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Tracking restoration of population diversity via the portfolio effect

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Abstract

1. Declines in diversity among populations managed together have diminished aggregate stability through a decreased portfolio effect. Although the portfolio effect has been quantified in a variety of ways, management recommendations for the recovery of lost diversity rarely specify the stability benefits possible through such improvements.

2. We introduce a metric, the Diversity Deficit (*DD*), that relates past losses and potential gains in aggregate stability to the changes in population diversity (i.e. covariability among population time series). We illustrate the use of this metric in retrospective analyses of the aggregate Sacramento River Fall-run Chinook salmon stock (*Oncorhynchus tshawytscha*), and project potential future improvements in stability through population diversity.

3. In the retrospective analysis, we removed individual time series from the stability calculations to determine their effects on times and locations of past losses in diversity and stability. We found an early threefold loss in stock stability resulting from the presence of a single tributary, the Sacramento River mainstem. Other shifts in stability resulted from an increase in variability of a single population, and from the synchronizing effects of low ocean survival that led to the 2008–2009 fishery closure. Only one, smaller increase in the *DD* (i.e. in lost stability) was due to portfolio-wide increases in covariabilities among tributary abundances.

4. In a prospective analysis using the *DD* applied to California salmon, we found that increasing biodiversity to the point of population independence and to its early high value would have reduced the probability of triggering a fishery closure.

5. *Synthesis and applications*. Analyses with the *Diversity Deficit (DD)* metric illustrate a way to identify the times and locations of losses in population diversity, and to quantify how much restoration of population diversity could increase stability, and thus benefit resource services. In our research, the benefit was a reduction in the probability of falling below a critical management threshold leading to fishery closure, but other tangible benefits (e.g. reduction in probability of extinction) would also be possible.

KEYWORDS
correlation, fisheries, management, population diversity, population synchrony, portfolio effect, restoration, Sacramento River Fall-run Chinook, salmon, stability

1 | INTRODUCTION

Ecological research has broadly supported an association between bio-diversity and the stability of ecosystem function and services (Cardinale, 2012; Duffy, 2009). Losses of biodiversity therefore raise concerns that the stability of ecosystem services will decline accordingly. Understanding and managing the potential for diversity losses to decrease stability in populations, communities and ecosystems are crucial tasks for agencies charged with ensuring persistent and predictable yield of natural resources (Cardinale et al., 2013; Koellner & Schmitz, 2006; McElhany, Ruckelshaus, Ford, Wainwright, & Bjorkstedt, 2000; Tilman, 1999).

The search for mechanisms underlying diversity–stability relationships has a rich history in ecology (Elton, 1958; Odum & Barrett, 2009; Tilman, 1996), motivating empirical and theoretical studies (e.g. Bai, Han, Wu, Chen, & Li, 2004; Cottingham, Brown, & Lennon, 2001; Ives & Carpenter, 2007; Lhomme & Winkel, 2002). An important step was the realization that pooling randomly fluctuating assets decreases variability, an effect termed the portfolio effect in ecology (Tilman, 1999), after the parallel concept in finance introduced by Markowitz (1952). However, while the financial concept is the same as in the eco-logical problem addressed here, the management questions differ. In finance, the question takes the form of selecting entities that vary in-dependently, while the choice of actions that maximize independence among assets (i.e. individual components of ecosystems, communities or population complexes) is relevant in ecology.

Although diversity–stability studies have conventionally focused on diversity among functional groups or species (e.g. Sax & Gaines, 2003), intraspecific population diversity may better represent avail-able ecosystem benefits (Luck, Daily, & Ehrlich, 2003; Worm et al., 2006). For example, unique spawning groups may preserve beneficial portfolio effects for metapopulations of Atlantic herring, an important forage fish (Secor, Kerr, & Cadrin, 2009). In alpine ecosystems, fine-scale habitat and genetic differences contribute to persistence of a rare plant through diverse subpopulation responses (Abbott, Doak, & Peterson, 2017). Here, we follow other studies in taking the view that population diversity, in the form of statistical differences among popu-lation abundances, contributes to ecosystem performance and is rele-vant to the conservation of resources (e.g. Downing, Brown, & Leibold, 2014; Hilborn, Quinn, Schindler, & Rogers, 2003; Luck et al., 2003).

Pacific salmon stocks are a model system for assessing the value of population diversity, and portfolio effects more generally, for three reasons. First, each component population can be locally adapted to its own unique freshwater spawning habitat, resulting in a diversity of life histories among populations (e.g. Rogers & Schindler, 2011). Second, multiple component populations contribute to a broader aggregate group that has management significance, as decisions are commonly made at the level of these aggregated commercial and recreational fish-ery stocks (Hilborn et al., 2003). Accordingly, maintaining high diversity is a management goal for conservation of salmon in the US and Canada (DFO (Fisheries and Oceans Canada), 2005; Griffiths et al., 2014; McElhany et al., 2000). Third, aggregate abundance has ecological sig-nificance. Evidence suggests that top predators such as brown bears and trout integrate across diverse salmon populations (Ruff et al., 2011;

Schindler et al., 2013). Indigenous groups may similarly depend upon asynchronous pulses from different Pacific salmon populations for a se-cure protein source throughout the year (Nesbitt & Moore, 2016). Thus, changes in salmon population diversity can have broad, significant ef-fects on riverine and marine ecosystem services (Griffiths et al., 2014).

The question of how to manage for population diversity has gained urgency for California's largest salmon population, the Sacramento River Fall-run Chinook (SRFC). The coherent decline across SRFC component populations (a symptom of increased aggregate variability) led to unprec-edented low returns of fish to freshwater in 2007 and 2008 and subse-quent closure of the associated fishery during 2008–2009. The SRFC is composed of several component populations spawning in different tribu-taries within the Sacramento River Basin. The proximate cause of the low returns in 2007–2008 was poor ocean productivity during the period of ocean entry for the 2004 and 2005 brood year cohorts (Lindley et al., 2009). However, that report also noted that several factors could have homogenized the SRFC component populations and that restoring pop-ulation diversity could reduce the incidence of such extreme, low stock abundances. Potential homogenizing factors included reduced access to unique spawning habitats (via dam construction and diversion of rivers for human use) and the domesticating effects of augmenting the stock with hatchery juveniles (Lindley et al., 2009), which now comprise most of the population (Barnett-Johnson, Grimes, Royer, & Donohoe, 2007).

While the portfolio effect framework holds promise for under-standing how increasing population diversity could improve stability and ecosystem services of salmon and other species (e.g. Abbott et al., 2017; Secor et al., 2009), management application has been limited because benefits are seldom quantified in a policy context. In general, decision makers choose policy instruments based on the improve-ments possible (e.g. how much would a policy reduce the probability of extinction, how much would it increase sustainable yield in a fish-ery?). Thus, scientific recommendations to increase population diver-sity immediately raise the policy questions "how much?" and "what will be the associated benefits?" Therefore, management decisions in the context of the portfolio effect must estimate how much increased population diversity can reduce the aggregate stock's variability, and how that greater diversity can improve persistence and yield of the stock. Managers must also be able to compare the ecosystem benefits of increasing population diversity to the effects of other possible man-agement steps that aim to reduce variability and increase persistence.

1.1 | Quantifying population diversity

Although the performance of the population portfolio effect has been quantified in several ways, here we directly use a definition of stabil-ity, the coefficient of variation (CV). The CV (i.e. the relative temporal variability) for an existing aggregate of n separate time series is,

$$CV_{Current} = \frac{\sqrt{\sum_{i=1}^{n} \sigma_i^2 + \sum_{i=1}^{n} \sum_{\substack{j=1 \\ i \neq j}}^{n} \sigma_i \sigma_j \rho(i,j)}}{\sum_{i=1}^{n} \mu_i} \qquad (1)$$

$CV_{Current}$ includes summed means (μ_i) and variances in abundance (σ_i^2) for each tributary i and summed covariances in abundance for each tributary pair i and j, $Cov(i,j)$. The covariances are the products of the correlations in abundance between tributaries i and j (i.e. $\rho(i,j)$) and the standard deviations (SDs) of these same tributary pairs, yielding, $Cov(i,j) = \sigma_i \sigma_j \rho(i,j)$.

Population stability conferred by the portfolio effect has been quantified in several ways, which are well-represented among studies of salmon. One method assumes the average CV among streams represents a number of identical streams, and then calculates what the reduction in that CV would be if all streams were statistically independent (Carlson & Satterthwaite, 2011; Schindler et al., 2010), based on an expression by Doak et al. (1998) for identical assets. Similarly, Anderson, Cooper, and Dulvy (2013) quantify the portfolio effect as the ratio of a single asset's CV to the aggregate CV. Notably, an average asset CV does not appear in the expression for stability (Equation 1), and therefore how well it represents the aggregate stability of assets with various means and variances is difficult to determine. Another expression used to represent the stability of groups of salmon populations is the Sharpe Ratio (Griffiths et al., 2014; Moore, McClure, Rogers, & Schindler, 2010). The Sharpe ratio would be similar to the inverse of $CV_{Current}$ (Equation 1), except that in Moore et al. (2010), the time series variable for the numerator in Equation 1 was the temporal variance among stream *productivities* (i.e. the residuals from the streams, resulting from a fit in logarithms to the Ricker stock–recruit curve), and the denominator of Equation 1 was the mean productivity across the streams. When the Sharpe ratio is derived from residual-based productivities, it would not be a direct quantification of the stability of the portfolio of abundances. Others have used variables associated with stability, rather than expressions for the stability state itself. For example "evenness," the degree of similarity of the mean abundances in assets, was identified as a characteristic favouring stability (Doak et al., 1998), hence was calculated for salmon by Satterthwaite and Carlson (2015). Presumably effects of evenness would be included in the direct calculation of an aggregate CV. Another quantity tied to the stability state of a portfolio is the Synchrony Index (Loreau & de Mazancourt, 2008), calculated for salmon by Satterthwaite and Carlson (2015). The Synchrony Index is the ratio of the numerator in Equation 1 to that same quantity if all entities were completely synchronous. The Synchrony Index provides the relative synchrony among populations, but does not translate relative synchrony into an absolute measurement of stability; for that, the CV must be calculated.

Management aiming to utilize the stabilizing benefits of population diversity requires a means of relating stability to that diversity. In Equation 1, population diversity is represented by the correlations in abundances (i.e. the ρ_{ij}'s), which are dimensionless constants reflecting the degree of similarity (or synchrony) among populations. Those correlations appear only in the covariance terms, the second term in the square root in the numerator. To focus on the effects of correlations on the CV, we subtract the first term in the square root,

$$CV_{Null} = \frac{\sqrt{\sum_{i=1}^{n} \sigma_i^2}}{\sum_{i=1}^{n} \mu_i}, \tag{2}$$

from Equation 1, to produce a variable termed the Diversity Deficit (DD),

$$DD = (CV_{Current} - CV_{Null}) \tag{3}$$

Quantification of the DD will allow managers to focus on the management implications of population diversity (i.e. the correlations between streams) for the stability of the aggregate stock. Because the correlations are multiplied by SDs to produce changes in the DD, the effects of population diversity on stability are essentially magnified by the SDs of abundances for each stream. Therefore, managers seeking to reduce variability through a stronger portfolio effect will be interested in how the SD of each tributary changes with time. In focusing on the effects of population diversity, we fully acknowledge that management could also be interested in changing other variables (e.g. the values of mean abundances) that can affect stability, but do not reflect changes in population diversity.

Here we demonstrate the use of the DD in management in both retrospective and prospective modes, using the fall-run of Chinook salmon in the Sacramento River as an example. The retrospective analysis identifies statistical characteristics of the existing time series that indicate where (i.e. which tributary) and when changes in diversity occurred. This is a first step in determining potential causes of lost population diversity. The prospective analysis calculates the improvement we could expect from reversing the losses in population diversity, in terms of a reduced likelihood of a fishery closure due to low abundance, a valuable addition for practical applications.

2 | MATERIALS AND METHODS

2.1 | Data sources

We used production (spawner abundances plus harvested fish) time series for California's Central Valley Chinook salmon runs from the 2010 CHINOOKPROD dataset maintained by the US Fish and Wildlife Service. We focused on five tributaries of the SRFC stock (Sacramento River mainstem, Battle Creek, Feather River, Yuba River and American River) and used data for 1957–2010, following Carlson and Satterthwaite (2011). To visualize potential covariability more clearly, we plotted a scale-free form of these time series, their logarithms normalized to zero mean and unit variance.

2.2 | Retrospective analysis of changing stability

To identify the sources of any increases in aggregate CVs, we employed several approaches to determine when and where past changes in correlation occurred.

2.2.1 | Components of changing CV and DD

We compared moving time window calculations of $CV_{Current}$, CV_{Null} and DD to quantify the statistical sources of temporal changes in the portfolio effect. We made moving time window calculations
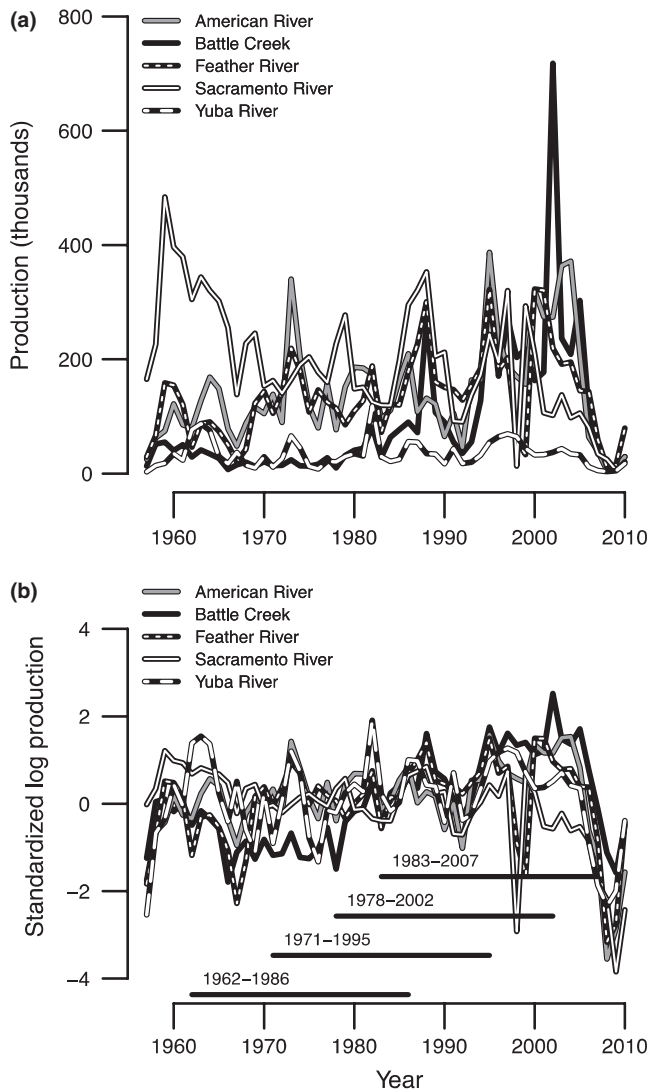
FIGURE 1 (a) Raw production (spawners plus catch) time series of the Sacramento River Fall-run Chinook stock divided by tributary from 1957 to 2010. Note that while this system as a whole is the Sacramento River Fall-run Chinook salmon stock, we refer to the spawners in the mainstem of the Sacramento River as the Sacramento "tributary." (b) Logarithms (base *e*) of Sacramento River Fall Chinook stock production time series for 1957–2010 normalized to zero mean and unit variance. Horizontal lines indicate the positions of the 25-year windows at times when the current and null values of aggregate CVs ($CV_{Current}$ and CV_{Null}; see text for explanation) were increasing rapidly as identified herein

of these variables for both 8-year and 25-year windows. We show the results for 25-year windows here, and the 8-year windows in Figure S1. We used the 25-year windows because they provided a more precise estimate of correlations, yet appeared to have adequate resolution (i.e. still able to detect sharp changes). The first comparison evaluated the difference between the time series of the aggregate CV calculated from the five tributaries ($CV_{Current}$) and the corresponding value of what the CV would have been if all correlations were zero (CV_{Null}). The third time series shows the *DD*, the difference between them.

2.2.2 | Removal of one tributary at a time

We removed the spawning populations of one tributary at a time from calculations of the *DD*s over 25-year sliding windows, then compared results to the calculation with all five tributaries visually to evaluate the robustness of our identification of the spatial and temporal changes in the portfolio effect. We also computed the correlation of the *DD* for each single tributary removed with that of the *DD* with all tributaries. The result is a measure of the sensitivity of our portfolio view to single tributaries (e.g. Britten et al., 2014).

2.2.3 | Past covariance and correlation structure

We computed covariances in abundances (i.e. production) between tributaries over sliding time windows to identify temporal changes in covariability evident in the *DD*. Calculations of covariance represent changes in covariability on the same scale as the other terms in $CV_{Current}$. To determine which covariance increases were due to changes in correlations, rather than simply changes in variances, we computed Pearson correlation coefficients for each tributary pair. Because the variance of the estimate of correlations between two series with no autocorrelation is the inverse of the sample size (Botsford & Paulsen, 2000), we calculated the standard error (*SE*) as the square root of the inverse of the window length, and used this value for the 90% confidence intervals (1.6 × *SE*). If we had included the effects of autocorrelation, the variance of the significance levels of the estimated correlations would be greater than those shown. We did not account for autocorrelation because the amount of autocorrelation would have been similar among the time series, hence would have little effect on comparisons.

2.3 | Prospective analysis of the effects of restoring diversity on fishery closures

The relationships between aggregate stability and managed levels of diversity (Equations 1 and 3) can also be used to provide managers with an estimate of the stability gains possible by achieving a certain level of diversity. Returns for past years represent unreplicated events, and thus they cannot be predicted to change by a specific amount under a specific, different scenario. However, it is a valuable exercise to extend the calculations beyond variance reduction to a quantity with greater relevance for SRFC managers: the potential for increased population diversity to reduce the probability of the fishery's closure. We compared the probability of future closure with the observed aggregate variance (in $CV_{Current}$) to the probability of closure with the variance reduced to two different levels: (1) the level existing at the start of the time series; and (2) that associated with CV_{Null} (i.e. by decreasing correlations to zero) calculated over the last 25 years of the time series. We focused on escapement values (number of spawners returning to freshwater) in this analysis rather than production because: (1) the population is managed for escapement (escapement threshold range = 122,000 to 180,000 fish); and (2) escapement and total production for the SRFC are correlated
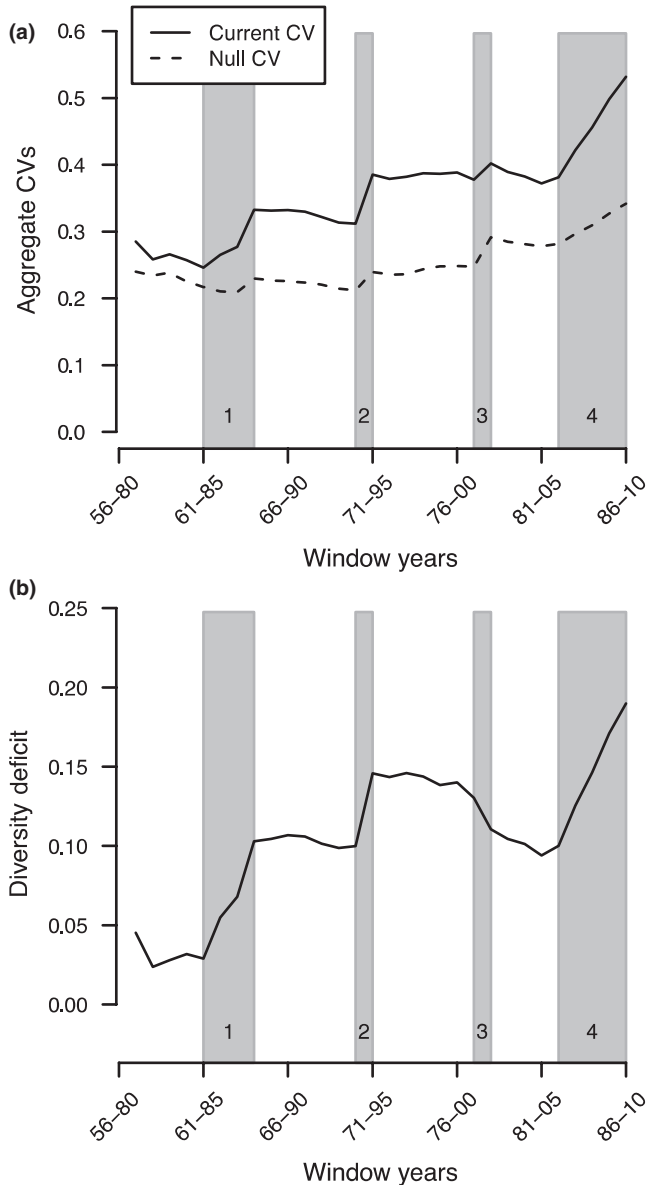
FIGURE 2 (a) Sliding 25-year windows of current versus null aggregate CVs ($CV_{Current}$ and CV_{Null}) for the Sacramento River Fall-run Chinook stock. The window range includes the first through last years of the 25-year time series for each calculated aggregate CV. (b) Sliding 25-year windows of the Diversity Deficit (DD; possible reduction in aggregate CV) relative to that achievable with all correlations equal to 0

($\rho = 0.86$). First, we fit a log-normal distribution to the escapement time series through 2010. Second, we found the new, reduced SD for the log-normal CV_{Null} by multiplying the SD for the log-normal $CV_{Current}$ by the ratio (on a non-logged scale) of the SDs of CV_{Null} to $CV_{Current}$. Third, we used the distribution with this new SD to calculate the probability of the fishery's closure (corresponding to the lower threshold of 122,000 returning spawners) under increased population diversity. We then compared the probability calculated with the SD for increased population diversity to the probability with the current, observed SD.

3 | RESULTS

For the SRFC, individual populations differ markedly in both their total abundance and their temporal patterns of abundance, with the Sacramento River mainstem population dominant in early years, and the Battle Creek tributary population dominant more recently (Figure 1a). Population variability generally appears to increase in recent years.

Relative correlation is visually more apparent in the time series of the normalized logarithm of production for the populations (Figure 1b). Populations appear to be relatively uncorrelated in early years, then become more correlated beginning in the mid-1980s. The populations then show divergent patterns in the late 1990s, when the Sacramento and Feather River populations decline for single years, and the other three populations do not. This is followed by more correlated dynamics during the SRFC stock collapse in the late 2000s (Figure 1b).

3.1 | Retrospective analysis of changing stability

3.1.1 | Components of changing *CVs* and *DD*

The $CV_{Current}$ for sliding windows generally increases in time, with four distinct shifts in value. These distinct shifts occur as the 25-year windows start to include each of the following end years: (1) 1986–1988, (2) 1995, (3) 2002 and (4) 2007 (Figure 2a). Following 2007, there is a steady increase in the $CV_{Current}$. These shifts are identified in subsequent figures as shaded regions. The CV_{Null} shows a similar saltatory pattern, with four smaller shifts in value that roughly coincide in 1988, 1995, 2002 and 2007, and an increasing trend near the end (Figure 2a). This similarity between $CV_{Current}$ and CV_{Null} suggests that changes in the mean-variance structure (i.e. Equation 2) are partly responsible for the distinct increases in $CV_{Current}$ over time. The first two shifts up in CV_{Null} appear to be less than those from the $CV_{Current}$ series, leading to an overall increase in the difference between the two series (i.e. the DD). The third shift (2002) is an important exception where the increase in the CV_{Null} appears to be greater than the increase in the $CV_{Current}$.

The time series of the DD (Figure 2b) shows the differences between the $CV_{Current}$ and CV_{Null} (displayed in Figure 2a) more clearly, and also is a direct indication of the amount by which lack of population diversity increases aggregate variability (i.e. decreases stability). Specifically, in the first shift, the DD increases from *c.* 0.03 to over 0.10 (Figure 2b), indicating a large loss in diversity. Following this approximately threefold change, the DD then plateaus to just over 0.10. The second shift in CV is associated with an increase in DD for 1995. However, the third shift in 2002 (increases in CV_{Null} and $CV_{Current}$) corresponds to a clear decline in DD. Note that this decline reflects the greater increase in CV_{Null} than in $CV_{Current}$ (Figure 2a). Because $CV_{Current}$ is CV_{Null} plus covariances (see Equations 1 and 2), the decline in $CV_{Current}$ suggests a decrease in covariances. In the fourth shift, the DD trends upward again (Figure 2b) as windows include more of the synchronous declines in 2007 and 2008. We also calculated the DD by replacing CV_{Null} with a CV that uses correlations from the first 25-year window; it shows only slight differences by comparison (Figure S2).
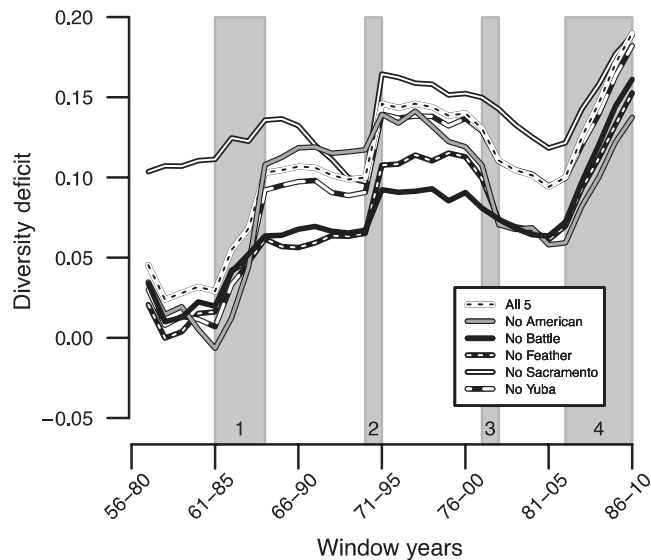
FIGURE 3 Sliding 25-year window calculations of the Diversity Deficit (*DD*; possible reduction in aggregate CV) for the Sacramento River Fall-run Chinook stock with: all five tributaries; American River tributary removed; Battle Creek tributary removed; Feather River tributary removed; Sacramento mainstem tributary removed; and Yuba River tributary removed
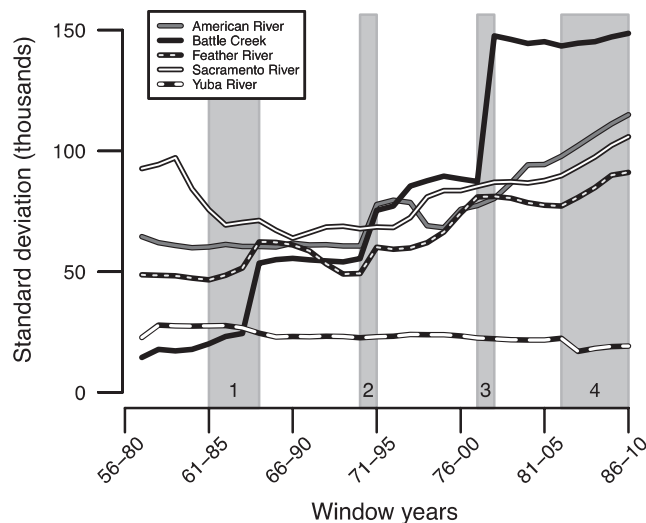

FIGURE 4 The 25-year sliding window standard deviations (*SD*s) for the five Sacramento River tributaries. The window range includes the first through last years of the 25-year production time series for each calculated *SD*

3.1.2 | Effects of single tributary removals

Plots of the *DD* with single tributaries removed (Figure 3) indicate the sensitivity of changes in the portfolio to the influence of single tributaries, while also providing clues to sources of increased SRFC variability over time. For example, without the Sacramento mainstem tributary, there was not the initial, rapid increase in the *DD* starting in 1986 that was present with all five tributaries included (Figure 3,

white dotted line). Instead, the *DD* was already quite high early in the series (Figure 3, white line). Thus, the cause of the first shift in *DD* must have involved the Sacramento mainstem, either through a change in its variance or a change in correlation with other tributaries. In addition, when the American River is removed (Figure 3, grey line), the second shift in *DD* is much smaller than the second shift with all five tributaries (Figure 3, white dotted line). Thus, elevated covariabilities associated with the American River were likely responsible for the increased *DD* at this point. Finally, when Battle Creek is left out of the calculations (Figure 3, black line), the third shift in *DD* during 2002 is much less compared to that with all five tributaries (white dotted line). This indicates that the third shift (the decrease) in *DD* was at least partly associated with Battle Creek.

Correlations between the *DD* computed with all five tributaries and each time series with a tributary removed indicated that three tributaries (first Sacramento mainstem, second American River and third Battle Creek) had important effects on the dynamics of the SRFC. However, the Sacramento mainstem population appears to contribute most to the loss of population diversity over time, resulting in the lowest correlation with all five tributaries (*r* = .85), followed by the American River tributary (*r* = .88), while the removal of other tributaries have less of an effect (*r* = .96–.99).

3.1.3 | Changes in tributary variability

As noted previously, changes in the amount of variability in each tributary can change the way that diversity affects stability because the *SD*s are the weightings in the sums over all correlations in the *DD*. There are early declines in variability of some tributaries, notably the Sacramento River, but the more interesting features here are the episodic upward shifts. Battle Creek has three substantial increases in *SD* at the times of the first, the second and the third shifts in the *DD* (Figure 4). Two other tributaries have a dramatic upward shift near the time of the second major shift in the *DD*. These increases in *SD*s merely amplify the effects of changing correlations. The effect of Battle Creek's large *SD* increase on the SRFC's aggregate variability is evident as a decline in *DD* when this tributary is removed (Figure 3, black line).

3.1.4 | Past covariance and correlation structure

Covariances between tributary pairs increase around the time of the first shift in *DD* for: Sacramento mainstem/Battle Creek, Sacramento mainstem/Feather River and Battle Creek/Feather River (Figure 5, upper right). Importantly, these shifts in covariance seem to stem from the changes in correlations (Figure 5, lower left). Notably, the correlations (and hence its covariances) for the Sacramento mainstem/Feather River increase from negative to positive values during these years. Thus, initially opposite dynamics between Sacramento River and Feather River may have helped keep the *DD* low prior to the first increase in 1986 (Figure 2b). Referencing the raw time series of production (Figure 1) supports the conclusion from the correlation analyses that the Sacramento River population declined prior
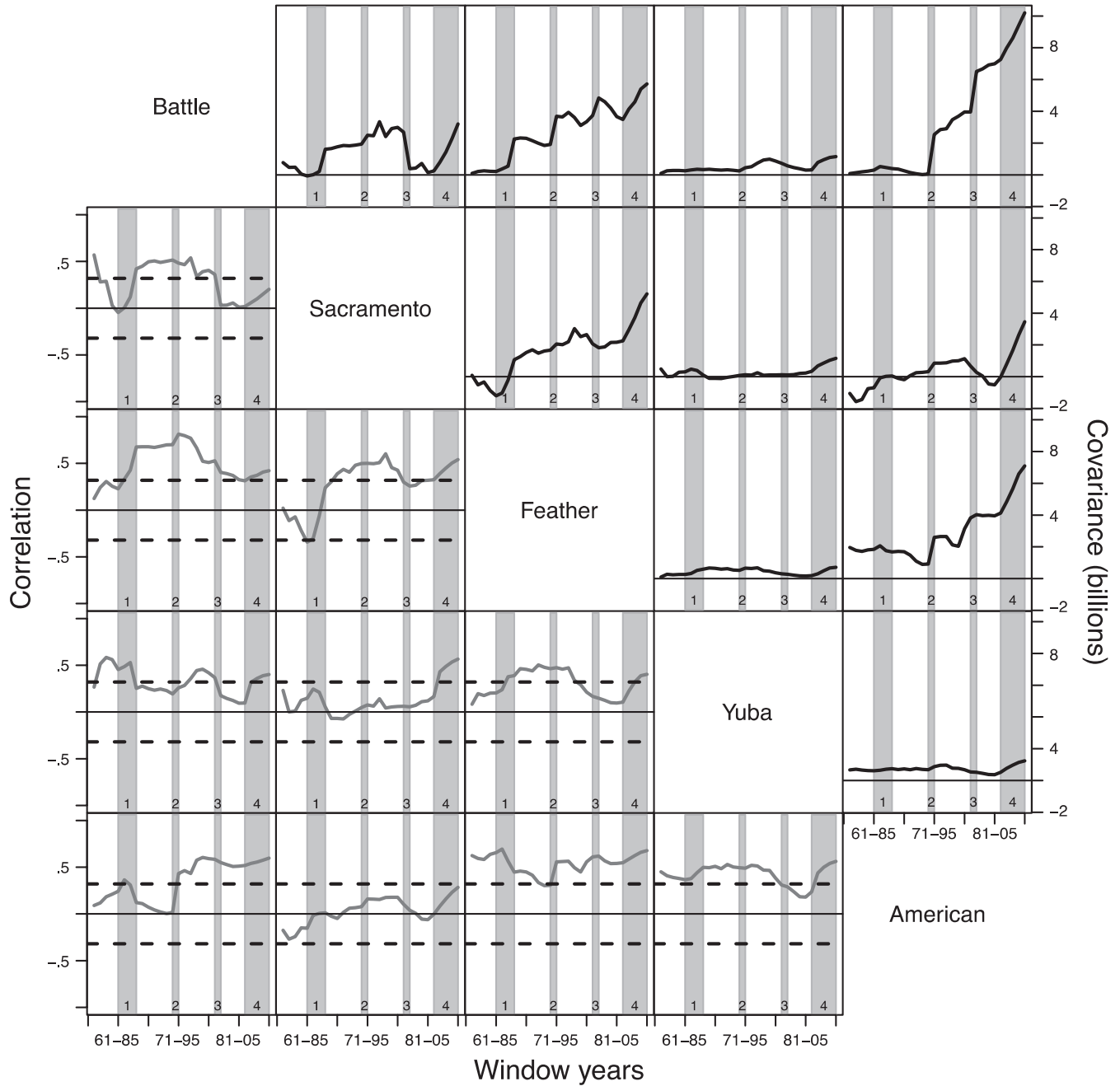
FIGURE 5 Matrix of population pair covariances (upper right; black lines) and correlations (lower left; grey lines) for the Sacramento River Fall-run Chinook stock. Each matrix element is a plot of the covariances or Pearson's correlation coefficients for one pair of tributaries within the stock, over sliding time windows. Correlation plots have dashed lines that define the 90% upper and lower confidence limits (1.6 × SE, where the SE is $1/\sqrt{\text{window length}}$). Tributary pairs are arranged from north to south, with labels along the diagonal

to around 1986, and these dynamics differed from those of Feather River. The increase in the *SD* identified above would have aided the upward shifts in covariances involving Battle Creek.

Concurrent with the second shift in the *DD*, covariances increase somewhat for American River/Feather River and Battle Creek/Feather River and more substantially for American River/Battle Creek. Indeed, prior to 1995, covariances between American River/Battle Creek were zero and increased by billions in 1 year (Figure 5). While the covariances associated with the American River appear to be driven by

increases in correlations (Figure 5, lower left), correlations do not appear responsible for most of the increased covariances between Battle Creek and the Feather River. Instead, increased *SD*s for Battle Creek and the Feather River are the likely causes.

During the third shift in the *DD*, a large decline in covariances to almost zero occurred for Battle Creek/Sacramento mainstem (Figure 5, upper right), and it appears to have been driven by a decline in correlation (Figure 5, lower left). A dramatic increase in covariance between the American River and Battle Creek (Figure 5,
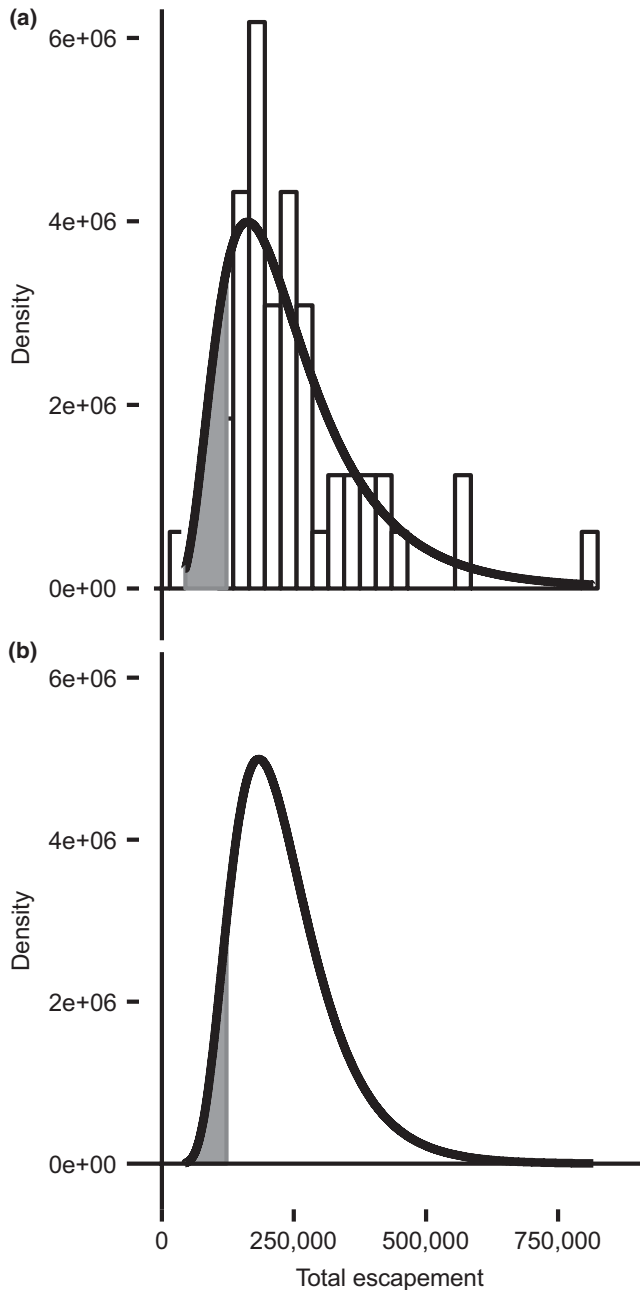
FIGURE 6 (a) Histogram of Sacramento River Fall-run Chinook stock escapement values (number of spawners) based on data from 1957 to 2010 (white bars) with a log-normal curve fit to them. (b) Distribution of escapement values if variance in stock abundances were reduced to that associated with the null CV (i.e. zero correlation; see text for further explanation). Shaded grey areas indicate the cumulative probabilities associated with closure of the fishery (less than or equal to 122,000 returning spawners)

3.2 | Reduction in the probability of the SRFC fishery closure

Based on a log-normal distribution with a mean and variance corresponding to the 1957–2010 escapement data, the *SD* of the distribution for the observed aggregate ($CV_{Current}$) was 142,939 fish (Figure 6a). If it had been possible to increase biodiversity to the point that tributaries were uncorrelated, this would have reduced the *SD* to 104,057 fish for CV_{Null} (Figure 6b). Such a reduction in *SD* would have decreased the probability of escapement values below the closure threshold from 0.14 (Figure 6a) to 0.08 (Figure 6b). If it were possible to increase biodiversity to the levels observed at the beginning (the first 25 years) of the time series, the *SD* of the distribution of annual abundances would have decreased to 63,013 fish. Consequently, the probability of escapement that would fall below the closure threshold would have decreased to 0.01 for this earliest observed, and therefore achievable, level of population diversity (results not shown).

4 | DISCUSSION

With continuing declines in biodiversity around the globe, natural resource policymakers and managers must determine the sources of diversity loss and the beneficial value of increasing population diversity to increase ecological persistence and stability.

In the specific application to SRFC salmon management, the results regarding times and places of changes in population diversity identify possible reducible causes of lost diversity. Most of the loss in diversity (a more than threefold increase in CV from 0.03 to 0.10) occurred at the point where the 25-year windows began to include the early to mid-1980s (Figure 2). Furthermore, the single tributary removed analysis indicates the Sacramento mainstem population contributed disproportionately to that increase (Figure 3); with only the four other tributaries, we would not have observed such a large loss in population diversity, or the associated reduction in stability. Moreover, direct examination of covariability (Figure 5) showed that the increased deficit in population diversity was due to positive jumps in covariability, and more specifically correlations, among the Sacramento mainstem, Battle Creek and Feather River, three adjacent locations. Early negative correlations between Sacramento mainstem and Feather River (before the first shift) may have resulted from a long, declining trend in Sacramento mainstem production that contrasted with increasing Feather River abundances.

With regard to possible exogenous causes of the first shift in *DD* (i.e. lost diversity), a recent analysis of hatchery practices indicated that while hatchery releases have continued since the 1950s, the practice of trucking hatchery juveniles to the estuary began in the early 1980s and has continued at a high level since the late 1980s (Huber & Carlson, 2015; Satterthwaite & Carlson, 2015). This practice was shown to increase the rate that salmon stray into other spawning streams upon returning to freshwater (Kormos, Palmer-Zwahlen, & Low, 2012), thus it could have diminished diversity. Satterthwaite and Carlson (2015) noted that the coincident increases in the 8-year

upper right) was not driven by an increase in correlation (Figure 5, lower left), so was likely caused by the dramatic increase in the *SD* of Battle Creek abundances. Finally, covariances for nearly all population pairs increase sharply in association with the fourth *DD* shift in 2007. In all scenarios, covariances with Yuba River are relatively constant, which is likely due to the population's low abundances (see Figure 1a).

windows of the Synchrony Index and estuary releases "strongly supports a role of estuary releases and straying in increasing synchrony." However, their synchrony index declined 20 years later to nearly the same level, while estuary releases remained at a high level. This may, in part, be due to the much lower precision in estimating correlations with 8-year, rather than 25-year windows (see Figure S1).

A second, smaller increase in *DD* (i.e. lost population diversity) (from 0.10 to 0.15; Figure 2b) occurred as sliding window analyses began to include the year 1995. The single tributary removed analysis identified American River as the likely cause of the *DD* increase around 1995, with the correlation analyses indicating that large increases in all three possible covariabilities among the American River, Battle Creek and Feather River were largely responsible.

The third shift in population diversity during 2002 essentially reversed earlier losses reflected in the *DD* from 1995 (Figure 2b). The single tributary removed analysis showed that Battle Creek played an important role in increasing independence among SRFC's component populations at that time (Figure 3). Our investigations of covariability suggested that a decoupling of Battle Creek from other tributary dynamics, particularly the Sacramento mainstem, contributed to the third shift in population diversity, a decline in 2002 (Figure 5). The covariance between Battle Creek and the American River also increased at that time (Figure 5, upper right), but the lack of increase in correlation at that time (Figure 5, lower left) suggests that the increase in the *SD* of Battle Creek in 2002 (Figure 4), was responsible. Battle Creek dynamics likely became decoupled from other tributaries because the number of spawners returning to Battle Creek rose quickly in 2002, while spawner abundances in other tributaries, particularly the Sacramento mainstem, did not (Figure 1a). Future studies could assess reasons underlying these divergent dynamics. Finally, all analyses suggest that no one tributary was responsible for the last identified decrease in population diversity, resulting instead from the synchronous decline of all populations in 2007 due to poor ocean conditions (Figure 1b).

The analyses of California salmon presented here illustrate an approach to quantifying the effects on stability of changes in both population diversity (*DD*) and asset (component population) variability, which could easily be adopted for other systems (e.g. herring as in Secor et al., 2009). Use of the *DD* in a retrospective analysis can reveal times and locations at which abrupt changes in population diversity and variability led to changes in aggregate stability. Importantly, these analyses focus on the statistical relationships in the time series, a useful precursor to identifying potential exogenous, causal variables. The *DD* can be used in a prospective analysis to determine resource management goals that could be achieved, a projection that rarely accompanies calls for increasing diversity. Here the goal was a potential reduction in fishery closures, but other performance measures are possible, such as avoiding a specified probability of extinction for the aggregate population. This approach to managing for population diversity is akin to methods currently used to manage species at risk, and catch in fisheries, where a quantitative expression of population persistence serves the role of a quantification of state. Calculations of the *DD* metric and other sliding window analyses would generally

be possible whenever abundance data were available, and they would provide a simple way to take advantage of the statistical information contained within empirical time series.

In summary, with the increasing number of instances of identified losses in population diversity around the globe, there is a need for decision makers: (1) to be able to quantify the current state of stability and population diversity, (2) to know what those have been under various past conditions, and (3) to know how much could be achieved through a strengthened portfolio effect. The analyses of the *DD* and variability described here, and illustrated with California salmon, outline an initial approach for managers and stakeholders, towards quantifying the increased stability associated with recovered population diversity.

AUTHORS' CONTRIBUTIONS

L.Y. and L.W.B. conceived the ideas and designed the analyses; L.Y. and D.P.K. analysed the data; and L.Y. and L.W.B. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Sacramento River Fall-run Chinook production estimates from the ChinookProd dataset are maintained by the U.S. Fish and Wildlife Service. Data from years 1952–2010 are available from the Dryad Digital Repository https://doi.org/10.5061/dryad.kt136 (Yamane, Botsford, & Kilduff, 2017).

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SUPPORTING INFORMATION

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