to 0.987 for a 21% reduction when excluding the Mokelumne River). By this measure, buffering is more effective in the SAC Basin, although some of this increased buffering may be attributable to the larger number of rivers pooled in our data set for the SAC Basin. (Similarly, this may explain why we observed less CV reduction when excluding Battle Creek or the Mokelumne River.) We can remove this sample size effect by considering how much reduction in CV we would expect after pooling together different numbers of rivers in an ideal system, with zero correlation between rivers and equal average abundances. According to eq. 1 of Doak et al. (1998), we would expect a 55.3% reduction in CV when pooling together five ideal rivers and 50.0% reduction in CV when pooling together four ideal rivers; thus we would expect a 10.6% larger reduction in the CV for the SAC Basin before accounting for the effects of evenness and correlation structure. Instead, we observed a 40.7% larger reduction in CV for the SAC Basin, suggesting stronger buffering effects in the SAC Basin even after accounting for the number of rivers in each system. Pooling all rivers together yielded a CV of 0.430 (Fig. 4*a*), a 2% reduction compared with pooling just the SAC Basin rivers, which numerically dominated total production (Fig. 2), and a 49% reduction compared with pooling just the SJ Basin rivers.

In general, the buffering effect, as measured by percent decrease in CV, increased with the number of stocks making up a stock complex (Fig. 4*b*). While we were unable to rigorously compare the fit of alternate model formulations, it would appear that there are diminishing returns in the amount of additional buffering achieved as additional rivers are added (a result expected from theory, see Doak et al. 1998). Note that for both basins, the minimum possible CV is achieved by pooling only a subset of the available rivers (Fig. 4*b*).

Degree of independence in dynamics between different rivers

Taking data from all years together, the mean pairwise correlation between rivers within the SAC Basin was 0.268 ± 0.260 (mean ± SD) compared with 0.313 ± 0.190 for the SJ Basin, 0.285 ± 0.230 for all within-basin pairings, and

0.135 ± 0.258 for rivers from different basins (Table 2). The difference in mean correlations for within-basin versus across-basin pairings was significant (Wilcoxon $W = 216$, $p = 0.039$ one-tailed), while the difference in mean correlations within each basin was not. Excluding Battle Creek and the Mokelumne River from this analysis reduced the mean pairwise correlation among SAC Basin rivers to 0.257 ± 0.258 and increased the mean for SJ Basin rivers to 0.390 ± 0.142, a statistically significant difference ($W = 126$, $p = 0.047$ one-tailed).

Taking all rivers together, there was a statistically significant decrease in pairwise correlation with increasing distance between rivers, but this effect was slight and only explained a small amount of total variation (Fig. 5; Mantel test $r = 0.3432$, $p = 0.0409$). Within basins, there was no significant effect of distance between rivers on their pairwise correlations ($r < 0.128$ for both basins). With Battle Creek and the Mokelumne River excluded, the relationships between geographical distance and correlation remained statistically insignificant ($p = 0.255$ for SAC Basin, $p = 0.331$ for SJ Basin).

Testing for evidence of a weakened PE

To test for changes in the strength of the PE through time, we compared the strength of the PE in the first and last 25 years of our data set. This does not represent a comparison with pristine conditions, but could detect evidence for ongoing deterioration of the PE. We found that for the SAC Basin, pooling rivers together reduced CV by 46% in the first 25 years but only 28% in the last 25 years, suggesting ongoing deterioration of the PE. By contrast, reduction in CV was similarly small in both halves of our data set for the SJ Basin (19% in first half, 23% in second half). The weakening PE in the SAC Basin seems to have been driven largely by increasing correlation among rivers (from 0.23 to 0.39), since evenness increased only slightly during this period (Shannon diversity index increased from 1.34 to 1.51). Correlations also increased somewhat for the San Joaquin system (from a mean of 0.31 to 0.37), but this was offset by increasing evenness (Shannon diversity index increased from 1.15 to 1.37).

Discussion

Our analysis of California's recently collapsed Central Valley fall-run Chinook salmon yielded several salient results. First, despite the genetically homogeneous (Williamson and May 2005) and collapsed (Lindley et al. 2009) state of this stock complex, some variance buffering in adult returns was achieved. For example, adult returns to the Central Valley were 2%–53% more stable (as measured by reduction in the CV of returns at various scales of aggregation) than the variability in component stocks. This reduction suggests that

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Fig. 4. Coefficient of variation (CV) in production as a function of the number of rivers pooled together to represent stock complex dynamics. In panel (*a*), we show the CV for individual rivers as well as the mean CV for individual rivers within each basin (error bars are ±1 standard error, SE), for each basin with all rivers pooled, and for the entire Central Valley with all rivers from both basins pooled together. In panel (*b*), we show the CV of each possible grouping of one, two, three, four, or five rivers from within each basin. Circles are from the SAC Basin; squares are from the SJ Basin.
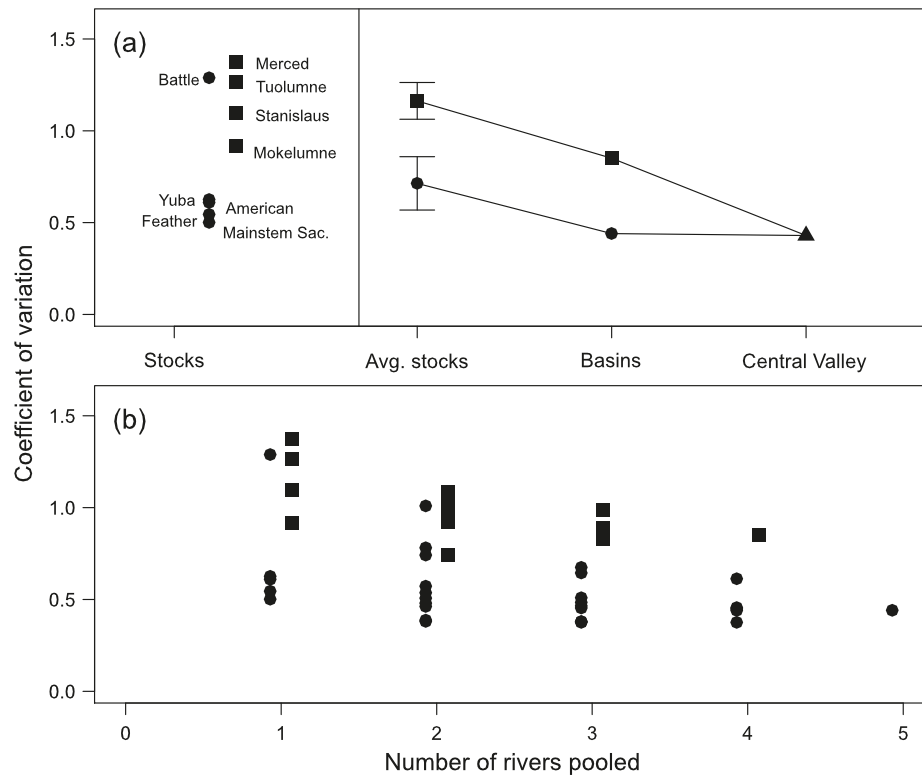
Table 2. Pairwise correlations between each pair of rivers, for all years combined.

|	Main.	Battle	Feather	Yuba	American	Stanislaus	Tuolumne	Merced
Mainstem	—	−0.110	0.085	0.188	−0.063			
Battle		—	0.487*	0.213	0.552*			
Feather			—	0.242	0.668*			
Yuba				—	0.422*			
Mokelumne					—	0.084	0.122	0.498*
Stanislaus	0.225	0.177	0.273	−0.062	0.02	—	0.551*	0.339
Tuolumne	0.374*	−0.098	0.062	−0.131	−0.105		—	0.281
Merced	−0.185	0.21	0.275	0.037	0.252			—

Note: An asterisk (*) indicates significant correlation at $p < 0.05$ in a one-tailed test after accounting for temporal autocorrelation. Within-basin correlations are shown above the diagonal (highlighted with dashes), across-basin correlations are shown below the diagonal. Note that the Mokelumne does not appear as a column and the American does not appear as a row, as this allows the most compact table.

some buffering exists against reaching dangerously low abundances and effective economic extinction of the fishery. The weak PE that we observed was due largely to the nonperfect correlations in returns among rivers even in the face of reduced genetic diversity (Williamson and May 2005). Moreover, we observed a weak but statistically significant decrease in pairwise correlations with increasing distance between the focal rivers and lower correlations across basins than within. It is possible that observation error may inflate our estimate of PE strength, but as noted earlier, some degree of buffering is a statistical inevitability — even in degraded systems. Moreover, observation error would only weaken our ability to find significant geographic patterns in correlations (see Appendix A). Together, these results underscore the im-

portance of maintaining multiple stocks even within degraded systems and highlight the possibility of improving buffering in degraded systems by fostering biocomplexity.

Second, despite the fact that some buffering was achieved in this degraded system, several lines of evidence suggest that the Central Valley fall-run Chinook stock complex represents a weak portfolio of stocks. For example, adult returns to the Central Valley as a whole were only 2% more stable (as measured by reduction in CV) than returns to the SAC Basin. This result reflects the considerable difference in adult returns to the two river basins. In particular, the SJ Basin contributes only a small amount to total adult returns to the Central Valley, and consequently, the variability in Central Valley production is driven largely by the variability in pro-

Fig. 5. Pairwise correlations between rivers within basins and across basins. The horizontal line at $y = 0$ indicates a correlation of zero and divides the plot into those correlations that are positive (above) versus negative (below). Circles are from the SAC Basin, squares are from the SJ Basin, and triangles represent cross-basin pairings.
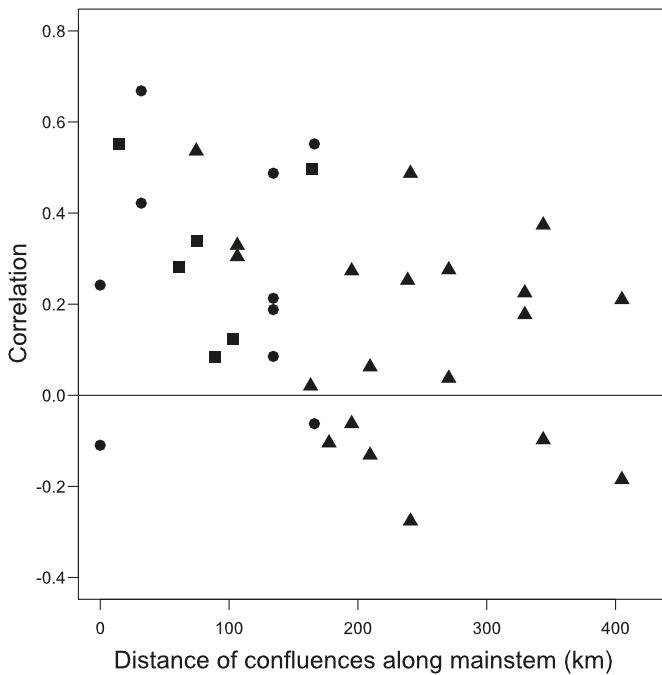
duction from the SAC Basin, and the small San Joaquin stocks contribute little buffering to the system. Moreover, production of rivers within the SJ Basin were more correlated (all pairwise correlations were positive, and 3/6 were significant) compared with production of rivers within the SAC Basin (all pairwise correlations were positive, and 4/10 were significant). One explanation for the apparently linked demography of the San Joaquin stocks is a shared environmental stressor that disproportionately impacts SJ Basin salmon. In general, salmon migrating downstream through the SAC Basin have a relatively direct downstream migration path to San Francisco Bay. In contrast, salmon migrating from the SJ Basin have to outmigrate through the south–middle delta to reach San Francisco Bay. This seemingly more difficult migration pathway (e.g., Brandes and McLain 2001) is a shared obstacle that the San Joaquin stocks must overcome and likely contributes to the higher observed correlations among the San Joaquin stocks.

Additional support for our conclusion of a weak PE in the Central Valley system derives from a comparison of the observed degree of reduction in CV to what would be achievable in an ideal system (even abundances with zero correlation). We found that pooling together the five rivers of the SAC Basin reduced CV by 38%, pooling together the four rivers of the SJ Basin reduced CV by 27%, and pooling together all nine rivers of the Central Valley reduced CV by 40%. In an ideal case, Doak et al. (1998, their eq. 1) show that the achievable reduction in CV would be 55%, 50%, and 67% for pooling together five, four, and nine populations, respectively. Thus, considerably less reduction in variance is achieved than in the ideal case, especially when pooling together the SAC and SJ basins. This is despite the

possibility that measurement error inflated our estimate of CV reduction.

Of course, even in a pristine system, we would not necessarily expect exactly equal abundances or lack of correlation among streams, since returns would be strongly affected by shared ocean conditions. Unfortunately, there are no data available to quantify how much buffering this system was capable of in the past or even how well correlated and how even in abundance the component rivers were. However, our comparison of the estimated strength of the PE in the first and last 25 years of our data set suggests a weakened PE in this stock complex in more recent years. This result seems to have been driven largely by increasing correlation among rivers within the SAC Basin — a pattern that was also observed among rivers of the SJ Basin although to a lesser degree. This does not represent a comparison with pristine conditions but nevertheless suggests evidence of recent deterioration of the PE in this stock complex.

Third, we observed "diminishing returns" in terms of how much buffering was achieved through the addition of more stocks, as measured by the CV, although of course adding rivers has the added benefit of increasing the total stock complex size. Additionally, we found that a careful choice of a few uncorrelated stocks actually produced better buffering, as measured by the CV, than all stocks combined. This latter result was unexpected and leads us to suggest that caution is warranted when interpreting buffering results using the CV approach.

Coefficient of variation as a metric of stability

Earlier work quantifying the PE in Bristol Bay sockeye salmon focused on a system with few anthropogenic impacts beyond harvest (e.g., Hilborn et al. 2003; Greene et al. 2010; Schindler et al. 2010). In stark contrast, Central Valley Chinook salmon are subject to multiple anthropogenic impacts that interact in complex ways, including loss of breeding and rearing habitat due to an extensive network of dams, extensive flow alterations both in rivers and through the Sacramento–San Joaquin Delta, substantial influence of hatchery-reared salmon, and the presence of mixed-stock fisheries that do not discriminate between relatively strong (hatchery-produced) and weak (naturally produced) stocks (for another example from a system experiencing multiple anthropogenic impacts, see Moore et al. 2010). Our expectation was that there would be little evidence of portfolio-induced buffering across the complexity hierarchy for the degraded Central Valley stocks, but this was not always the case — a result that led us to consider some of the weaknesses of the CV as a metric of stability.

Somewhat unexpectedly, for example, we observed a high degree of variance buffering in the severely degraded SJ Basin stocks, as measured by reduction in CV. Returns to the SJ Basin are typically an order of magnitude less than returns to the SAC Basin, and yet pooled returns to the SJ Basin were reduced by nearly as much as pooled returns to the SAC Basin (38% vs. 27% reduction in CV compared with the mean CV for individual rivers within a basin for the SAC and SJ basins, respectively). Because the CV is calculated as the standard deviation divided by the mean, variation in the CV among stocks can reflect differences in standard deviation about the mean or differences in the means themselves. In

the case of the SJ Basin stocks, the high CVs observed for these stocks appear to be the consequence of the low mean returns.

Moreover, the buffering observed in the SJ Basin extended across the full complexity hierarchy from individual rivers to the basin (described above) and from the basin to the Central Valley. In contrast, efficient buffering within the SAC Basin was observed only when comparing individual rivers with the basin but not when comparing CVs for the SAC Basin with the Central Valley. This result highlights an important point, which is that effective buffering requires both low correlation among constituent stocks and comparable means. In other words, fluctuations in a large stock complex, like the Sacramento, will not be buffered through the addition of a small stock complex, like the San Joaquin, even if the two are negatively correlated (see also Doak et al. 1998, their eq. 6). Shared ocean conditions may limit the extent to which river dynamics can be decoupled, even if their environments and hatchery production practices are quite different. To that end, it is interesting to note that reduced correlations across basin boundaries may reflect differential use of the ocean by different stocks. Within the Central Valley, Myers et al. (1998) noted a tendency toward maturation at younger ages along with spawning later in the year for San Joaquin salmon, suggesting some difference in their ocean ecology. In other systems, Koseki and Fleming (2006) suggested that ocean dynamics operating at different spatial scales may be important in determining the dynamics of jack versus hooknose coho (*Oncorhynchus kisutch*). In a follow-up paper, Koseki and Fleming (2007) suggest differential importance of freshwater versus ocean conditions in synchronizing naturally produced versus hatchery fish. A better understanding of the spatial distribution of different components of population complexes would greatly improve our ability to understand the factors driving variation in their dynamics.

For all of these reasons, we suggest some caution in using CV as a metric of stability. Other important metrics that could be monitored include those with mechanistic links to reduced variability, such as (*i*) correlations among components of a stock complex (e.g., Rogers and Schindler 2008), (*ii*) life history diversity including age composition (e.g., Greene et al. 2010) or the timing of migrations, and (*iii*) evenness among components of a stock complex (e.g., this study) — all of which could be monitored through time. Of course, evenness that results from a uniform decrease in mean abundance is not an effective buffer against risk, and negative trends in overall abundance are an obvious sign of trouble regardless of CV.

Management implications

Our results suggest that for the most effective buffering in this system, restoring the SJ Basin populations should be prioritized. If even a single population within this basin could be increased to a size comparable to one of the SAC Basin populations, this would contribute substantial buffering to the system because of the generally low correlations across basins. One major question then becomes whether it is better to improve production in the SJ Basin by improving the environment, which may take a long time, or through hatchery production, which may foster homogeneity among rivers. Here we argue that restoring environmental heterogeneity,

which is the template that gives rise to local adaptations and diverse life history portfolios, will pay larger dividends in the long run. Projects designed to improve access to rivers in the southern part of the SJ Basin, for example, could restore populations with different life histories than those in the northern SJ Basin rivers, thereby improving the buffering capacity of the system. It is believed that the San Joaquin once supported a very large (but since extirpated) spring run (Yoshiyama et al. 1998). Both spring- and fall-run fish were found on multiple rivers in the SJ Basin, with "very large" populations on the Merced, Tuolumne, and upper San Joaquin rivers (Yoshiyama et al. 1998). A late fall run may have occurred on some rivers as well. Even partially restoring these numbers and this life history diversity would considerably aid buffering in the Central Valley Chinook salmon complex.

Moreover, ameliorating passage through the Sacramento–San Joaquin Delta holds substantial promise for improving the buffering capacity of the larger stock complex. If indeed difficult passage is why the San Joaquin run sizes are currently low, improving passage has the potential to increase run sizes on several San Joaquin rivers simultaneously, assuming they have adequate habitat to support larger populations. In addition, removing this shared bottleneck may lead to different limiting factors on the different rivers, thereby reducing correlations between them. Having multiple rivers with larger, less correlated runs will greatly increase buffering induced by the PE within this salmon stock complex. In general, managers of other systems need to consider how restoring a particular part of a system will contribute to the evenness and correlation structure of the complex and target restoration accordingly.

Finally, because one of our goals was to understand the buffering capacity in this collapsed stock complex given the current state of habitat and management activities in the Central Valley, we did not treat differently rivers with ($n = 5$) and without ($n = 4$) hatcheries. In the future, we plan to explicitly test how hatchery management activities influence evenness and correlation structure among these populations to illuminate the impact of management on the buffering capacity and stability of this stock complex.

Acknowledgements

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Appendix A

Simulations exploring the impact of observation error on estimated portfolio effect (PE) strength and power to detect geographic patterns in correlations among rivers

Because of varying degrees of documentation of the individual estimates making up the GRANDTAB data set, we cannot directly model observation error in our production estimates. However, we can attempt to remove some of the effect of observation error by smoothing our production estimates via a moving average. This builds upon part of the method described by Holmes (2001) for population viability analysis of noisy data. Although our analysis does not require every step of a method originally focused on estimates of mean and variance in growth rate, we do take the first step of estimating total population size (including both returning spawners and fish in the ocean) as a weighted sum of sequential counts, with the side benefit of reducing observation error. An equivalent approach (through scaling outputs back down to the magnitude of annual returns rather than total population size) using a moving average rather than a moving sum has previously been used to smooth salmon counts for comparisons across watersheds (e.g., Fujiwara 2008). We chose to use the running average approach for easier comparison with the mean and SD in returns used in the body of the paper. Since we cannot estimate the temporally varying proportion of fall-run Central Valley Chinook, which return at different ages (primarily ages 2, 3, or 4), we took an unweighted moving average of estimated returns over 3 years to yield a smoothed trajectory. This averaging likely reduced the contributions of both observation error and real population changes to variation in estimated returns. The smoothing reduced the SD in returns for each river by 19%–26% (SAC Basin) or 10%–21% (SJ Basin).

As a conservative test of the influence of observation error on generating patterns documented in the main text, we repeated our analysis on this smoothed data, which likely had "true" variation removed as well. To examine the potential for observation error to create spurious results, we regard the smooth trajectories as "true" and compare the results of analyzing the smoothed trajectories with trajectories to which we have added normally distributed error with mean 0 and a SD equal to 5%–150% of the SD for each river in the original (presmoothing) data set. We chose normally distributed observation error since even though population sizes are often lognormally distributed (because of a multiplicative process and thus multiplicative process error), counts themselves are

Fig. A1. Estimated strength of portfolio effect (PE, as proportional reduction in coefficient of variation (CV), solid symbols and solid lines) and pairwise correlations (open symbols and dashed lines) among rivers for simulations based on smoothed trajectories as a function of the amount of simulated noise (as percentage of standard deviation (SD) in the raw data for each river) added back in. Circles are from the SAC Basin, squares are are from the SJ Basin, and triangles represent cross-basin pairings. Error bars are ±1 SD from 100 simulations at each level of added noise.
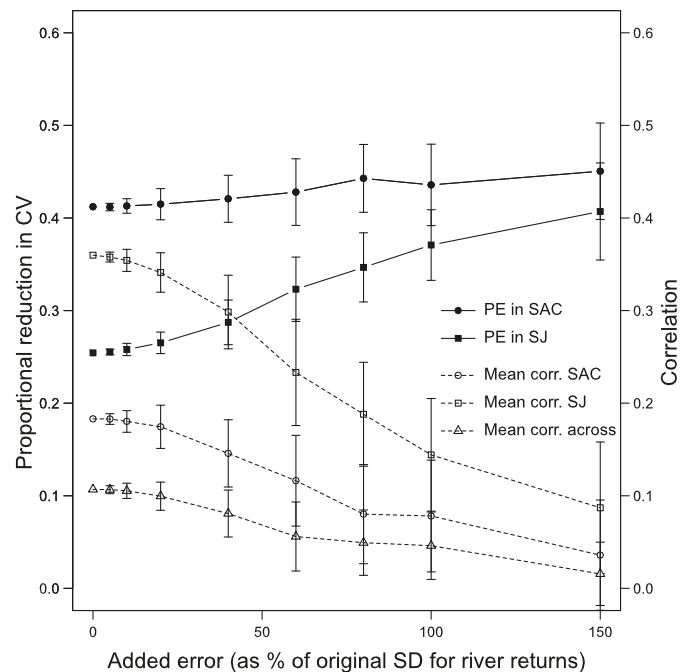
additive and thus likely have normally distributed errors. As a result, it is possible to generate a negative population size in our counts with large simulated error, which we convert to zero. For this reason, we excluded Battle Creek from our analysis, since (in addition to concerns raised in the main text) its large SD combined with low estimated returns prior to the 1980s meant that we would most often encounter negative population estimates when adding noise to Battle Creek.

Our main results from the text are closely matched by an analysis of the smoothed data set (noting that numeric comparisons should be made with the analyses that exclude Battle Creek). We observed more reduction in the coefficient of variation in the SAC Basin (41%, was 34%) than in the SJ Basin (25%, was 21%), with mean correlations among rivers highest within the SJ Basin (0.36, was 0.31), lowest across basins (0.11, was 0.14), and intermediate within the SAC Basin (0.18, was 0.26).

As we increased the simulated observation error (Fig. A1), we tended to underestimate correlations among rivers and tended to overestimate the degree to which CV was reduced by the PE, although the effects were small for added error on the order of 20%–30% of the original SD. Both of these effects are to be expected — adding uncorrelated noise will reduce correlations between trajectories and as a result lead to more effective buffering when adding noisy trajectories together.

Thus it is possible that we overestimated the strength of

the PE in the system — however we reiterate that some degree of PE is a statistical inevitability. Observation error would not lead us to find higher correlations or less buffering in the SJ Basin than in the SAC Basin, unless observation error made up a much larger proportion of variation in estimated SAC Basin returns. Likewise observation error might lead us to underestimate cross-basin correlations, but since it would similarly affect our estimates of within-basin correlations, it would not lead us to find lower correlations across basins than within either basin. It is possible that large observation error in the SAC Basin but not SJ Basin would lead us to underestimate within-SAC and across-basin correlations but not within-SJ correlations, with the result that when pooling together all within-basin correlations (half of which will be influenced by large observation error) they are higher than across-basin correlations (all of which will be influenced by large observation error). However, this seems unlikely since our main results are robust to an attempt to reduce the effects of observation error, and in fact we found a stronger PE (41% reduction in CV vs. 34%) and lower mean correlations (0.18 vs. 0.26) for the SAC Basin in the smoothed data set. Thus it appears that our smoothing removed more correlated signal (or bias) than uncorrelated noise. Also, despite whatever observation error was present, we still found statistically significant correlations for 4/10 (2/6 excluding Battle Creek) pairings in the SAC Basin.

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