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Restoring freshwater habitat mosaic to promote phenotypic diversity and resilience of vulnerable salmon populations

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Cordoleani F.[1,2], Phillis C.[3], Sturrock A.[4], Willmes, M.[1,5], Whitman G.[6], Holmes E.[6], Weber P. K.[7], Johnson R.C.[2,6]

[1] Institute of Marine Sciences, Fisheries Collaborative Program, University of California Santa Cruz Santa Cruz, 1156 High Street, Santa Cruz 95064, USA

[2] National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Southwest Fisheries Science Center, 110 McAllister Way, Santa Cruz 95060, USA

[3] The Metropolitan Water District of Southern California, 1121 L Street, Suite 900, Sacramento 95814, USA

[4] School of Life Sciences, University of Essex, Wivenhoe Park, Colchester CO4 3SQ, United Kingdom

[5] Norwegian Institute for Nature Research, 5685 Torgarden, 7485 Trondheim, Norway

[6] University of California Davis, Center for Watershed Sciences, One Shields Ave, Davis 95616, USA

[7] Physical and Life Sciences, Lawrence Livermore National Laboratory, Livermore 94550, USA

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Abstract

Phenotypic diversity drives salmon resilience in the face of increasing environmental variability. But what happens when human activities fundamentally alter the habitat complexity that drives this diversity? And how can we restore habitats to recover diverse phenotypes that can persist in a warming climate? Here we looked at the impact of a large floodplain restoration effort on the abundance and climate resilience of the three remaining core natural spring-run Chinook salmon populations in the California Central Valley (Butte, Mill and Deer Creek). Butte Creek fish, that have unrestricted floodplain access, had higher overall productivity and faster juvenile growth compared to Mill and Deer Creek spring-run populations, and the proportion of floodplain inundation was positively correlated with Butte Creek adult abundance two years later. Butte Creek also had lower within-population phenotypic diversity and the smallest increase in population stability after the floodplain restoration (lowest decrease in coefficient of variation (CV)) compared with Mill and Deer Creek populations. The late-migrating juvenile (i.e., yearling) strategy, which was disproportionately important for the Mill and Deer Creek populations during droughts, was uncommon among Butte Creek adults (averaging 60% for Mill and Deer Creek vs. 0.3% of Butte Creek returns), and high interannual escapement variability, with relatively low adult abundances following some particularly dry years (e.g., return years 2010, 2017) was observed for Butte Creek, suggesting higher climate vulnerability for this population. We hypothesize that this is due to the limited availability of cold water pools in the Butte Creek watershed that are necessary to support late-migrating juveniles during the summer before they migrate to the ocean. Increased spring-run stock complex stability was found, post-floodplain restoration, when combining the three spring-run populations (i.e., lower aggregate CV). However, increased Mill, Deer and Butte Creek population dynamics synchronization was also observed post-restoration, which might increase the stock complex vulnerability to extreme climatic events. This study underscores the importance of restoring a connected mosaic of aquatic habitats across modified landscapes, such as cold water refuge and floodplains, to preserve multiple life-history pathways important for increasing salmon stock complex stability and abundance. These landscape-scale process-based habitat restoration efforts are likely to be crucial for the successful long-term recovery of vulnerable species in a rapidly changing climate.

Introduction

Habitat loss and homogenization from human activities (e.g., dam construction, agriculture) combined with climate warming, are major drivers of species extinctions (IPCC 2007; Kiehl 2011; IPBES 2019). Billions of dollars are invested annually to restore degraded or lost habitats for the recovery of vulnerable species, however, decisions often have to be made with limited data and across ecological and jurisdictional boundaries (BenDor et al. 2015;

Keeley et al. 2022). Recovering imperiled populations thus remains a daunting issue, and effective recovery actions and policies will be needed to avoid widespread human-induced extinctions (Bolam et al. 2023). A current limitation is that most conservation objectives focus on short-term abundance increases through localized habitat restoration efforts, but they rarely account for the interdependencies among habitats (Keeley et al. 2022), and the impact of future climate change which could lead to decreased (or increased) success in the long-term (Battin et al. 2007). With landscape simplification occurring at global scale (Foley et al. 2005) and projected temperature rises of at least 1.5°C in the next two decades (IPCC 2019), it is critical to understand how habitat restoration can enhance the resilience of vulnerable species to a warming climate.

Recent studies have demonstrated the importance of habitat heterogeneity and connectivity for providing long-term species stability through a changing environment, often resulting in increased population abundance (habitat mosaic concept; Stanford et al. 2005; Brennan et al. 2019). Furthermore, phenotypic diversity, which is widespread in nature, has been widely proposed as a mechanism leading to increased population and community stability, by buffering populations against environmental changes and extreme climatic events (the portfolio effect concept; (Hilborn et al. 2003; Miner et al. 2005; Ives and Carpenter 2007; Schindler et al. 2010; Cordoleani et al. 2021). However, there is limited research on the interaction between these ecological concepts - portfolio effect and habitat mosaic - and their potential application in informing restoration efforts. Specifically, little attention has been given to restoring habitat complexity at the stock complex scale to promote phenotypic diversity and enhance long-term species recovery goals.

Habitat contraction and simplification is of particular concern for species with a limited habitat range such as species that use freshwater for at least some parts of their life cycle (e.g., salmonids). In California's Central Valley (CCV), spring-run Chinook salmon (*Oncorhynchus tshawytscha*; CVSC) are at the southern edge of the native species' range, spawning and growing in a heavily modified freshwater environment. Spring-run were once the most abundant Chinook salmon run in the CCV, found in every major watershed and important contributors to the freshwater and ocean fisheries (Yoshiyama et al. 1998). Two important habitat features were critical to their success; 1. access to high elevation cold water habitats, for adult holding and spawning as well as for over summer juvenile rearing (yearling juvenile phenotype), and 2. floodplain access for winter and spring season juvenile rearing (Moyle et al. 2017). However, as a result of mining activities and the construction of large dams without fish passage that have eliminated access to 80% of CVSC historical spawning habitat (Yoshiyama et al. 2001), and of various water diversion projects and habitat reclamation for farming or urban use that led to about 93% reduction of the amount of floodplain habitats in the CCV (Herbold et al. 2018), the CVSC stock complex was listed as threatened under the US Endangered Species Act in 1999 (Lindley et al. 2004). Only three tributaries of the Sacramento River (a major CCV watershed) - Mill, Deer and Butte Creek - host self-sustaining core natural spring-run populations, with the rest of the stock complex including one hatchery population (Feather River Hatchery), one recovering core population (Battle Creek), and various dependent populations (e.g., Yuba River). Mill and Deer Creek watersheds, which are very close geographically (Figure 1), provide access to some of the few remnant high elevation thermal refugia left in the CCV, that have been shown to benefit juvenile salmon during extensive warm periods by supporting the expression of the now-rare yearling phenotype (Cordoleani et al. 2021). On the other hand, Butte Creek watershed, which is at much lower elevation (Figure 1), provides a unique access to a recently restored ecologically functional floodplain, which has been shown to be a food-rich and high growth potential environment for juvenile salmon (Cordoleani et al. 2022).

The extensive habitat restoration that took place in the Butte Creek watershed during the 1990s resulted in improved access for Butte Creek juveniles to the floodplain. However, the extent to which the restoration efforts altered life history expression in the long term and the stability of the adult stock remains unknown. This large-scale restoration effort thus provides a unique opportunity to study the long-term effects of restoration on salmon population dynamics, and to evaluate the implications for the broader stock complex.

Here, we first investigated the impact of habitat restoration on adult abundance by comparing annual trends before vs. after restoration and by correlating adult abundance to floodplain inundation area. Second, we explored Butte Creek spring-run phenotypic diversity using otolith (earstone) strontium isotope ratios (^{87}Sr/^{86}Sr) and daily growth increments to reconstruct juvenile emigration strategies and growth rates from 2003 to 2018. We compared trait distributions from Butte Creek with those previously reported for Mill and Deer Creek (Cordoleani et al. 2021). We then quantified the strength of the portfolio effect before vs. after restoration and with different CVSC population combinations. Finally, we discuss the results in the context of performing landscape-scale process-based restoration efforts to enhance the productivity and long-term stability of salmon stock complexes in the face of future environmental change.

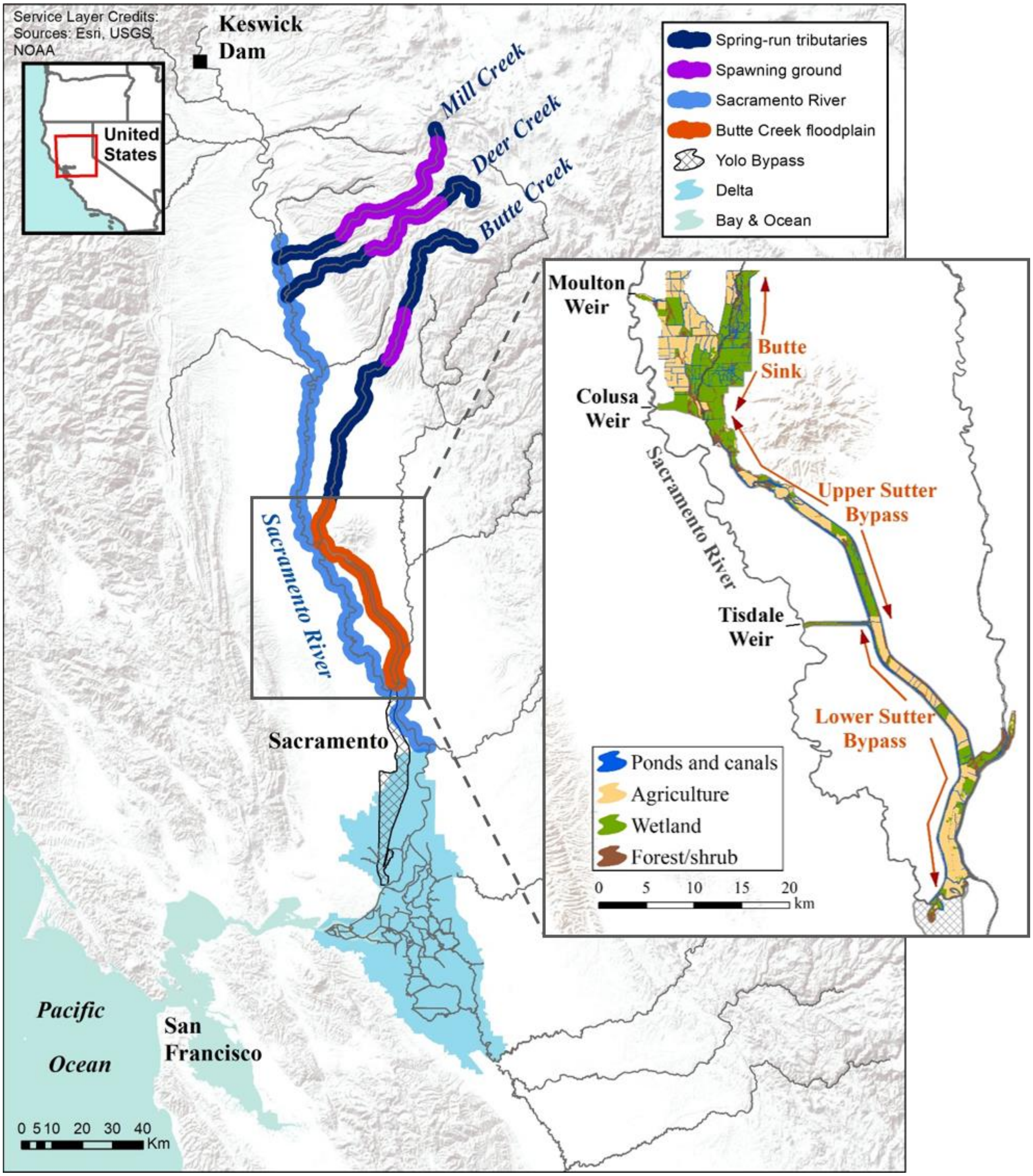

Figure 1. Map of current distribution of California Central Valley self-sustaining spring-run Chinook salmon populations (i.e., Mill, Deer and Butte Creek). Delta = Sacramento-San Joaquin River Delta, Bay = estuary between Suisun and San Francisco Bays. Inset map shows a detailed hydromorphology of Butte Creek floodplain (Butte Sink and Sutter Bypass) with land use coverage from the National Land Cover Database, the USDA Cropland Data Layer, and the National Water Information System.

Material & Methods

Study system

This study focuses on the three self-sustaining natural populations of the CCV spring-run Chinook Salmon stock complex: Mill, Deer and Butte Creeks. Those three creeks are tributaries of the Sacramento River**,** which is the largest watershed of California, USA, and drains the northern half of the CCV (Buer et al. 1989). Mill and Deer Creeks originate in the Lassen National Forest and connect to the Sacramento River upstream of Butte Creek. Because of their geographical proximity and geological similarity both watersheds have a similar isotopic signature (Johnson et al. 2016), and will be combined for the otolith isotope and growth analyses described below.

Butte Creek originates on the western slopes of the Sierra Nevada mountains, and is at much lower elevation than Mill and Deer Creek. Butte Creek flows into the Butte Sink and Sutter Bypass (Figure 1; hereafter called the “Butte Creek floodplain”), which constitutes a flood bypass of approximately 214 km^2. It is the uppermost flood bypass in the Sacramento Valley, and it is a crucial piece of the Central Valley flood management program, relieving pressure on the levees of the Sacramento and Feather Rivers ([CVFMPP] Central Valley Flood Management Planning Program 2010). Due to the heavy channelization of the major waterways, including the Sacramento River, flood bypasses have replaced a large portion of the historical floodplains in CCV, and can functionally act as natural floodplains by receiving surplus river water during high winter and spring flow events and providing a food-rich environment for juvenile salmon (Cordoleani et al. 2022). Floodwaters from the Sacramento River spills into Butte Creek floodplain through Moulton, Colusa, and Tisdale weirs (Figure 1). Ultimately, floodplain waters drain into the lower Sacramento River and, during large flooding events, into the Yolo Bypass, a similar flood bypass (Sommer et al. 2001; Figure 1).

An extensive habitat restoration effort program started in the lower Butte Creek watershed in the early 1990s, which included restoration of off-channel habitats, dam and weir removals and screening of water diversions (e.g., Lower Butte Creek Project; ICF Jones & Stokes 2009). Therefore, Butte Creek spring-run Chinook Salmon have ready access to this seasonal floodplain each year, while Mill and Deer Creek spring-run Chinook populations can only access it when conditions are wet enough that one of the Sacramento River weirs overtops.

Spring-run population productivity and floodplain access

We used spring-run adult returns (i.e., escapement) as an index of population productivity. Spring-run escapement data come from California Department of Fish and Wildlife’s monitoring program (GrandTab data; https://www.calfish.org/ProgramsData/Species/CDFWAnadromousResourceAssessment.aspx), and represent the estimated number of adult Chinook Salmon that "escaped" the ocean and river fisheries and successfully migrated upstream to a natural spawning area. While escapement estimates represent the number of adult salmon available for spawning, these numbers may vary from the actual number of salmon that ultimately succeed in spawning, due to pre-spawning mortality events that particularly impact CVSC during drought conditions.

The adults considered in this study were assumed to come back to spawn to their natal stream at age three, which corresponds to the dominant age at spawning for CVSC populations (Fisher 1994). Based on CVSC adult spawning timing (i.e., September - October) and juvenile emigration timing (i.e., October to May), we have the following relationship: primary juvenile emigration year = adult return year - 2. In other words, adults that came back to spawn in year Y were primarily emigrating from the freshwater as juveniles during year Y - 2 (Table S1).

To investigate the impact of Butte Creek restoration efforts on spring-run population productivity, we analyzed the relationship between 2004 - 2020 escapement estimates and the proportion of the floodplain that was inundated two years prior (corresponding to the juvenile emigration year). First, to estimate the floodplain inundation area, we used a stage-inundation relationship. This involved determining wetted areas from Landsat NDWI calculations and matching the date of imagery with the associated mean daily stage at Meridian Pass Road (floodplain location; CDEC Station ID: BSL; Figure S1A). We then transformed absolute floodplain inundation area to proportion of inundation (i.e., proportion = 1 means that the entire floodplain is inundated). We fit a Gompertz model (Tjørve and Tjørve 2017), and estimated the parameters of the stage-proportion of inundation relationship using a nonlinear least squares model, using the *nls* function from the *stats* package in R version 4.2 (R Core Team 2022) (Figure S1B). Subsequently, a linear regression was fitted between annual Butte Creek escapement estimates and the average proportion of floodplain inundated during the October-May juvenile emigration period, using the *lm* function in R. The same analysis was carried out for Mill and Deer Creek populations that only have access to the floodplain in question during weir overtopping events.

Spring-run juvenile life history and growth rate reconstructions

Otolith sampling

Adult Butte Creek spring-run otoliths were collected from carcasses retrieved during annual spawner surveys performed by CDFW (McReynolds et al. 2007), between 2003 and 2018 (Table 1). Otoliths were extracted from a total of 544 Butte Creek adults and used for strontium isotope ($^{87}Sr/^{86}Sr$) analysis. Combined, these data span a wide range of freshwater hydrological conditions and water year types from wet to critically dry (Table S1).

Table 1. Butte Creek otoliths summary. Escapement values represent the number of adult spawners estimated to have returned to Butte Creek watershed in a given year. Escapement data comes from CDFW GrandTab (https://www.calfish.org/ProgramsData/Species/CDFWAnadromousResourceAssessment.aspx). N = number of otoliths used for Sr isotope and growth analyses. % Adult analyzed = (N/Escapement) * 100.

Year	**Escapement**	**N_{Sr}**	**% Adult analyzed for Sr isotope**	**N_{growth}**	**% Adult analyzed for growth**
2003	17404	28	0.16%	24	0.14%
2005	17592	28	0.16%	24	0.14%
2006	6537	48	0.73%	38	0.58%
2007	6871	33	0.48%	0	0%
2008	11046	55	0.50%	0	0%
2009	2687	47	1.75%	0	0%
2010	1991	47	2.36%	28	1.41%
2011	4871	20	0.41%	18	0.37%
2012	16317	24	0.15%	20	0.12%
2014	5083	23	0.45%	20	0.39%
2015	569	46	8.08%	40	7.03%
2016	5731	47	0.82%	30	0.52%
2017	515	47	9.13%	32	6.21%
2018	2362	45	1.90%	36	1.52%

Strontium isotope analysis

Sagittal otoliths were prepared at UC Davis per established techniques (Johnson et al. 2016). The otoliths were ground on both sides in the sagittal plane using 600 and 1500 grit wet/dry sandpaper to expose the primordia and surrounding microstructure. The surfaces were then polished using 3 µm and 1 µm Al_2O_3 lapping films. Finished samples were mounted to a 1 cm square glass pedestal using Gorilla Glue^{TM}. The otoliths' dorsal side was photographed in 20x magnification using a Qimaging digital camera (MicroPublisher 5.0 RTV) mounted to a Olympus BX60 microscope. Following imaging otoliths were analyzed for $^{87}Sr/^{86}Sr$ at the UC Davis Interdisciplinary Center for Inductively-Coupled Plasma Mass Spectrometry by Laser Ablation on their Multi Collector Inductively Coupled Mass Spectrometer. We used the otolith strontium isotope analytical methods described in Barnett-Johnson et al. (2008) to reconstruct juvenile freshwater habitat-use and migration histories. In brief, $^{87}Sr/^{86}Sr$ of freshwater habitats (the "isoscape") varies as a function of watershed lithologies and weathering patterns, and because there is negligible biological fractionation of strontium isotopes during incorporation into the otolith matrix, the otoliths directly record the signature of the surrounding water and dietary sources. $^{87}Sr/^{86}Sr$ is a particularly powerful tool in the California Central Valley, because the spatial heterogeneity in rock types results in significant differences in isotope values among most of the salmon-bearing watersheds (Ingram and Weber 1999; Barnett-Johnson et al. 2008). Consequently, variations in $^{87}Sr/^{86}Sr$ across Central Valley watersheds has proven useful for determining population of origin and reconstructing juvenile rearing and migration behaviors (Sturrock et al. 2015, 2020; Johnson et al. 2016; Phillis et al. 2018; Willmes et al. 2018; Cordoleani et al. 2021).

Movement reconstruction

Otolith radius was used as a proxy for fish size at natal and freshwater exit. The otolith radius for each $^{87}Sr/^{86}Sr$ measurement was estimated by measuring the distance from the otolith core to the center of each laser pit along a standardized 90˚ axis (Barnett-Johnson et al. 2007). Strontium isotope profiles representing changes in $^{87}Sr/^{86}Sr$ values as a function of otolith distance from the core were created for each otolith. Specific location $^{87}Sr/^{86}Sr$ threshold values were used to identify the movement of Central Valley spring-run Chinook juveniles from one rearing region to the other. These values come from a Central Valley isoscape database (Table S2; Barnett-Johnson et al. 2008; Sturrock et al. 2015; Phillis et al. 2018). Four regions were considered: Natal tributary, which encompasses the entire Butte Creek watershed, including Butte Creek floodplain (hereon "Butte Creek"), Sacramento River, Sacramento-San Joaquin Delta (hereon "Delta"), and San Francisco-San Pablo Bay & Ocean (hereon "Bay & Ocean"). We used changes in $^{87}Sr/^{86}Sr$ and threshold exceedance values along the otolith transect to identify three key habitat shifts (1) natal tributary exit, (2) Delta entry, and (3) freshwater exit (exit location is Chipps Island, river kilometer 73). Otolith radius at natal exit was calculated by linearly interpolating between otolith distances at the $^{87}Sr/^{86}Sr$ measurements on either side of the $^{87}Sr/^{86}Sr$ threshold value between Sutter Bypass and the Sacramento River at Elkhorn (i.e., point of natal tributary exit; threshold value = 0.7056; Table S2). The Sacramento River at Freeport $^{87}Sr/^{86}Sr$ value threshold (threshold value = 0.70761; Table S2) was used to identify the migration of spring-run juveniles from the mainstem Sacramento River into the Delta. Finally, otolith radius for freshwater exit was calculated by linearly interpolating between the otolith distances for $^{87}Sr/^{86}Sr$ measurements either side of the Chipps Island threshold value of 0.7078 (Table S2).

Hierarchical clustering analysis

A hierarchical cluster analysis (Legendre and Legendre 1998) based on the otolith radius at natal exit was performed for the 544 adults sampled, to identify whether several juvenile life history strategies could be observed within the spring-run Butte Creek population. The clustering was performed in R version 4.2 (R Core Team 2022) using the function *hclust* with the Ward 2 method and Euclidean distance. To estimate the optimal number of clusters across we used the *Nbclust* package (Charrad et al. 2014) which uses 30 different clustering indices.

Fish size reconstruction

We applied an otolith radius – fork length relationship for Central Valley fall-run Chinook salmon, developed in Sturrock et al. (2020), to reconstruct fish sizes at natal and freshwater exit. While applying individual otolith-fish size calibration curves for specific ESUs is recommended to avoid spurious size reconstructions (Zabel et al. 2010), given the protected status of CVSC, lethal sampling of juveniles to develop such curves was not possible. Additionally, the use of Central Valley fall-run as surrogates is appropriate as Central Valley fall- and spring-run Chinook salmon spawn and emigrate at similar sizes and exhibit overlapping geographic distributions. The reconstructed natal and freshwater exit sizes for Butte Creek juveniles ranged from 33 mm to 146 mm and 49 mm to 152 mm respectively (Figure S3).

Otolith growth chronologies

Otoliths increment numbers were estimated from digitized otolith images using Image Pro Premier 9.0 (Media Cybernetics), and were used as a proxy for fish age as they permit estimation of the number of days since fish emergence. Moreover, habitat-specific freshwater juvenile growth rates were reconstructed from increment widths measured in each isotopically distinct habitat region of the otolith. Each otolith reading was assigned a score of "certainty" on a scale of 1-5, 5 being the highest certainty. This index is a combination of the reader's confidence in the accuracy of the increment placement and the quality or readability of the image (i.e., how likely it is that another reader would get the exact same increment width measurements). Otoliths with poor readability (i.e., certainty score < 3) were eliminated from the analysis. A total of 310 otoliths (from escapement years 2003, 2005-2006, 2010-2012, 2014-2018; Table 1) were used for the growth analysis.

We estimated the number of days spent in each key habitat (i.e., natal tributary, Sacramento River and Delta) for Butte Creek and Mill and Deer Creek populations, and compared their freshwater growth rates. As mentioned earlier Mill and Deer Creek populations were combined for the growth analysis.

Spring-run stock complex stability

To assess the stability of each spring-run population as well as the overall stability of the spring-run stock complex through time, we calculated the coefficient of variations (CVs) in adult returns for each population independently and for grouped populations (e.g., Mill + Deer + Butte), for the pre-floodplain restoration (i.e., 1970-1994) and the post-restoration (i.e., 1995-2019) time periods, similar to the metrics calculated by Carlson and Satterthwaite (2011) for CCV fall-run Chinook salmon. Similar to Carlson and Satterthwaite (2011), we used escapement as an index of productivity, rather than a recruits-per-spawner index for instance, because we did not have reliable juvenile production estimates. Additionally, because increased synchronization between populations from the same stock complex is predicted to decrease the overall stock portfolio stability (Markowitz 1952; Moore et al. 2010), we assessed the degree of independence between spring-run population dynamics by estimating pairwise Pearson correlations between all pairs of populations.

Results

Spring-run population production and floodplain access

After habitat restoration efforts starting in the early 1990s, Butte Creek spring-run escapement abundance increased significantly, with about a 2000% increase in average abundance (post-restoration mean $N_{1995\text{-}2019}$ = 8578.5 ± 6714.4 SD vs. pre-restoration mean $N_{1970\text{-}1994}$ = 404.4 ± 412.1 SD; Figure 2). The Butte Creek population is now the most abundant spring-run Chinook Salmon population in the stock complex. In contrast, Mill and Deer Creek populations, which used to play a more important role in the stock complex productivity, have experienced a steady decline in adult abundance and are now at relatively low escapement levels (Mill Creek post-restoration mean $N_{1995\text{-}2019}$ = 597.8 ± 419.6 vs pre-restoration mean $N_{1970\text{-}1994}$ = 776.0 ± 782.1 SD, and Deer Creek post-restoration mean $N_{1995\text{-}2019}$ = 955.6 ± 803.2 SD vs pre-restoration mean $N_{1970\text{-}1994}$ = 1255.6 ± 1864.2 SD; Figure 2).

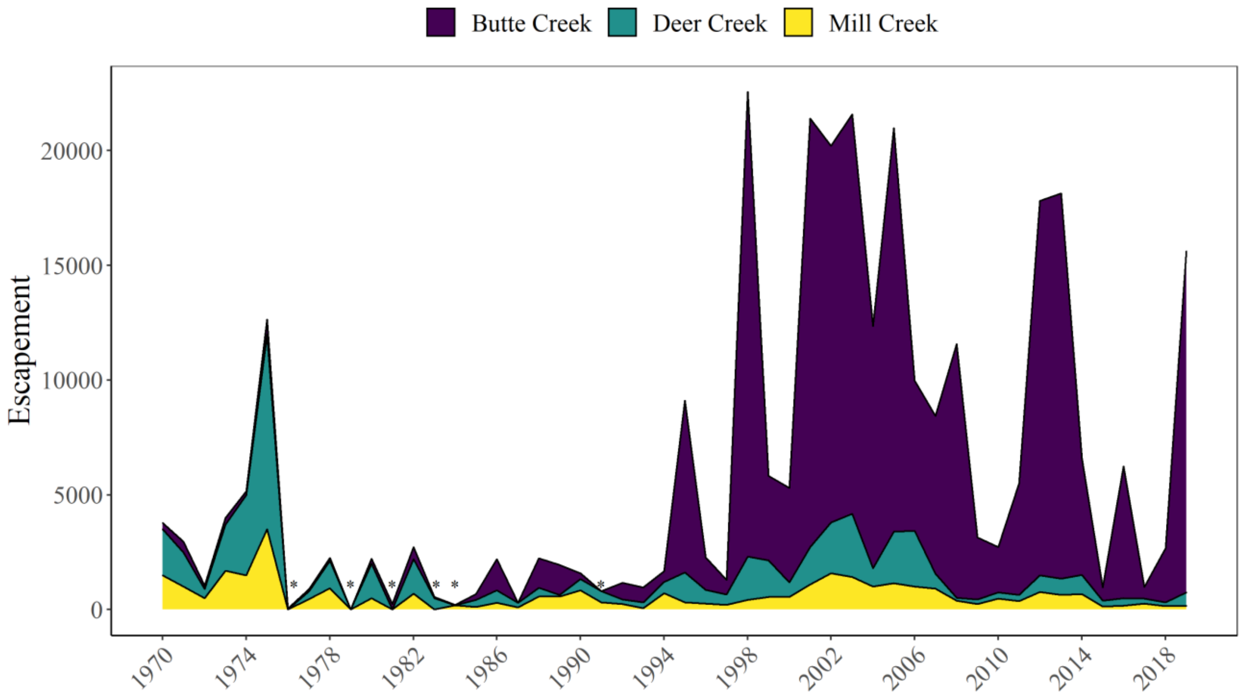

Figure 2. Annual spring-run escapements to Butte, Mill and Deer Creek from 1970 to 2019. Asterisks show years where abundance estimates were missing for at least one population.

A significant positive relationship was found between the proportion of Butte Creek floodplain inundation and Butte Creek escapement levels two years later (representing adult returns for the typical dominant return age), over a wide range of hydrological conditions (Figure 3). No significant correlations were found, however, between the proportion of Butte Creek floodplain inundation and Mill and Deer Creek escapement levels two years later, which may be expected due to limited opportunities for Mill and Deer Creek juveniles to access the floodplain (on average 20 days per year for Colusa weir; Table S1). Weak correlations were also found between river flows in the mainstem Sacramento River and the Delta and Mill and Deer Creek escapement sizes (Figure S2).

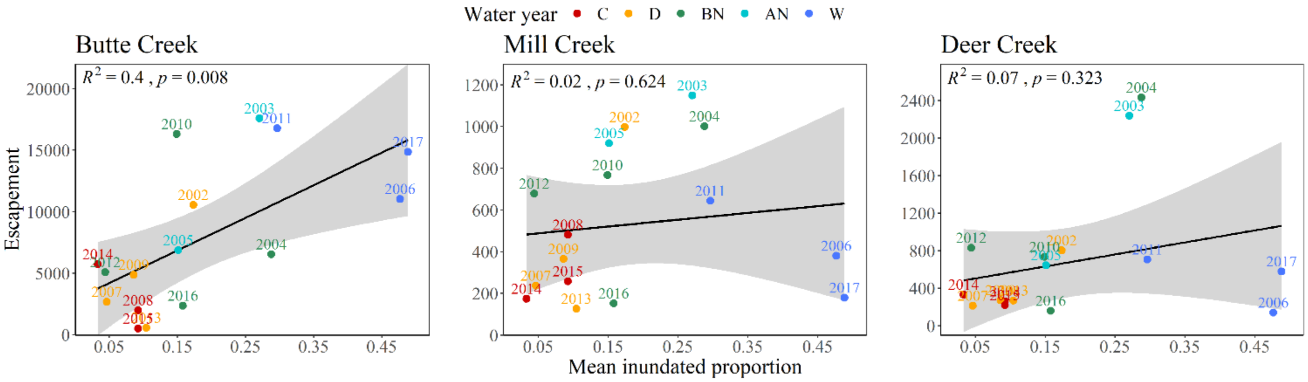

Figure 3. Relationships between spring-run adult returns (‘Escapement’) to Butte, Mill and Deer Creek from 2004 to 2020 relative to the average proportion of Butte Creek floodplain inundated during October-May juvenile emigration period experienced 2 years prior. Years shown on the figures correspond to juvenile emigration years (Emigration Year = Return Year - 2). We used the California Department of Water Resource water-year (Water year) classification to describe the range of hydrological conditions during the emigration period, with C = critical, D = Dry, BN = Below Normal, AN = Above Normal, W = Wet (https://cdec.water.ca.gov/reportapp/javareports?name=WSIHIST).

Spring-run juvenile life history strategy diversity

While recent Butte Creek spring-run spawner abundance is usually several magnitudes greater than the Mill and Deer Creek populations, a wider range of juvenile life history strategies was found in Mill and Deer Creek spring-run fish. Specifically, otolith isotope profiles and the hierarchical clustering analysis revealed three distinct juvenile life history types in Butte Creek population (Figure 4A, “Otoliths analysis” section in Sup. Mat.), that we referred to as “early”, “intermediate” and “late” migrants, following Cordoleani et al. (2021). However, while we kept the same nomenclature, the three life history types were not entirely comparable to Mill and Deer Creek early, intermediate and late life history strategies, and were more closely aligned with the fry, parr and smolt groups observed in Sturrock et al. (2015, 2020) (i.e., fry < 55 mm, parr = 55-75 mm, smolt = 75-110 mm), with the majority of the fish belonging to the intermediate emigration type (n=270), followed by the late type (n=177), and then the early type (n=97). Furthermore, the size and age distributions of the three life history strategies at natal and freshwater exit were more uniform and constrained for Butte Creek than for Mill and Deer Creek (Figures 4B-E). In general, Butte Creek juveniles left their natal grounds smaller and earlier than their Mill and Deer Creek counterparts, and the yearling strategy was largely absent (e.g., average size and age at natal exit was 74 mm ± 13 mm vs 87 mm ± 33 mm & 71 days ± 22 days vs 144 days ± 79 days respectively; Figure 4, Table S3). Additionally, Butte Creek juveniles consistently entered the bay and ocean at more similar and smaller sizes, which were earlier ages than Mill and Deer Creek fish, regardless of the migrant strategy (average size and age at freshwater exit was 83 mm ± 11 mm vs 106 mm ± 23 mm, and 83 days ± 19 days vs 176 days ± 65 days respectively; Figure 4). This could in part be explained by the limited number of yearling sized fish (i.e. size > 110mm at natal exit) in the Butte Creek sample, that migrate to the ocean much larger than the other migrant types after oversummering in freshwater. This is consistent with juvenile trapping data from the natal reaches of the three tributaries, that show larger numbers of yearling fish in Mill and Deer Creek (approximately 10% vs. 1% of raw catch data, respectively; Figure S4).

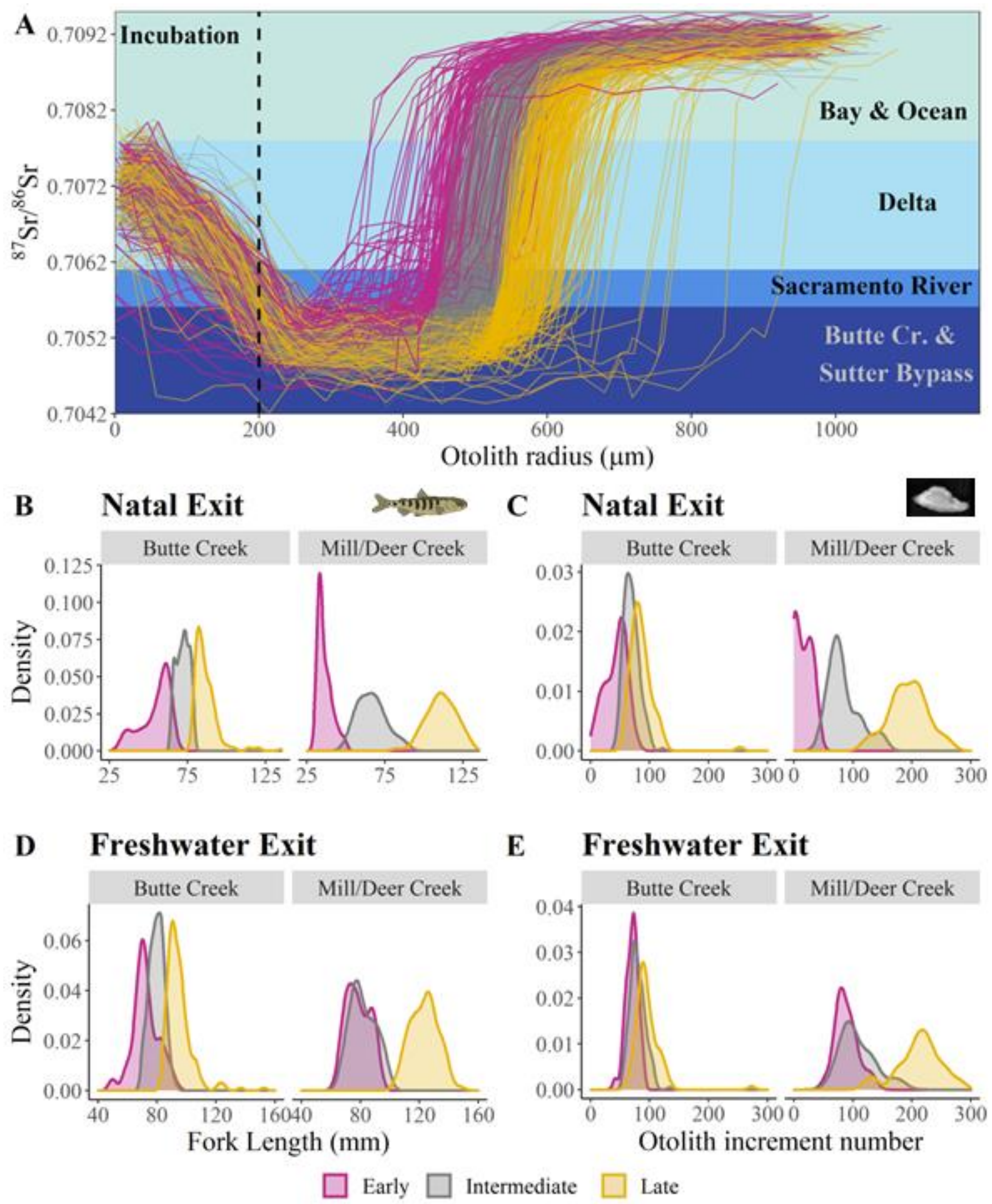

Figure 4. A. Butte Creek otolith strontium isotope profiles for all years combined and colored by life history type. Life-history types were classified using a hierarchical cluster analysis based on otolith radius at natal exit. Fish size distributions for each population (i.e., Butte, Mill/Deer Creek) and life-history type when they emigrated out of the natal stream (B) and out of freshwater (D). Otolith increment number (a proxy for fish age) distributions for each population and life-history type when they emigrated out of the natal stream (C) and out of freshwater (E). Note that due to the similarity in Mill and Deer Creek watershed isotopic signatures, Mill and Deer Creek otoliths were combined for the strontium analysis.

This larger uniformity in Butte Creek spring-run juvenile rearing and migratory strategies also translates into lower interannual variability in the number of days spent in each of the three isotopically defined freshwater regions (i.e., Natal tributary, Sacramento River, and Delta; Figures 5A and 5B). Each year, the majority of Butte Creek juveniles spent most of their time rearing in the Butte Creek watershed (including both the spawning ground and Butte Creek floodplain) and a short amount of time in the lower Sacramento River and Delta (71 days ± 22 days and 12 days ± 10 days on average), suggesting that they underwent smoltification while rearing in the natal tributary and used downstream habitats primarily as a migratory corridor. Contrary to the Mill and Deer Creek populations, where yearlings dominated the adult returns in some years (Cordoleani et al. 2021), only one sampled Butte Creek fish left freshwater as a yearling, having spent about 8 months in the Butte Creek watershed in 2017 before emigrating at 146 mm FL.

Differences in juvenile growth were also observed among spring-run populations (Figure 5C). Butte Creek juveniles exhibited faster early growth rates than their equivalents from Mill and Deer Creek (first 83 days - the median age at freshwater exit for Butte Creek - growth of 0.63mm/day vs 0.45 mm/day respectively; Figure 5D).

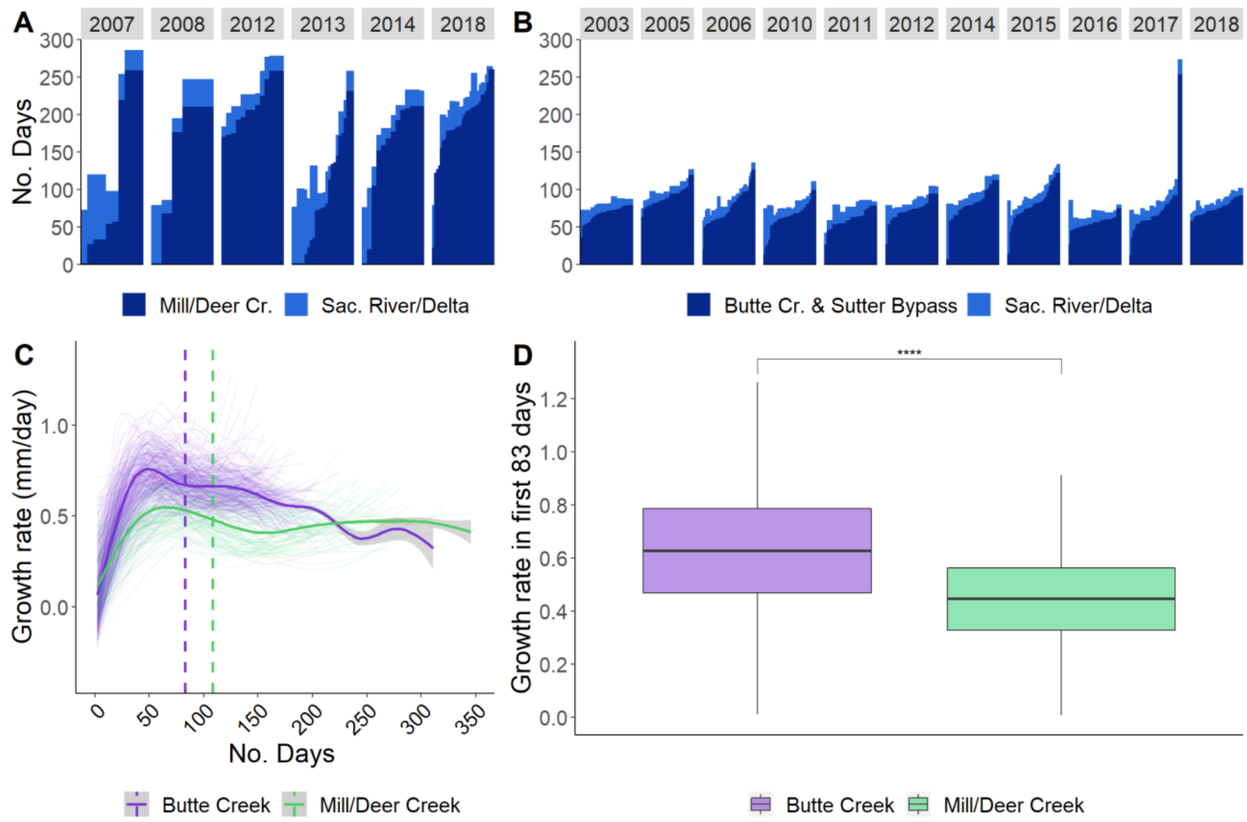

Figure 5. Number of days spent by each fish (individual bars) in the natal tributary (dark blue) and Sacramento River/Delta (light blue) across escapement years for Mill and Deer Creek (A) and Butte Creek (B). Each bar represents one adult (note varying widths), and the bar height represents their age at freshwater exit based on Sr isotope analysis and otolith daily increments. (C) Butte (purple) and Mill/Deer Creek (green) juvenile individual smoothed growth profiles (thin lines) and average profiles

(bold lines) obtained using the *gam* function in R (R Core Team 2022). The vertical dashed lines show the median number of days (i.e., age) at freshwater exit for each population (i.e., 83 days for Butte Creek and 108 days for Mill/Deer Creek). (D) Boxplot comparing Butte Creek and Mill/Deer Creek growth rates during the first 83 days after emergence (the median age at freshwater exit for Butte Creek). The horizontal line in each box represents the median value, lower and upper hinges of the boxes correspond to the 25th and 75th percentiles. The upper and lower whiskers extend from the hinge to the largest and smallest value no further than 1.5 × interquartile range (IQR) from the hinge. Wilcoxon test showing significant differences in early growth rates between populations. Note that, similar to the strontium analysis, Mill and Deer Creek populations were combined for the otolith growth analysis.

Spring-run stock complex stability

While Butte Creek spring run population had the lowest CV (i.e. highest population stability) during the pre-Butte Creek floodplain restoration period (i.e., 1970-1994), its CV did not decrease as much as for Mill and Deer Creek populations during the post-restoration period (i.e., 1995-2019; Figure 6A). However, the large Butte Creek population increase after 1994 also led to a significant increase in the post-restoration abundance of Butte, Mill and Deer Creek populations combined, and a 38% decrease in the combined populations' post-restoration CV (combined populations pre-restoration CV = 1.02 vs post-restoration CV = 0.74; Figure 6). Additionally, during the pre-restoration period a strong correlation was found between Mill and Deer Creek population dynamics ($r = 0.94$), but very little correlation was found between Butte and Mill Creek or Butte and Deer Creek abundances ($r = -0.07$ in both cases). However, the correlation between Butte and Mill Creek or Butte and Deer Creek abundances increased significantly during the post-restoration period ($r = 0.61$ and $r =0.6$, respectively), while the correlation between Mill and Deer Creek abundances slightly decreased ($r = 0.77$), suggesting an overall increased synchronization of the stock complex dynamics.

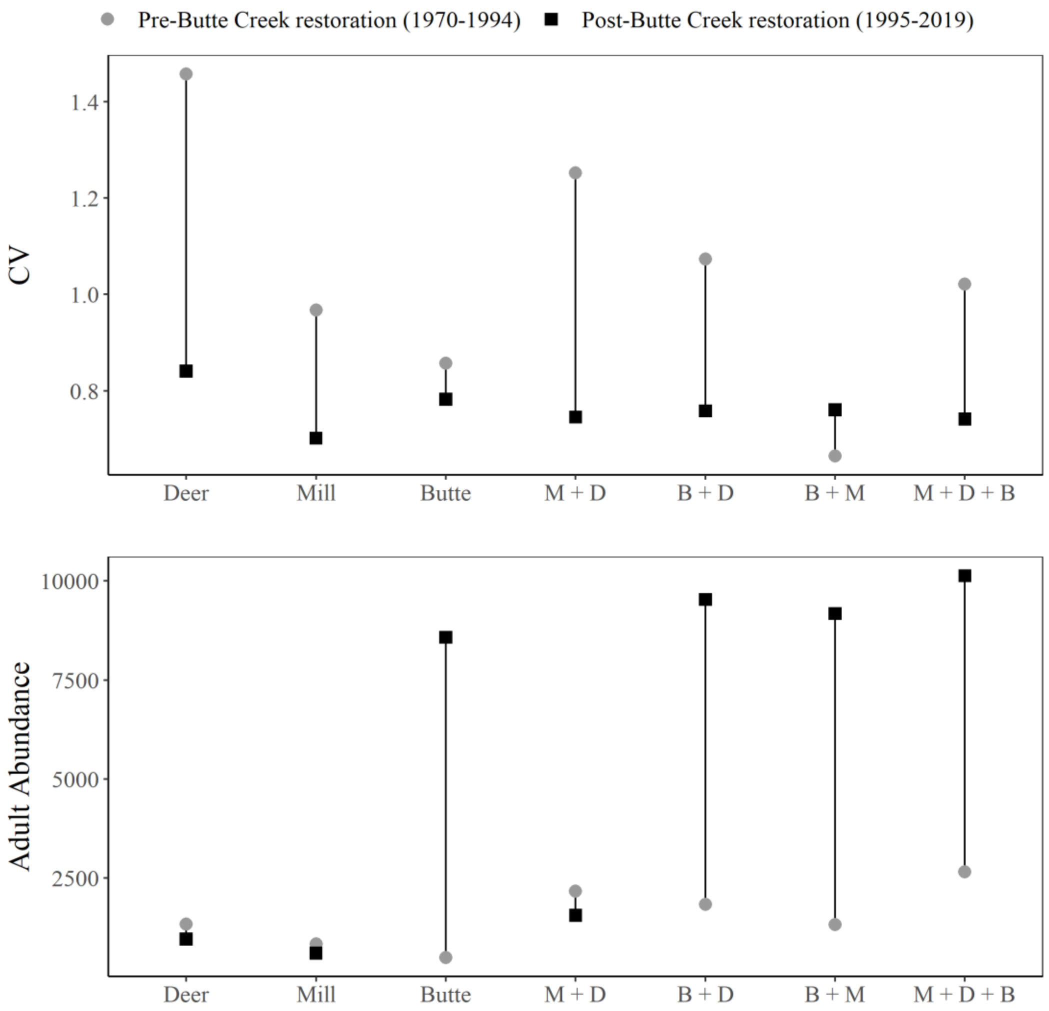

Figure 6. A. Coefficient of variations (CVs) and B. Average adult abundances, for each spring-run population separately and for aggregated populations, estimated for both pre-Butte Creek restoration (1970-1994, gray circle) and post- Butte Creek restoration (1995-2019, black square) periods. M = Mill Creek, D = Deer Creek, and B= Butte Creek.

Discussion

Spring-run Chinook salmon populations in the Central Valley (CVSC) have experienced dramatic declines as a result of combined anthropogenic factors that dramatically reduced the quantity and access to high quality freshwater spawning and rearing habitats (Lindley et al. 2004). The CVSC stock complex is also particularly vulnerable to a warming climate as they need cold freshwater refugia for adults to hold in the summer until they spawn in the fall, and for juvenile yearlings to rear over-summer before migrating to the ocean in the fall (Moyle et al. 2017). One exception is the Butte Creek spring-run Chinook population that has seen a large increase in overall productivity after extensive Butte Creek watershed restoration efforts that started in the early 1990s. This restoration action is considered one of the most successful salmon recovery efforts in the CCV, and allowed Butte Creek Chinook to have unrestricted access to one of the last CCV ecologically functional floodplains (i.e. Butte Creek floodplain) during flooding season.

Here we found that Butte Creek spring-run adult abundance was positively correlated with increased floodplain inundation area two years prior, while Mill and Deer Creek abundances, which have a limited floodplain access, did not show a correlation. This demonstrates the importance of Butte Creek floodplain to recovering Butte Creek spring-run. For Mill and Deer Creek spring-run populations, other factors, such as water temperature or non-linear relationship with flow and floodplain inundation, might have a stronger influence on population size. Additionally, while CCV spring-run adults are assumed to predominantly return to spawn at age-3, some inter-annual adult age structure variability has been observed, among Feather River and Butte Creek spring-run populations particularly, with a non-negligible proportion of age-4 spawners in some years (McReynolds et al. 2007; Satterthwaite et al. 2018). Furthermore, it has been shown in other Pacific Northwest watersheds that yearlings tend to mature later than earlier migrants (Hankin and Logan 2010), raising the possibility for Mill and Deer Creek spring-run populations, which are characterized by a large proportion of yearling migrants (Cordoleani et al. 2021), to harbor a greater proportion of age-4 spawners than previously thought. Consequently, having accurate estimates of annual spawner age structure in Mill, Deer and Butte Creek spring-run adult cohorts could help refine the relationship between environmental factors, such as floodplain inundation, and population productivity.

Access to off-channel habitats in the lower Butte Creek watershed has also been previously related to enhanced juvenile salmon growth (Cordoleani et al. 2022), and likely explains the high growth rates that were observed among Butte Creek juveniles compared to Mill and Deer Creek fish (average fish length growth rates of 0.63 mm/day vs 0.45 mm/day respectively). In comparison, fish reared in enclosures in off-channel habitats in the Butte Creek floodplain in 2019 had an average growth rate of 0.55 mm/day (Cordoleani et al. 2022), slightly lower than what we report here. However, Butte Creek juvenile growth rates from this study were within the range of growth rates measured in free-swimming and enclosure fish reared in the Yolo Bypass (a similar floodplain downstream of Butte Creek floodplain; Figure 1), with growth rates ranging from 0.55 to 0.80 mm/day (Sommer et al. 2001; Katz et al. 2017). This fast early-life growth allowed Butte Creek juveniles to leave the natal reaches and exit the freshwater earlier than Mill and Deer Creek juveniles, potentially avoiding critically warm en-route migration conditions, especially during dry years, and leading to better growth and survival opportunities in the ocean (Woodson et al. 2013; Satterthwaite et al. 2014).

While this habitat restoration provides a great example of ways to provide high growth benefits and improve the overall abundance of vulnerable Chinook salmon populations, we did not find support for it promoting population phenotypic diversity and stability. These restoration efforts favored one main juvenile life-history strategy: most Butte Creek juveniles reared in the Butte Creek watershed, including Butte Creek floodplain, and migrated in the spring (earlier than Mill and Deer Creek juveniles) to the ocean at parr (55-75 mm) or smolt (75-110 mm) sizes. Only a small proportion of juveniles were found to quickly leave Butte Creek and rear in downstream habitats (i.e., lower Sacramento River and Delta), and only one confirmed yearling fish reared over summer in Butte Creek and migrated to the ocean in the fall. While juveniles are sometimes observed in the upper Butte Creek watershed in the summer (California Department of Fish and Wildlife, personal communication), the rarity of the yearling phenotype in the spawner population is likely related to the elevated summer and early fall water temperatures observed in both Butte Creek spawning ground and floodplain habitat (Figure S5), making it unsustainable for juveniles to survive over summer and during their fall migration. This constrained migration pattern is consistent with juvenile trawl catch data at Chipps Island (point of freshwater exit) in the San Francisco Estuary, where genetically identified Butte Creek spring-run fish were observed passing this location over a compressed time window and at very similar sizes (Thompson and Meek 2022). In comparison, Mill and Deer Creek spring-run populations exhibited various distinct juvenile life history strategies and a higher interannual variability. Specifically, the late migrating (i.e. yearling) strategy, supported by access to cold-water refugia, was found to be key for Mill and Deer Creek spring run populations to persist through years of delayed ocean upwelling or drought conditions (Cordoleani et al. 2021). Similarly, the threatened population of fall-run Chinook salmon from the Clearwater River (Idaho), known for its cool summer temperatures, predominately exhibited this life-history strategy (Hegg et al. 2013). Furthermore, while Butte Creek abundance sharply increased post-floodplain restoration (increase > 2000%), it is also characterized by high interannual escapement variability, with relatively low adult abundances following some particularly dry years (e.g., return years 2010, 2017), which led to the lowest post-restoration decrease in the CV (indicating population stability) among the three spring-run populations. This suggests that Butte Creek fish are highly vulnerable to environmental extremes such as drought events and wildfires, potentially limiting their adaptation to a warming climate. On the other hand, Mill and Deer Creek populations' lower post-restoration CV (i.e., higher population stability) is likely not related to the floodplain restoration effort but due to their chronically low abundances, with very infrequent years of high returns.

These recent low adult abundances have put Mill and Deer Creek populations at high risk of extinction, while the large abundance increase in Butte Creek population observed after 1994 drives the overall CVSC stock complex abundance and allows a determination of a decrease in the overall stock extinction risk (Johnson et al. 2022). When combining the three spring-run population’s abundances a decrease in the overall CV was observed, post-floodplain restoration, indicating an increase in portfolio effect stability at the stock complex level. However, while the strong correlation found between Mill and Deer Creek adult abundances was expected because of the watersheds’ geographical proximity, hydrological and genetic similarities between these two populations (Lindley et al. 2007; Johnson and Merrick 2012), an increase in the correlations between Butte and Mill, and Butte and Deer Creek adult abundances post-restoration indicates an overall increase in the synchronization of the stock complex dynamics, which, contrary to the CV decrease, is expected to reduce the strength of the portfolio effect stability. This study shows the limitation of using the CV when assessing population stability, for populations that are close to extinction, and the importance of additionally looking at population diversity and synchrony indicators to help gaining insight into how to enhance the resilience of each populations as well as the overall stock complex to environmental perturbations. Recent increases in synchrony have also been reported among CCV fall-run Chinook salmon populations (Satterthwaite and Carlson 2015) and threatened Chinook salmon populations in the Snake River basin (Oregon, Washington, Idaho; Moore et al. 2010), and were found to be coincident with increased off-site hatchery releases in the CCV, and an increase in hatchery propagation and large dam numbers in the Snake River. Although there is a spring-run hatchery in the Feather River watershed, its influence on natural Mill, Deer and Butte Creek spring-run populations is thought to be small if any. Further investigation would be needed to identify the potential impact of environmental factors in their common marine ecosystem (e.g., North Pacific Gyre Oscillation) in promoting synchrony for the CVSC stock complex.

This study provides a missing link between the "spatial diversity" metric used in the viability assessment of Chinook salmon stocks in the CCV - that accounts for the diversity of ecoregions represented in the stock complex but does not explicitly incorporate an habitat component (Lindley et al. 2007) - and watershed-scale restoration efforts generally implemented in the CCV to increase Chinook population abundance, by highlighting the importance of developing restoration actions specifically targeted at places on the landscape that promote habitat heterogeneity and asynchronous population dynamics to enhance the buffering of the entire stock complex to catastrophic disturbances. More globally, most conservation objectives focus on short-term biodiversity increases that would be achieved through localized habitat restoration efforts, assuming that "if you build it, they will come" ("Field of Dreams" hypothesis; Palmer et al. (1997)). However, these efforts may not fully account for landscape-scale physical and ecological processes that are crucial for maintaining healthy populations in a dynamic environment. As our climate rapidly changes, it is essential to reassess conservation approaches and prioritize building adaptive capacity in species in order to achieve long-term recovery goals (Lawler 2009; Prober et al. 2019; Rilov et al. 2020). Here we highlight the importance of landscape-scale, process-based conservation approaches that reconcile two key ecological concepts: habitat mosaic and portfolio effect. Specifically, this involves restoring habitat heterogeneity and connectivity to support a diverse mosaic of habitats that can foster the expression of multiple phenotypes and enhance resilience of vulnerable species like Chinook salmon in a warming climate (Herbold et al. 2018; Coleman et al. 2022). This may require expanding the CVSC stock-complex's geographical distribution to include lost ecoregions (Lindley et al. 2007), through population re-introduction into habitat above impassable dams and natural barriers watersheds, which would provide access to cold water habitat that is predicted to persist in a warming climate (FitzGerald et al. 2021; Cordoleani et al. 2021). This would also reduce extinction risks of the core CVSC populations, that currently belong to the same ecoregion, as a result of local catastrophic climate events. Additionally, this study shows strong support for designing habitat restoration and flow management efforts that recreate ecologically functional floodplains, such as the Butte Creek floodplain and Yolo Bypass, and re-connect them to mainstem rivers to provide multi-population benefits (Yarnell et al. 2015, 2020). The landscape-scale restoration efforts proposed to improve the resilience of the CVSC stock complex could be seen as comparable to the development of marine protected areas, which promote connectivity between populations and habitats, and is recognized as a powerful conservation policy tool for the recovery of marine species worldwide (Lubchenco et al. 2003; Giakoumi et al. 2018; Devillers et al. 2019; Duarte et al. 2020).

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