








## ARTICLE

## Freshwater Ecology

## Restoring freshwater habitat mosaics to promote resilience of vulnerable salmon populations

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## Abstract

Phenotypic diversity and abundance drive 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 both diversity and abundance to support salmon persistence in a warming climate? Here, we looked at the impact of a large watershed 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, which have floodplain access, had higher overall productivity and faster juvenile growth compared with Mill and Deer Creek populations, and the proportion of floodplain inundation was positively correlated with Butte Creek adult abundance two years later. While Butte Creek exhibited significant increases in abundance post-restoration (~2000%), it generally exhibited lower phenotypic diversity and only a marginal increase in population stability after restoration based on the coefficient of variation (CV). In particular, Butte Creek salmon tended to exhibit larger drops in escapement following dry years (e.g., return years 2010, 2017) compared with Mill and Deer Creek populations, presumably due to limited inundation of its downstream floodplain. The late-migrating juvenile strategy (i.e., yearling), which disproportionately supported Mill and Deer Creek populations during droughts, was

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uncommon among Butte Creek adults (averaging 60% of returns for Mill and Deer Creek vs. 0.3% for Butte Creek). Increased spring-run stock complex stability was found, post-restoration, when combining the three spring-run populations (i.e., lower aggregate CV). However, among-river pairwise correlations also suggested increased synchronization in population abundances post-restoration, potentially due to increasing frequency and severity of extreme climatic events (e.g., droughts and ocean warming). This study underscores the importance of restoring a connected mosaic of aquatic habitats across modified landscapes, such as cold water refugia and floodplains, to preserve multiple (across-population) life history pathways 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.

#### KEYWORDS

floodplain, habitat mosaic, life history strategy, portfolio effect, restoration, spring-run Chinook Salmon, warming climate

## INTRODUCTION

Habitat loss and homogenization from human activities (e.g., dam construction, agriculture) combined with climate warming are major drivers of species extinctions (IPBES, 2019; IPCC, 2007; Kiehl, 2011). 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). The 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 near term (IPCC, 2023), 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

(shifting habitat mosaic concept; Brennan et al., 2019; Stanford et al., 2005). 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; Ives & Carpenter, 2007; Miner et al., 2005; Schindler et al., 2010). 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 landscape or stock complex scale to promote phenotypic diversity and enhance long-term species recovery goals (Beechie et al., 2013, 2023; Lindley et al., 2007).

Habitat contraction and simplification are of particular concern for taxa such as salmonids that rely on freshwater habitats for parts of their life cycle (Bănăduc et al., 2022). In California's Central Valley (CCV), spring-run Chinook Salmon (*Oncorhynchus tshawytscha*; CVSC) are at the southern edge of the species' native range, spawning and growing in a heavily modified freshwater environment. Spring-run, now listed as threatened under the US Endangered Species Act, were once the backbone of California's commercial salmon fishery and found in every major watershed (Lindley et al., 2004; Yoshiyama et al., 1998). Two habitat features were particularly critical to their success: (1) access to high-elevation cold water habitats, for adult holding and spawning as well as

for juvenile oversummer rearing (yearling 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 impassable dams 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 >90% loss of CCV floodplain habitats (Herbold et al., 2018), the status of the CVSC stock complex continues to worsen (Johnson et al., 2023). Only three tributaries of the Sacramento River (a major CCV watershed) continue to host self-sustaining core natural spring-run populations, namely Mill, Deer, and Butte Creek. The rest of the CVSC stock complex includes one hatchery population (Feather River Hatchery), one recovering core population (Battle Creek), and various dependent populations (e.g., Antelope Creek). Mill and Deer Creek watersheds, which are geographically very close (Figure 1), provide access to some of the few remnant high-elevation thermal refugia left in the CCV, which 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), has access to an 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, which included dam and weir removals and screening of water diversions, resulted in improved passage and floodplain access throughout the watershed. In other systems, dam removal had significant impacts on habitat complexity and juvenile salmon life history diversity (Munsch et al., 2023; Williams et al., 2018). The extent to which the Butte Creek restoration efforts also altered abundance and life history expression, and the stability of the ESU remain unknown. The restoration of Butte Creek watershed is a rare example of addressing several limiting factors within a single watershed rather than spreading out restoration resources across several watersheds. Therefore, it provides a unique opportunity to study the long-term effects of landscape-scale restoration on salmon population dynamics in a variable Mediterranean climate 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 versus after restoration and by correlating adult abundance to floodplain inundation area. Second, we explored Butte Creek spring-run phenotypic diversity using otolith (ear stone) strontium isotope ratios ( $^{87}\text{Sr}/^{86}\text{Sr}$ ) 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 versus after restoration and with different CVSC population combinations. Finally, we discuss the results in the context of implementing process-based restoration efforts to enhance productivity and among-population asynchrony to promote the long-term stability of salmon stock complexes in the face of environmental change.

## MATERIALS AND METHODS

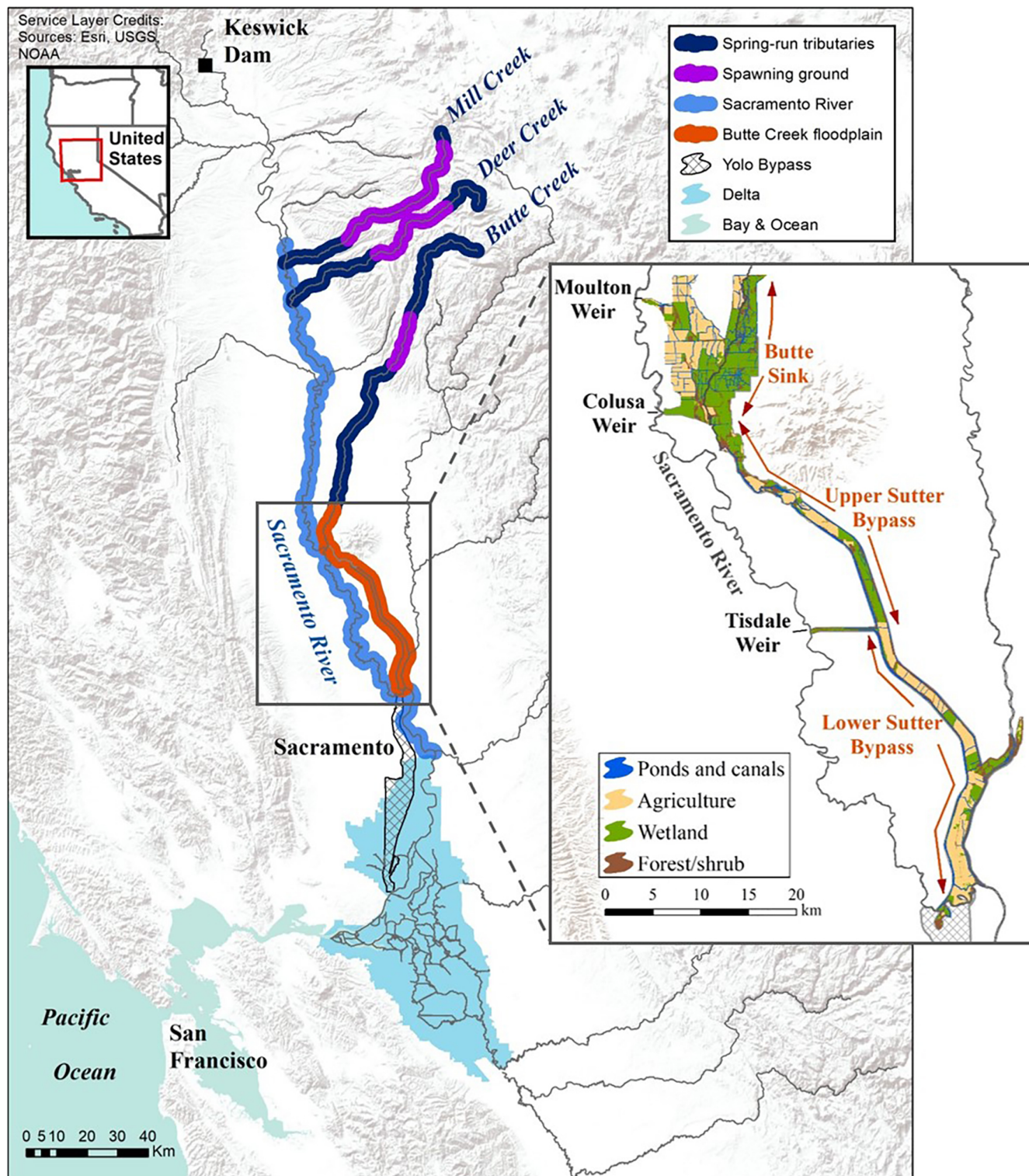
### Study system

This study focuses on the three self-sustaining natural populations of the CCV spring-run Chinook Salmon stock complex: Mill, Deer, and Butte Creeks. These 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 similar strontium isotope ranges (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 a 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<sup>2</sup>. It is the northernmost 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, 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 spill 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 program started in the lower Butte Creek watershed in the early 1990s,





**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.

which included the establishment of minimum instream flows, dam removal, addition of fish ladders and diversion screens, and altered water conveyance structures

(e.g., Lower Butte Creek Project; ICF Jones & Stokes, 2009), resulted in improved adult passage and decreased juvenile stranding throughout the watershed. As a result



of existing habitat and restoration actions, Butte Creek spring-run Chinook Salmon have abundant access to seasonal floodplain during their downstream migration 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

Spring-run adult returns (i.e., escapement) were used as an index of population productivity. Spring-run escapement data were sourced from the 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, the actual number of salmon that ultimately succeed in spawning is lower due to pre-spawning mortality, which is typically less than 10% (Garman, 2016) but has exceeded 90% during extreme drought conditions (Johnson et al., 2023; Nichols, 2022).

While imperfect (see caveats in [Discussion](#)), the adults considered in this study were all assumed to come back to their natal stream to spawn at age 3, which corresponds to the dominant age at spawning for CVSC populations (Fisher, 1994) (mean = 82% in Satterthwaite et al., 2023). Based on CVSC adult spawn timing (i.e., September–October) and juvenile emigration timing (i.e., October–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 (Appendix S1: Table S1).

To investigate the impact of Butte Creek restoration efforts on spring-run population productivity, we analyzed the relationship between 2004 and 2020 escapement estimates and the proportion of the floodplain that was inundated two years prior (corresponding to the dominant juvenile emigration year). First, a stage–inundation relationship was used to estimate the floodplain inundation area. 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; Appendix S1: Figure S1a). Floodplain inundation area was then transformed into proportion of inundation (i.e., proportion = 1 means that the entire floodplain is

inundated). A Gompertz model (Tjørve & Tjørve, 2017) was fitted and the parameters of the stage-proportion of inundation relationship were estimated using a nonlinear least squares model, using the `nls` function from the `stats` package in R version 4.3.2 (R Core Team, 2023) (Appendix S1: Figure S1b). Subsequently, the `lm` function in R was used to fit a linear regression between annual Butte Creek escapement estimates and the average proportion of floodplain inundated during the October–May juvenile emigration period. The same analysis was carried out for Mill and Deer Creek populations that only have access to the Butte Creek floodplain 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 ( $^{87}\text{Sr}/^{86}\text{Sr}$ ) analysis. Combined, these data span a wide range of freshwater hydrological conditions and water year types from wet to critically dry (Appendix S1: Table S1).

#### 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- and 1- $\mu\text{m}$   $\text{Al}_2\text{O}_3$  lapping films. Finished samples were mounted to a 1-cm square glass pedestal using Gorilla Glue. The otoliths' dorsal side was photographed in 20 $\times$  magnification using a Qimaging digital camera (MicroPublisher 5.0 RTV) mounted to an Olympus BX60 microscope. Following imaging, otoliths were analyzed for  $^{87}\text{Sr}/^{86}\text{Sr}$  at the UC Davis Interdisciplinary Center for inductively coupled plasma mass spectrometry by laser ablation on their multi-collector inductively coupled mass spectrometer. Otolith strontium isotope analysis was used to reconstruct juvenile freshwater habitat use and migration histories (Barnett-Johnson et al., 2008). In brief,  $^{87}\text{Sr}/^{86}\text{Sr}$  of freshwater habitats (the "isotope") varies as a function of watershed lithologies and weathering patterns, and

**TABLE 1** Butte Creek otoliths summary.

Year	Escapement	Sr isotope analysis		Growth analysis	
		<i>N</i>	Percentage of adults analyzed	<i>N</i>	Percentage of adults analyzed
2003	17,404	28	0.16	24	0.14
2005	17,592	28	0.16	24	0.14
2006	6537	48	0.73	38	0.58
2007	6871	33	0.48	0	0
2008	11,046	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	16,317	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

Note: 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* is the number of otoliths used for Sr isotope and growth analyses. Percentage of adults analyzed = (*N*/Escapement) × 100.

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.  $^{87}\text{Sr}/^{86}\text{Sr}$  is a particularly powerful tool in the CCV, because the spatial heterogeneity in rock types results in significant differences in isotope values among most of the salmon-bearing watersheds (Barnett-Johnson et al., 2008; Ingram & Weber, 1999). Consequently, variations in  $^{87}\text{Sr}/^{86}\text{Sr}$  across Central Valley watersheds have proven useful for determining the population of origin and reconstructing juvenile rearing and migration behaviors (Cordoleani et al., 2021; Johnson et al., 2016; Phillis et al., 2018; Sturrock et al., 2015, 2020; Willmes et al., 2018).

## Movement reconstruction

Otolith radius was used as a proxy for fish size at natal and freshwater exit given a linear relationship between otolith size and fish size at early life stages (Sturrock et al., 2020). The otolith radius for each  $^{87}\text{Sr}/^{86}\text{Sr}$  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  $^{87}\text{Sr}/^{86}\text{Sr}$  values as a function of otolith distance from the

core were created for each otolith. Specific  $^{87}\text{Sr}/^{86}\text{Sr}$  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 (Appendix S1: Table S2; Barnett-Johnson et al., 2008; Phillis et al., 2018; Sturrock et al., 2015; Willmes et al., 2018). The Butte Creek migratory corridor was separated into four geographic regions: (1) Natal tributary, which encompasses the entire Butte Creek watershed, including Butte Creek floodplain (hereon “Butte Creek”), (2) Sacramento River, (3) Sacramento-San Joaquin Delta (hereon “Delta”), and (4) San Francisco-San Pablo Bay and Ocean (hereon “Bay & Ocean”). Changes in  $^{87}\text{Sr}/^{86}\text{Sr}$  and threshold exceedance values were used along the otolith transect to identify the shifts between each region: (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  $^{87}\text{Sr}/^{86}\text{Sr}$  measurements on either side of the  $^{87}\text{Sr}/^{86}\text{Sr}$  threshold value between Sutter Bypass and the Sacramento River at Elkhorn (i.e., point of natal tributary exit; threshold value = 0.7056; Appendix S1: Table S2). The Sacramento River at Freeport  $^{87}\text{Sr}/^{86}\text{Sr}$  value threshold (threshold value = 0.7076; Appendix S1: 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  $^{87}\text{Sr}/^{86}\text{Sr}$  measurements on either side of the Chipps Island threshold value of 0.7078 (Appendix S1: Table S2).

## Hierarchical clustering analysis

A hierarchical cluster analysis (Legendre & 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 4.3.2 (R Core Team, 2023) using the function `hclust` with the Ward 2 method and Euclidean distance. The `Nbclust` package (Charrad et al., 2014) was used to estimate the optimal number of clusters across, based on 30 different clustering indices.

## Fish size reconstruction

An otolith radius–fork length relationship for Central Valley fall-run Chinook Salmon, developed by Sturrock et al. (2020), was applied 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 to 146 mm and 49 to 152 mm, respectively (Appendix S1: Figure S3).

## Otolith growth chronologies

Otoliths increment numbers were estimated from digitized otolith images using Image Pro Premier 9.0 (Media Cybernetics) and 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, with 5 representing 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.

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

## Spring-run stock complex stability

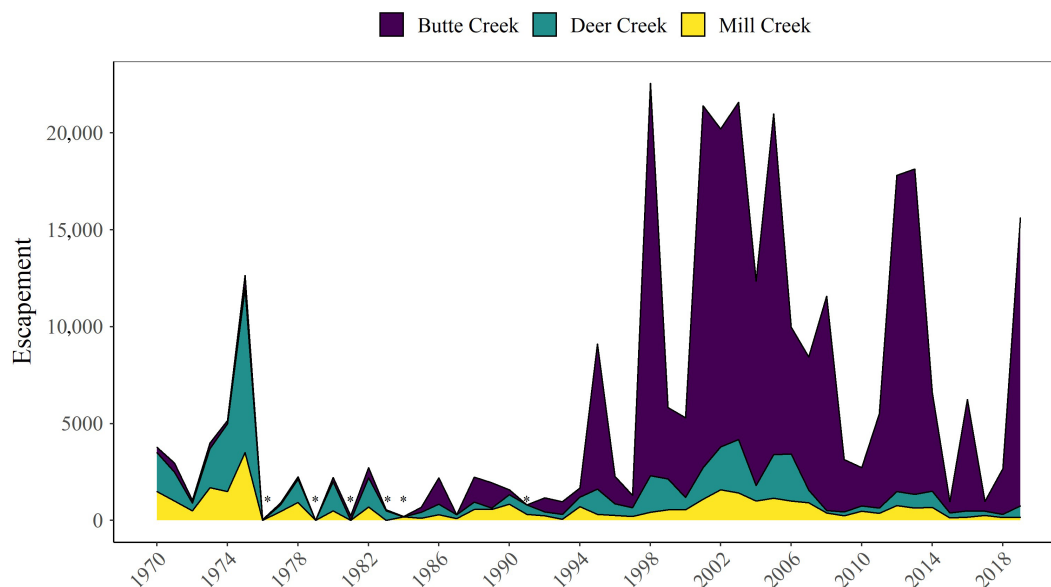
To assess the stability of each spring-run population as well as the overall stability of the spring-run stock complex through time, the CVs in adult returns were calculated for each population independently and for grouped populations (e.g., Mill + Deer + Butte), for the pre-restoration (i.e., 1970–1994) and post-restoration (i.e., 1995–2019) periods, similar to the metrics calculated by Carlson and Satterthwaite (2011) for CCV fall-run Chinook Salmon. Similar to Carlson and Satterthwaite (2011), escapement was used as an index of productivity. 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), the degree of independence between spring-run population dynamics was also assessed by estimating pairwise Pearson correlations between all pairs of populations.

## RESULTS

### Spring-run population production and floodplain access

After habitat restoration efforts started in the early 1990s, Butte Creek spring-run escapement abundance increased significantly, with about a 2000% increase in average abundance (post-restoration mean  $N_{1995-2019} = 8578.5 \pm 6714.4$  SD vs. pre-restoration mean  $N_{1970-1994} = 404.4 \pm 412.1$  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





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

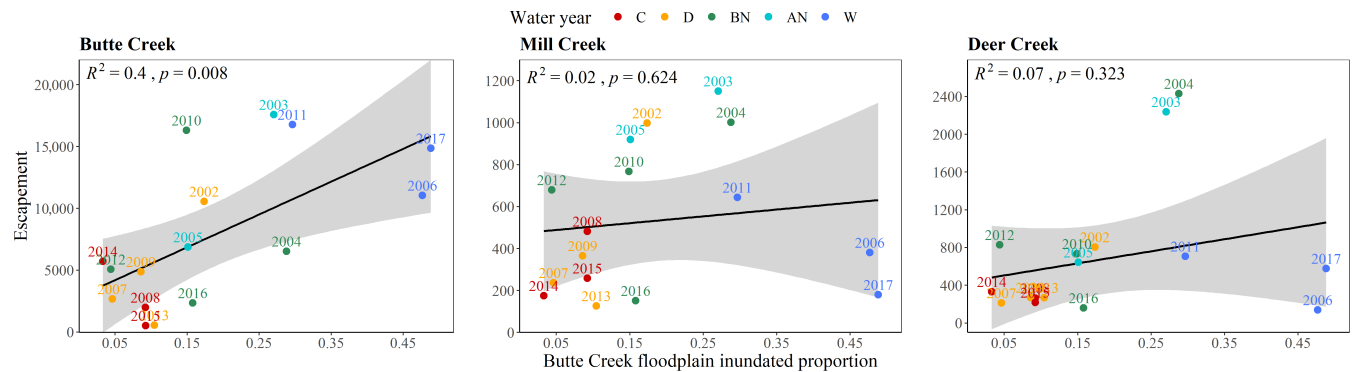
are now at relatively low escapement levels (Mill Creek post-restoration mean  $N_{1995-2019} = 597.8 \pm 419.6$  vs. pre-restoration mean  $N_{1970-1994} = 776.0 \pm 782.1$  SD, and Deer Creek post-restoration mean  $N_{1995-2019} = 955.6 \pm 803.2$  SD vs. pre-restoration mean  $N_{1970-1994} = 1255.6 \pm 1864.2$  SD; Figure 2).

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 Butte Creek floodplain (on average 20 days per year for Colusa weir; Appendix S1: 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 (Appendix S1: Figure S2). Collectively, these results suggest that the relationship in Figure 3 is not simply a generic “wet year effect” shared across watersheds.

### Spring-run juvenile life history strategy diversity

While recent Butte Creek spring-run spawner abundance is usually several orders of magnitude 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 indicated three distinct juvenile life history types in Butte Creek population (Figure 4a, “Otoliths analysis” section in Appendix S1), which 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 with 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 (Figure 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., median [quartiles, Q1–Q3] size and age at natal exit was 74 mm [67–81 mm] vs. 113 mm [82–126 mm] and 70 days [59–82 days] vs. 176 days [74–207 days], respectively; Figure 4; Appendix S1: Table S3). Additionally, Butte Creek juveniles consistently entered the bay and ocean at more similar and smaller sizes/earlier ages than Mill and Deer Creek fish, regardless of the migrant strategy (median [Q1–Q3] size and age at freshwater exit was 83 mm [76–90 mm] vs. 113 mm



**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 the October–May juvenile emigration period experienced two years prior. Years shown on the figures correspond to juvenile emigration years, assuming all individuals returned at age 3 (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>).

[82–126 mm], and 81 days [72–91 days] vs. 197 days [107–223 days] respectively; Figure 4; Appendix S1: Table S3). This could in part be explained by the limited number of yearling-sized fish (i.e., size >110 mm at natal exit) in the Butte Creek sample, which 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, which show larger numbers of yearling fish in Mill and Deer Creek (approximately 10% vs. 1% of raw catch data, respectively; Appendix S1: Figure S4).

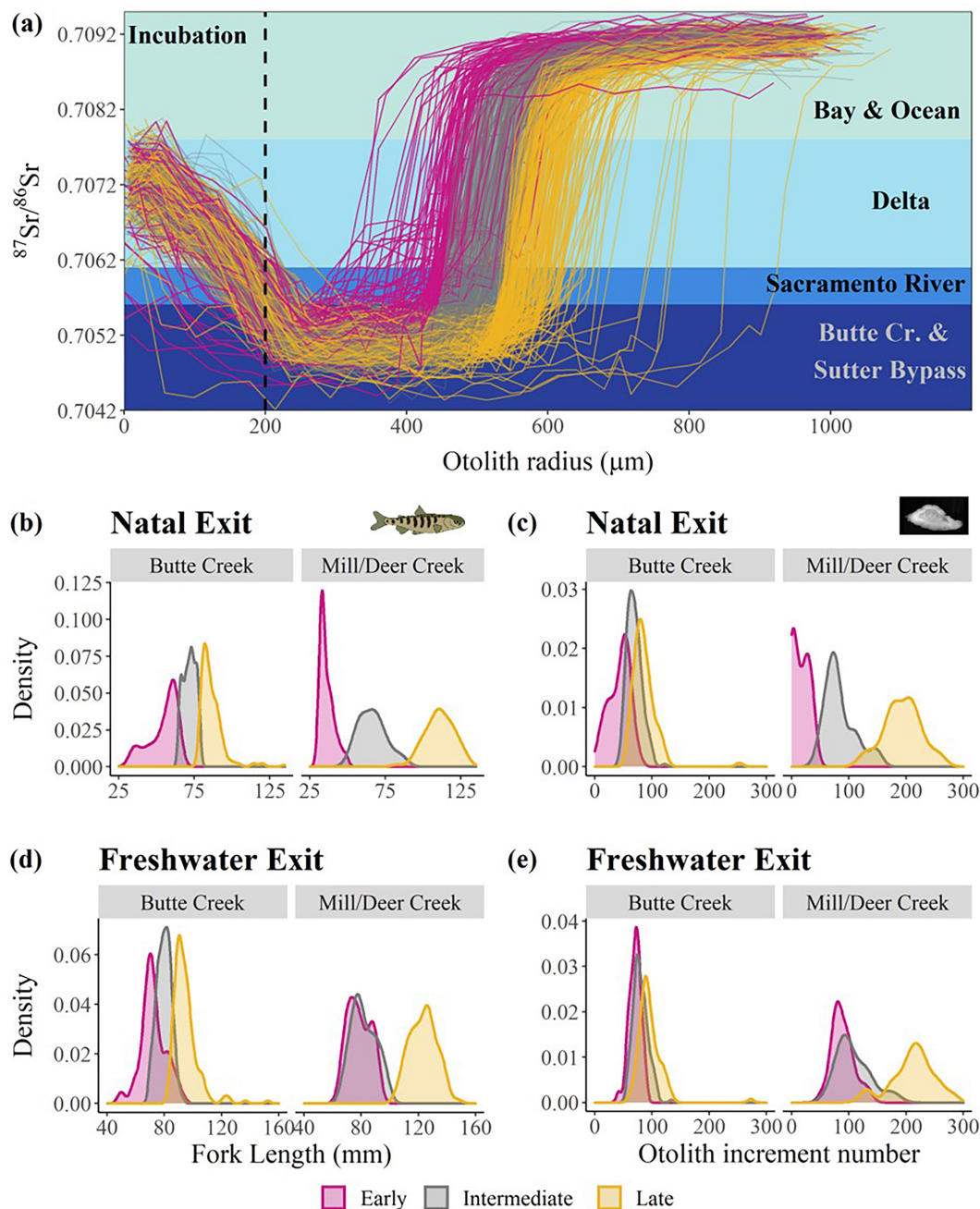
This increased uniformity in Butte Creek spring-run juvenile rearing and migratory strategies also translated into lower interannual variability in the number of days spent in each of the three isotopically defined freshwater regions (i.e., Natal tributary, Sacramento River, and Delta; Figure 5a,b). 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 (median [Q1–Q3] rearing time was 70 days [59–82 days] and 10 days [8–13 days], respectively), suggesting that they underwent smoltification while rearing in the natal tributary and used downstream habitats primarily as a migratory corridor. Contrasting to the Mill and Deer Creek populations, where yearlings dominated the adult returns for many 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 81 days—the median age at freshwater exit for Butte Creek—median growth of 0.62 vs. 0.44 mm/day respectively; Figure 5d).

### 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 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 abundances ( $r = 0.94$ ), 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 considerably during the post-restoration period ( $r = 0.61$  and  $r = 0.60$ , 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.



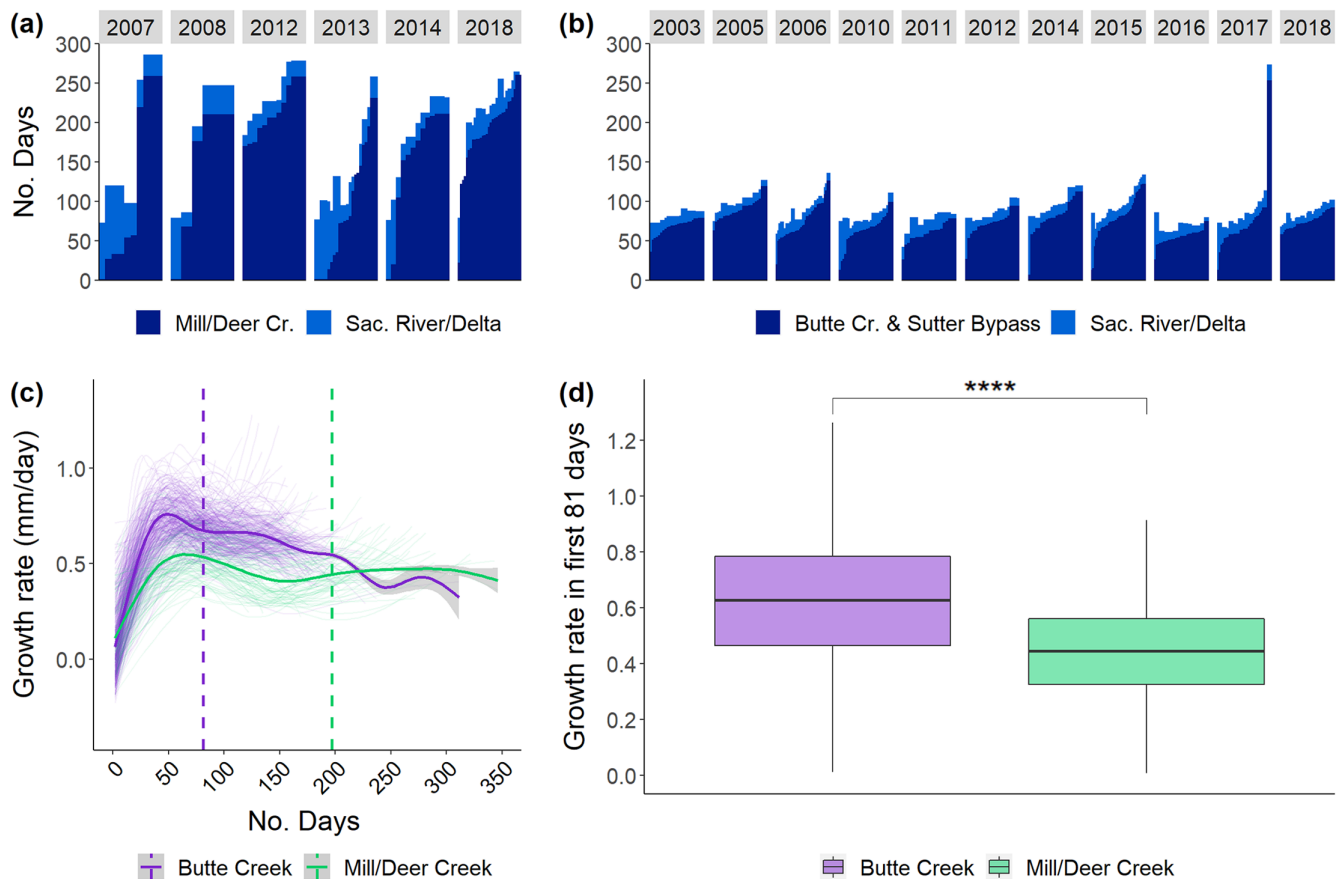
**FIGURE 4** (a) Butte Creek otolith strontium isotope profiles for all years combined and colored by life history type. Life history types were classified using a hierarchical cluster analysis based on otolith radius at natal exit. Fish size distributions for each population (i.e., Butte, Mill/Deer 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.

## 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; Munsch et al., 2022; Yoshiyama et al., 1998). The CVSC stock complex is also particularly vulnerable to warming 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 oversummer before migrating to the ocean in the fall (Moyle et al., 2017). One exception is the Butte Creek spring-run Chinook





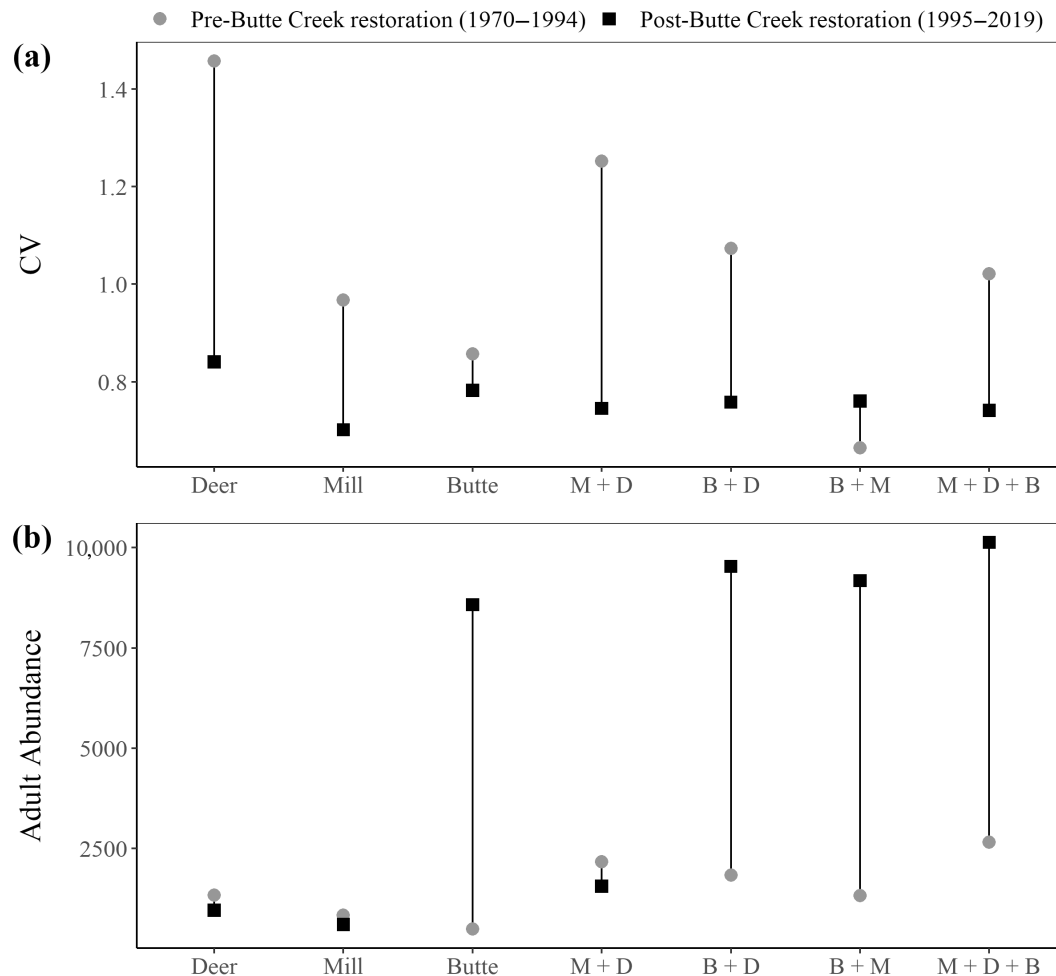
**FIGURE 5** Number of days spent by each fish (individual bars) in the natal tributary (dark blue) and Sacramento River/Delta (light blue) across escapement years for Mill and Deer Creek (a) and Butte Creek (b). Each bar represents one adult (note varying widths), and the bar height represents their 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 loess function in R (R Core Team, 2023). The vertical dashed lines show the median number of days (i.e., age) at freshwater exit for each population (i.e., 81 days for Butte Creek and 197 days for Mill/Deer Creek). (d) Boxplot comparing Butte Creek and Mill/Deer Creek growth rates during the first 81 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  $1.5 \times$  interquartile range from the hinge. Wilcoxon test shows 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.

population that has exhibited a large increase in overall productivity after extensive watershed restoration efforts that started in the early 1990s. This restoration action is considered one of the most holistic and successful salmon recovery efforts in the CCV, with abundance increases of ~2000% following passage improvements throughout the watershed. This multi-life-stage approach highlights that when limiting factors are mitigated and juvenile fish can experience the benefits of access to one of the last CCV ecologically functional floodplains (i.e., Butte Creek floodplain), population recovery can be realized.

Here we found that following restoration activities, 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 the Butte Creek floodplain to recovering Butte Creek spring-run. For example, 2006 outmigrants across the CCV experienced high river flows but poor ocean conditions that resulted in low numbers of returns and the ultimate collapse of the fishery in 2008–2009 (Lindley et al., 2009). The fact that Butte Creek escapement remained above 10,000 spawners in 2008 is a testament to the buffering effects of floodplain access, with ~50% floodplain inundation area apparently providing significant growth and survival benefits to its outmigrants.

For Mill and Deer Creek spring-run populations, other factors, such as water temperature, nonlinear relationships with flow/floodplain inundation, and/or their



**FIGURE 6** (a) Coefficients of variation (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. B, Butte Creek; D, Deer Creek; M, Mill Creek.

different outmigration pathway including a far longer stretch of the mainstem Sacramento River might have a stronger influence on population size. Importantly, in contrast to Butte Creek, Mill and Deer Creeks experienced relatively low numbers of returns in 2008 and 2019 (dominant outmigration years 2006 and 2017, respectively) despite having experienced relatively wet conditions during outmigration. As mentioned above, 2006 outmigrants experienced poor ocean conditions that resulted in the ultimate collapse of the fishery (Lindley et al., 2009), while low returns in 2016–2017 following the extreme 2014–2015 drought resulted in low juvenile production and thus low returns in 2019.

It is important to note that a significant relationship between Butte Creek escapement and its floodplain inundation area two years prior was observed despite the noise undoubtedly introduced by our oversimplified assumption that all spawners had returned at age 3. While natural-origin CCV spring-run adults do predominantly

return to spawn at age 3 (60%–99%; mean = 82% for 2010–2014, 2016, 2018; Satterthwaite et al., 2023), some interannual adult age structure variability has been observed, for Feather River and Butte Creek spring-run populations particularly, with a non-negligible proportion of age-2 and age-4 spawners in some years (McReynolds et al., 2007; Satterthwaite et al., 2018, 2023). It has been shown in other Pacific Northwest watersheds that yearlings tend to mature later than earlier migrants (Hankin & 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 with Mill and Deer Creek fish (median fish length growth rates of 0.62 vs. 0.44 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, reconstructed 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 (Katz et al., 2017; Sommer et al., 2001). 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 migration conditions later in the spring, especially during dry years, and leading to better growth and survival opportunities in the ocean (Satterthwaite et al., 2014; Woodson et al., 2013).

Butte Creek provides a textbook example of how salmon populations at risk of extinction can respond to coordinated watershed-level restoration. By focusing efforts to take advantage of existing high-quality habitat and eliminating several key demographic bottlenecks, important growth and survival benefits can be unleashed to increase abundance by several orders of magnitude. Yet at the population level, Butte Creek appears to exhibit lower phenotypic diversity than the other spring-run strongholds (Mill and Deer Creek). Indeed, most Butte Creek juveniles reared in their natal watershed and floodplain then migrated to the ocean in the spring (earlier than Mill and Deer Creek juveniles) at parr (55–75 mm) or smolt (75–110 mm) sizes. Only a small proportion of juveniles were found to leave the Butte Creek watershed as fry 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. The limited rearing of Butte Creek juveniles in the mainstem Sacramento River and Delta (which have been characterized by poor growth and survival in other studies, e.g., Sommer et al., 2001), suggests that—when there is sufficient habitat within a natal watershed—non-natal rearing in downstream habitats is uncommon. While juveniles are sometimes observed in the upper Butte Creek watershed in the summer (California Department of Fish and Wildlife, Tracy McReynolds, Chico Field Office, personal communication), the rarity of the

yearling phenotype in the spawner population is presumably related to the elevated summer and early fall water temperatures observed in both Butte Creek spawning ground and floodplain habitat (Appendix S1: Figure S5), making it unlikely 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 & 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 high-elevation 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, this life history strategy is predominant in Chinook Salmon populations found in more northern latitudes, as a result of low “growth opportunities” for juvenile salmons due to cool water temperatures and decreased daylight hours (Taylor, 1990). While Butte Creek abundance sharply increased post-restoration, it has also been characterized by high interannual escapement variability in recent decades, with relatively low adult abundances following some particularly dry years (e.g., return years 2010, 2017). This—and the strong relationship with floodplain inundation area—suggests that Butte Creek spring run are still vulnerable to drought. However, post-restoration, they appear to have a much greater ability to “bounce back” from extreme climate events, which we attribute to their higher average abundance largely relating to the increased passage, water supply, and floodplain access. On the other hand, Mill and Deer Creek populations’ lower post-restoration CV (i.e., higher population stability) is likely unrelated to the Butte Creek 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 increase in Butte Creek population size observed after 1994 now drives the overall CVSC stock complex abundance and decreases the overall stock extinction risk (Johnson et al., 2023). When combining the abundances of the three spring-run populations, a decrease in the overall CV was observed post-restoration, suggesting an increase in portfolio effect stability at the stock complex level. However, this observation was contradicted by an increase in pairwise correlations between Butte and Mill, and Butte and Deer



Creek abundances across the same time period ( $r < 0$  to  $r > 0.6$ ), suggesting an overall increase in among-stock synchronization. Recent increases in synchrony have also been reported among CCV fall-run Chinook Salmon populations (Satterthwaite & 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. It is likely that the increasing climate volatility in California (Swain et al., 2018)—that affects both their freshwater and marine ecosystems (e.g., North Pacific Gyre Oscillation)—is driving this increased synchrony in the CVSC stock complex. Collectively, these results highlight potential limitations of using the CV for assessing population stability, particularly for populations that are close to extinction. It is also important to consider abundance and other diversity and synchrony indicators to understand how to enhance the resilience of individual and grouped populations to environmental perturbations (Carlson & Satterthwaite, 2011).

The geomorphological and hydrological differences between watersheds give rise to critical among-population life history diversity (Schindler et al., 2015). Here, differences in the frequency of outmigration phenotypes (early, intermediate, and late) between Butte Creek and Mill/Deer Creek spring run will likely play an important part in the recovery of the spring-run ESU. For example, California is predicted to have increased whiplash weather, with more frequent periods of extreme droughts followed by floods (Swain et al., 2018). California's late spring and summer river temperatures often exceed the physiological tolerance limits for this species, reducing survival during spring outmigration and making access to cold water critical for overwintering (Crozier et al., 2019). Cordoleani et al. (2021) demonstrated that the yearlings on Mill and Deer Creek are functionally the only outmigrant phenotype that survives during droughts in the Central Valley, due to their access to cold overwintering habitats and delayed outmigration into the fall when downstream river temperatures are cooler. Butte Creek spring run outmigrate during a more compressed time window in the spring and thus a greater proportion of their juvenile production may be impacted by droughts. However, in average to high precipitation years with increased floodplain inundation, Butte Creek juveniles appear to exhibit disproportionately high survival, resulting in large increases in adult abundance. This asynchrony in outmigration phenotypes between

watersheds—and their respective survival advantages under differing hydroclimatic conditions—will likely play a critical role in the ongoing persistence of this ESU in a changing California climate. If individual spring-run populations are lost or if there is increased synchrony in outmigration phenotypes, we would anticipate an increased risk of extinction.

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 a habitat component (Lindley et al., 2007)—and watershed-scale restoration efforts generally implemented in the CCV to increase Chinook population abundance. While the juvenile outmigration diversity for Butte Creek spring run was found to be narrower than for Mill and Deer Creek populations, this work highlights the importance of large-scale restoration efforts to promote increased abundance and asynchrony in among-population dynamics to support recovery of the stock complex as a whole. Specifically, this work demonstrates the increased value in prioritizing a variety of restoration actions that promote habitat heterogeneity across watersheds (e.g., cold water refuge in Mill and Deer Creeks and floodplains on Butte Creek) to buffer the entire stock complex to catastrophic disturbances. More globally, most conservation objectives focus on short-term abundance benefits 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; Moore & Schindler, 2022; 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 the abundance and resilience of vulnerable species like Chinook Salmon in a warming climate (Coleman et al., 2022; Crozier et al., 2019; Herbold et al., 2018). This may require expanding the CVSC stock complex's geographical distribution to include lost ecoregions, through population re-introduction into habitat above impassable dams and natural barriers watersheds, which would provide access to cold water habitat for

spawning and rearing even in a warming climate (Cordoleani et al., 2021; FitzGerald et al., 2021). Also, using targeted restoration efforts in sections of the migratory corridor identified as survival bottlenecks—in the Central Valley, the mainstem Sacramento River and Delta—can have dramatic effects on productivity (e.g., Ogston et al., 2015). 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 (Pander et al., 2018; Yarnell et al., 2015, 2020). Collectively, such efforts would boost abundance and amplify asynchrony among populations and lead to a further reduction in the extinction risk of the CVSC stock complex, which is currently relying on core populations belonging to the same ecoregion that are likely to all be impacted by the same local catastrophic climate events (Lindley et al., 2007). The landscape-scale restoration efforts proposed to improve the resilience of the CVSC stock complex could be seen as comparable with the development of marine protected areas, which are designed to promote connectivity between populations and habitats, and is recognized as a powerful conservation policy tool for the recovery of marine species worldwide (Devillers et al., 2019; Duarte et al., 2020; Giakoumi et al., 2018; Lubchenco et al., 2003).

## AUTHOR CONTRIBUTIONS

Flora Cordoleani, Corey Phillis, Anna M. Sturrock, Malte Willmes, and Rachel C. Johnson conceived the study. Flora Cordoleani led data collection and analyses. George Whitman conducted the otolith microchemistry and microstructure analyses. Flora Cordoleani, Corey Phillis, Anna M. Sturrock, Malte Willmes, Eric Holmes, Peter K. Weber, Carson Jeffres, and Rachel C. Johnson contributed to data analyses and manuscript writing.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interests.

## DATA AVAILABILITY STATEMENT

Data and code (Cordoleani, 2023) are available from Zenodo: <https://doi.org/10.5281/zenodo.8057726>.


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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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