

# One hundred-seventy years of stressors erode salmon fishery climate resilience in California's warming landscape

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## Abstract

People seek reliable natural resources despite climate change. Diverse habitats and biologies stabilize productivity against disturbances like climate, prompting arguments to promote climate-resilient resources by prioritizing complex, less-modified ecosystems. These arguments hinge on the hypothesis that simplifying and degrading ecosystems will reduce resources' climate resilience, a process liable to be cryptically evolving across landscapes and human generations, but rarely documented. Here, we examined the industrial era (post 1848) of California's Central Valley, chronicling the decline of a diversified, functional portfolio of salmon habitats and life histories and investigating for empirical evidence of lost climate resilience in its fishery. Present perspectives indicate that California's dynamic, warming climate overlaid onto its truncated, degraded habitat mosaic severely constrains its salmon fishery. We indeed found substantial climate constraints on today's fishery, but this reflected a shifted ecological baseline. During the early stages of a stressor legacy that transformed the landscape and -- often consequently -- compressed salmon life history expression, the fishery diffused impacts of dry years across a greater number of fishing years and depended less on cool spring-summer transitions. The latter are important given today's salmon habitats, salmon life histories, and resource management practices, but are vanishing with climate change while year-to-year variation in fishery performance is rising. These findings give empirical weight to the idea that human legacies influence ecosystems' climate resilience across landscapes and boundaries (e.g., land/sea). They also raise the question of whether some contemporary climate effects are recent and attributable not only to increasing climate stress, but to past and present human actions that erode resilience. In general, it is thus worth considering that management approaches that prioritize complex, less-modified ecosystems may stabilize productivity despite increasing climate stress and such protective actions may be required for some ecological services to persist into uncertain climate futures.

## KEY WORDS

biocomplexity, climate change, disturbance, diversity, habitat mosaic, historical ecology, natural resources, shifting baselines

## 1 | INTRODUCTION

The reliability of ecosystem services under uncertain climate futures is a global concern (Barange et al., 2018; NOAA, 2016; Oremus, 2019). Reliable production emerges from diverse, intact ecosystems because disasters befalling finer scales of biological organization (e.g., habitats, species, life histories) can be mitigated at greater spatial and organizational scales (e.g., ecosystems, meta-populations) by ecologically redundant, finer-scale counterparts (Naeem & Li, 1997; Tilman & Downing, 1994) and because individuals integrate across events and habitat attributes that are unpredictable and highly variable over time and space (Armstrong et al., 2013; Brennan et al., 2019; Levin, 1992; Schindler et al., 2015). A common argument that emerges from this literature is that people may promote climate-resilient resources by conserving and restoring processes that maintain and define diverse landscapes and life histories that enable production systems to spread risk and actualize adaptive responses (e.g., Beechie et al., 2013; Hughes et al., 2003; Mantua & Francis, 2004; Timpane-Padgham et al., 2017).

One of the defining challenges of the Anthropocene, exemplified by fisheries, is to promote reliable natural resources despite the interactive effects of climate change and ecosystem modification. The world's largest sockeye salmon (*Oncorhynchus nerka*) fishery, produced by the Bristol Bay watershed (Alaska, USA), has demonstrated that complex, pristine ecosystems can reliably produce resources despite climate variation (Hilborn et al., 2003). This system steadily produced salmon for centuries across climate regimes because regional climate effects were locally, differentially filtered across many different populations maintained by a complex, diverse landscape (Hilborn et al., 2003; Rogers et al., 2013). Yet, many ecosystems are transformed and continue to be simplified and stressed (Lotze et al., 2006), suggesting that transformed ecosystems presently experiencing severe climate forcing may reflect states that emerged only after modification by human stressors and that actualizing climate-resilient productivity will require people to prioritize biological and habitat diversity (e.g., Battin et al., 2007; Eliason et al., 2011; Hughes & Connell, 1999; Worden et al., 2010). While there is widespread concern that stressor legacies may erode resources' climate resilience over landscapes and human generations, documentation of this process is comparatively rare.

Here, we examined the interconnected history of salmon, human stressors, and commercial salmon fishing in California's Central Valley from the 1848 Gold Rush to the present. This system presents a striking example of a formerly complex production system transformed within a naturally dynamic, recently warming climate. We review the ecology of the salmon population complex, synopsize human actions that impacted salmon habitat and -- often consequently -- life history diversity, quantify the evolution of fishery responses to climate across this transformative period, and discuss the implications for salmon and other natural resources produced by modified systems. We present an analysis of long-term datasets to test the hypothesis that stressors have tightened the relationship between the fishery and annual climate conditions. Because

appreciating these findings requires substantial biological and historical context, we framed this paper as a review that synthesized information from other informative reviews (e.g., Herbold et al., 2018; Lindley et al., 2009; Madgic, 2013; Williams, 2006; Yoshiyama et al., 1998) that prompted our hypothesis, and then we present an analysis of empirical data to test this hypothesis. As is true of all historical studies, we referenced data and descriptions that were contemporaneous with past events using inference informed by present-day perspectives to reconstruct a reasonable representation of the historical Central Valley. We have, therefore, taken care to specify throughout the paper whether we are referring to analyses of empirical data or offering inference, often in light of contemporary literature. Our overarching goals were to (1) confront well-founded but largely theoretical arguments with empirical data to see if stress and simplification to a formerly-diversified production system indeed eroded climate resilience and (2) communicate the importance of often-referenced, but potentially esoteric concepts like "diversity," "habitat mosaic," "life history," and "lost climate resilience" via the real-world contexts of the Central Valley's landscape, climate, salmon, and fishery.

## 2 | INTRINSIC BUT THREATENED RESILIENCE OF SALMON PRODUCTION SYSTEMS

Pacific salmon (*Oncorhynchus* spp.) are iconic, keystone, anadromous fishes that support reliable fishing in complex ecosystems (Greene et al., 2010; Hilborn et al., 2003; Schindler et al., 2010, 2015). Salmon spawn in natal freshwater habitats, creating many reproductively-isolated, locally-adapted populations nested across landscapes (e.g., basins, rivers, streams). Within and among species, salmon express many life histories that inhabit different places in different seasons for different lengths of time for different purposes (e.g., growth, migration, reproduction), mature across a range of ages (Pacific salmon are semelparous), and exploit natural variation in opportunities spread across landscapes and seasons to maximize habitat benefits, altogether stabilizing production (Armstrong et al., 2013, 2021; Brennan et al., 2019; Greene et al., 2010; Schindler et al., 2010). Additionally, life history and habitat diversity give rise to asynchronous population outcomes that stabilize abundances of stocks (i.e., aggregate populations fished for together), similar to stabilizing effects of diversified financial portfolios (Galland et al., 2021; Greene et al., 2010; Hilborn et al., 2003; Schindler et al., 2010). However, salmon fisheries throughout much of their range are becoming less resilient (Griffiths et al., 2014). Human stressors have altered and simplified many salmon ecosystems (Nehlsen et al., 1991), threatening life history diversity (Beechie et al., 2006), and eroding asynchrony among individual populations required to stabilize regional productivity (Carlson & Satterthwaite, 2011; Moore et al., 2010). In addition, stressors limit salmon from actualizing adaptive responses to climate stress (Crozier et al., 2019; Herbold et al., 2018). In summary, resilient salmon production emerges from

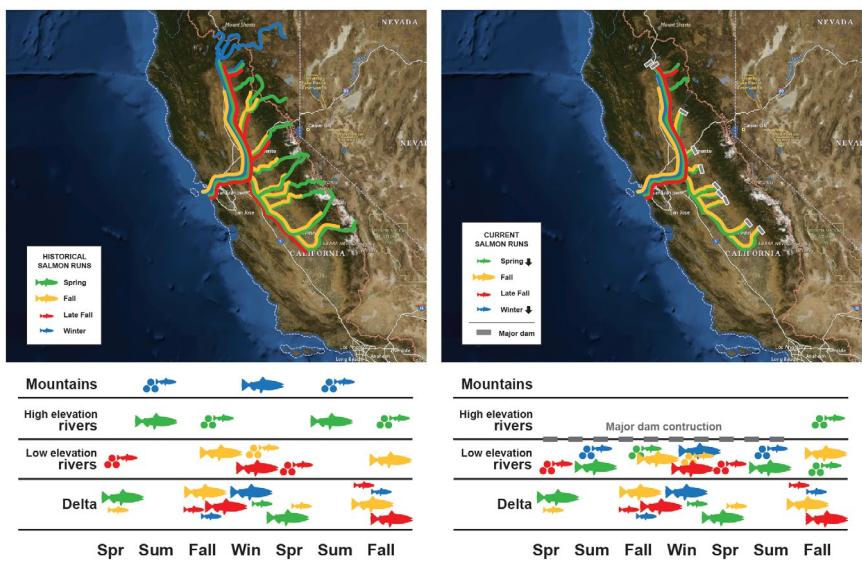
diverse salmon biologies and the habitat mosaics that support them (Brennan et al., 2019; Greene et al., 2010; Rogers & Schindler, 2008; Schindler et al., 2010), but human stressors threaten this resilience (Crozier et al., 2019).

Historically, California's Central Valley ( $47,000 \text{ km}^2$ ) likely epitomized the need and opportunity for climate resilience via diversification. The Central Valley is bounded by mountains and includes a vast network of rivers and streams branching from the Sacramento and San Joaquin River mainstems, which meet to flow through a formerly  $1820 \text{ km}^2$ , highly productive wetland delta (Whipple et al., 2012) and then San Francisco Bay. California's warm, dry summers are predictable, but annual precipitation is not. Indeed, multi-year droughts are common (Dettinger, 2011; Meko et al., 2014), yet atmospheric rivers can fuel storms that historically flooded the valley and created a massive, seasonal estuary (Madgic, 2013; Null & Hulbert, 2007). The landscape supports a gradient in water temperatures across elevations, which is especially relevant to cold water fish during summer when aquifers, springs, and snowmelt prolong the availability of cold water at higher elevations while waters at low elevations become quite warm (FitzGerald et al., 2021). Thus, California's Mediterranean climate is overlaid onto a habitat mosaic composed of desert rivers, seasonally-inundated floodplains, delta wetlands, and mountainous, forested streams that filter and decouple localized conditions from the region's climate.

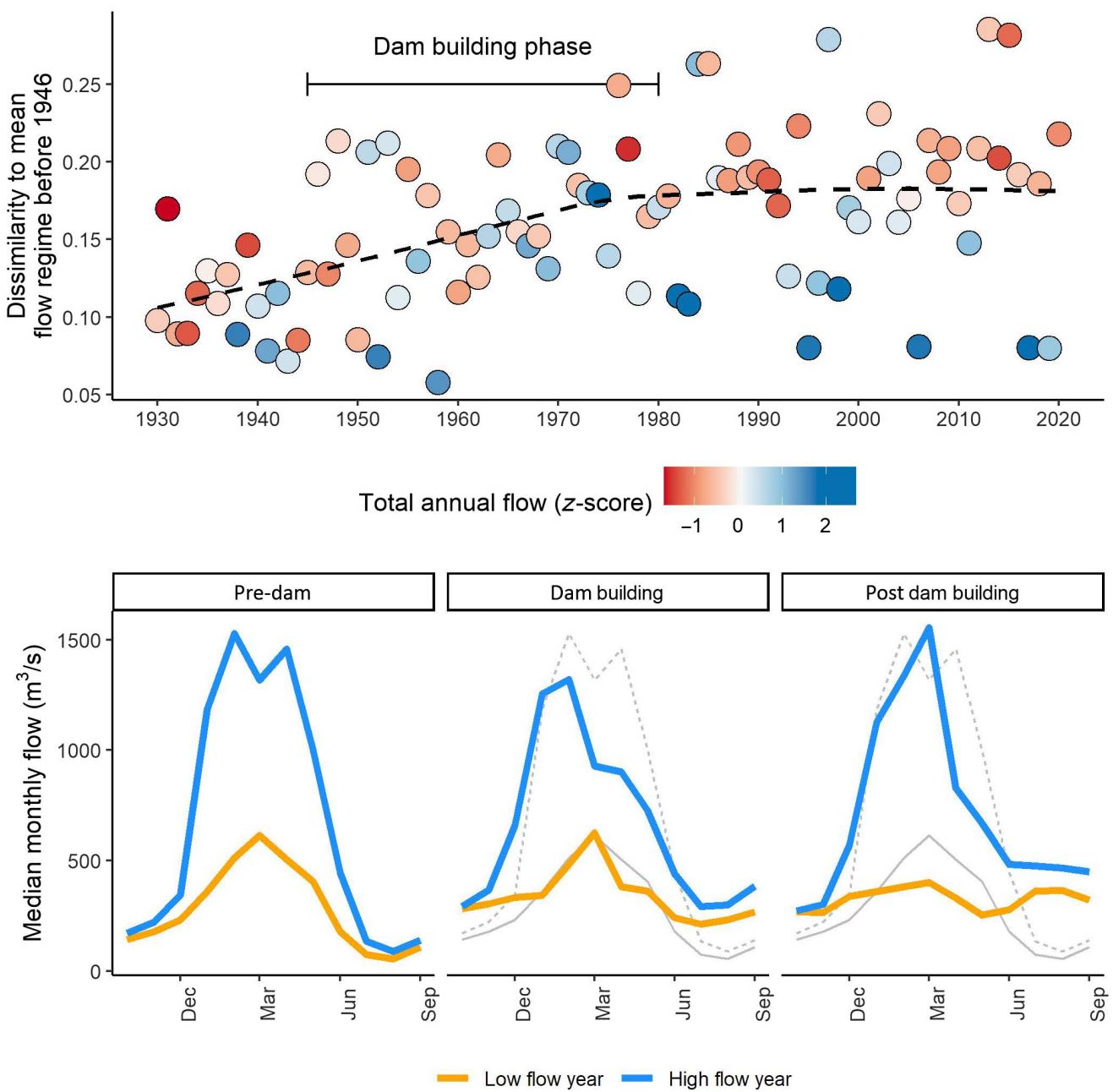
Within this landscape and climate are salmon spawning populations at the southern extent of their species' natural range that require cold, amply-flowing water (e.g., Michel, 2019; Notch et al., 2020; Sturrock et al., 2015). Historically, four Chinook salmon

(*Oncorhynchus tshawytscha*) life history templates staggered their life cycles across the seasons and rugged landscape (Herbold et al., 2018; Williams, 2006; Yoshiyama et al., 1998), presumably spreading risk across seasons and habitats (Figure 1). The Winter, Spring, Fall, and Late-fall runs -- named for the season in which adults re-enter the watershed -- apparently represented alternative approaches to avoid the lower watershed during summer, when and where water quality forced by warm, dry weather was most severe (Yoshiyama et al., 1998). The historical landscape and seasonal climate dynamics supported two general migratory approaches, each presumably balancing a suite of ecological trade-offs that included climate constraints. Adults could enter the watershed during the winter or spring, migrate extensively to higher elevations before summer, then spawn in the summer or early fall (Yoshiyama et al., 1998). This generally enabled offspring to migrate to the sea while the weather remained wet and cool. Alternatively, adults could stay at sea during the summer, enter the watershed during the fall, and spawn shortly thereafter at lower elevations (Yoshiyama et al., 1998). This latter approach required offspring to migrate to sea later, risking passage through the lower watershed during spring-summer transitions when annual water quality may have already turned unfavorable (Figure 2, bottom). Indeed, contemporary research suggests that juvenile survival is greater during colder spring-summer transitions (Kjelson et al., 1982) and the lower landscape is only inhabitable during spring-summer transitions if water is cold and amply-flowing (Munsch et al., 2019).

In addition to spreading risk across habitats and seasons, historical stocks also presumably spread risk across years (sensu Greene



**FIGURE 1** Top: The Central Valley's rugged, varied landscape and the historical (left), and contemporary (right) use of its landscape by salmon life histories. Fish sizes in legends correspond roughly with relative run abundances, with down arrows indicating sharply declined runs. Note that, for legibility, smaller tributaries and streams and the destruction of wetlands and floodplains over time are not shown (details on habitat changes: Herbold et al., 2018, Whipple et al., 2012, and Figure 4). Basemap by USGS. Bottom: Conceptual model of salmon life history across the Central Valley's historical (left) and contemporary (right) landscape. Dams block most high elevation habitats, but Spring Runs use the few remaining accessible portions. Letters across the bottom refer to seasons. Figure by Su Kim (NWFSC/NOAA) [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]



**FIGURE 2** Evolution of water regulation on the annual flow regime. Top: Flow patterns of individual years compared to median flow patterns of years before Shasta Dam was completed. With increasing water regulation, the flow regime diverged from natural patterns and only now approaches natural patterns during especially wet years. Dashed line is fit by local regression. Bottom: Water regulation reduced flows during the wet portion of the year when juvenile salmon migrate to sea. Low and high flow years are split according to the median value of total flow for all years. Dashed lines on the right two panels repeat the left panel's pre-dam flows.

Source: USGS flow gage 11425500 (USGS, 2021) [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

et al., 2010; Schindler et al., 2010). By completing their life cycles across a range of ages (primarily ages 3–5, Williams, 2006), abundances of the population complex returning to spawn would have depended less on the environmental state of any singular past year; thus, diffusing impacts of annual climate conditions such as drought or poor ocean conditions across multiple return years. Furthermore, some juveniles reared for a year in fresh water before migrating to sea (Williams, 2006), presumably requiring high elevation habitats to

access cold water during the summer (Beechie et al., 2006; Williams, 2006) and diversifying the lower-watershed conditions experienced by juveniles hatching in the same year (*sensu* Greene et al., 2010; Schindler et al., 2010). Altogether, the Central Valley's landscape and climate probably always influenced salmon habitat experiences, survival, and adaptations.

Thus, one may envision a historical salmon production system that diversified its relationship with regional climate variation

by spreading risk across life histories, habitats, seasons, and years (Figure 3, top panel). Productivity probably relied on favorable climate conditions in general, but a diversity of habitats and salmon would have untethered longer-term productivity from volatile conditions experienced at the finer scales of particular habitats, seasons, or years, potentially culminating in fishing opportunities that were more reliable than California's climate (*sensu* Levin, 1992).

### 3 | PEOPLE IN THE CENTRAL VALLEY AND 170 YEARS OF INDUSTRIAL-ERA STRESSORS

People have lived in the Central Valley since time immemorial, with archeological evidence suggesting large, cohesive groups have been present for at least 6000 years (Madgic, 2013). Various groups of Indigenous people lived across (Yoshiyama, 1999, his Figure 2) and modified (e.g., fire clearing, Mann, 2005) but did not industrialize the landscape. Unsurprisingly, the watershed, climate, and salmon are integral to Indigenous cultures. Among the Indigenous names for the Sacramento River and its tributaries are *Num-tee-pom-all-way-nem*, *Ol-te-ma*, and *We-nem-mem* (Madgic, 2013). Additionally, Indigenous legends describe massive floods (Madgic, 2013) and Indigenous people historically living in flood-prone lowlands did not construct permanent housing (Madgic, 2013). Many Indigenous groups participated in community activities centered on capturing and processing salmon (Madgic, 2013; Yoshiyama, 1999; Yoshiyama & Fisher, 2001) while avoiding excessive localized capture, which probably promoted sustainable harvest (Lufkin, 1991). Indigenous people harvested all salmon runs, with predictable harvests following food-scarce winters in some locations providing important nutrition, although it is noteworthy that people in the Central Valley harvested many other natural resources as well (Yoshiyama, 1999). Indigenous populations declined as a consequence of disease, conquest, and oppression by European immigrants during the early industrial period (McEvoy, 1986; Yoshiyama et al., 1998) or even earlier before Europeans recorded disease impacts (Mann, 2005). Quantitative estimates of Indigenous salmon harvest are uncertain, but they may have approached levels on the order of the industrial era's commercial fishery (Yoshiyama, 1999).

The 1848 California Gold Rush ushered in a new era characterized by explosive population growth and industrialization, which continues to the present (Figure 4). The influx of miners, railroad workers, and settlers transformed rivers and drained the Sacramento-San Joaquin River delta (Madgic, 2013, Whipple et al., 2012, Herbold et al., 2018, their Figure 4). Primarily between 1850 and 1920, 97% of delta wetlands were lost and its waterways were converted to channelized aqueducts within a largely agricultural, unshaded landscape (Whipple et al., 2012). Additionally, people in the late 1800s introduced nonnative salmon predators, which are present today and often valued by anglers (Madgic, 2013).

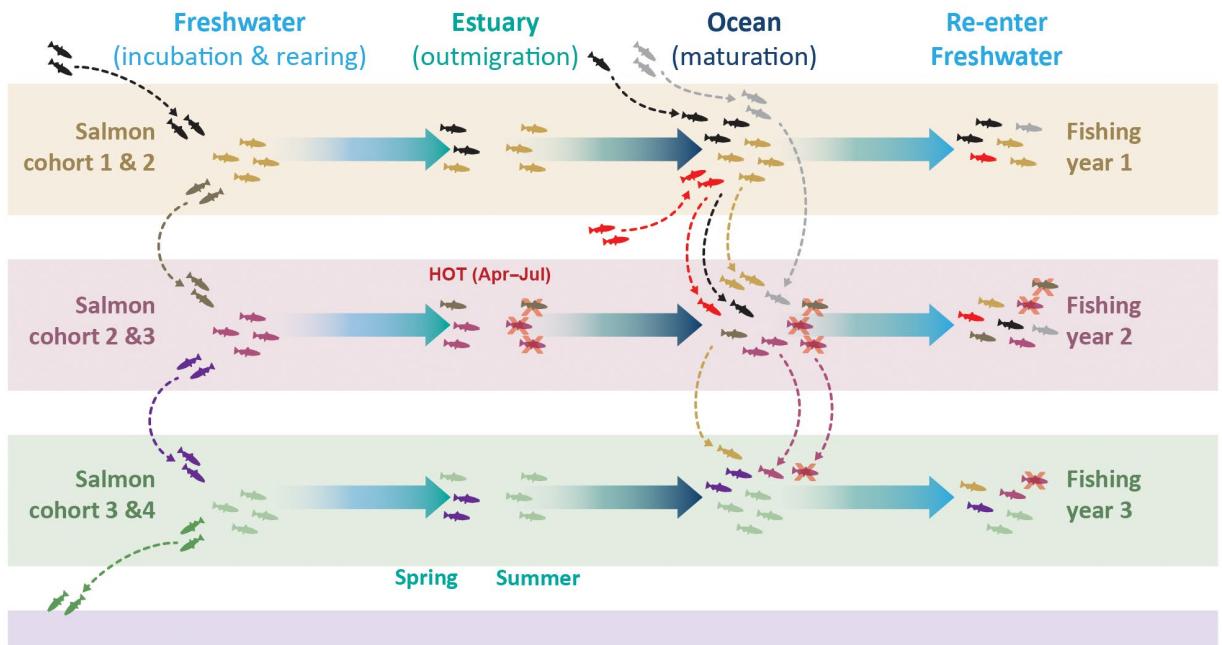
Circa 1850, the commercial salmon fishery was established using gill and fyke nets in the lower watershed, and several

canneries opened in the following decades (Yoshiyama et al., 1998). For context, the system's entire history of commercial fishing lies within its timeline of industrial stressors (Yoshiyama et al., 1998), and cannery entrepreneurs as early as 1866 believed that habitat destruction was imperiling salmon (Lichatowich, 1999). As is clear from monthly market sales in the 1890s, the commercial fishery harvested all salmon runs (Figure 5), and would continue to do so as late as the 1950s (California Fish Commission, 1900; Yoshiyama et al., 1998). Moreover, Winter and Spring Run salmon were highly valued by the river fishery because fishers could capture these fish en route to their high elevation habitats well before spawning season when meat quality degrades (Yoshiyama et al., 1998). During the early to mid-1900s, boat motors proliferated and the fishery shifted from the river to the ocean, providing access to higher quality meat regardless of salmon life history, but introducing fishing pressure on salmon that would not have matured that year (McEvoy, 1986). Ocean fishing would be expected to remove older fish from the population complex, either as a simple numerical phenomenon and/or by selecting evolutionarily against older maturation ages (Barnett et al., 2017). Indeed, analysis of otoliths (ear stones) as early as 1919 suggests a general pattern of Central Valley salmon maturing at age 3–5, then age 3–4, then age 3 becoming increasingly predominant (Satterthwaite et al., 2017; Williams, 2006).

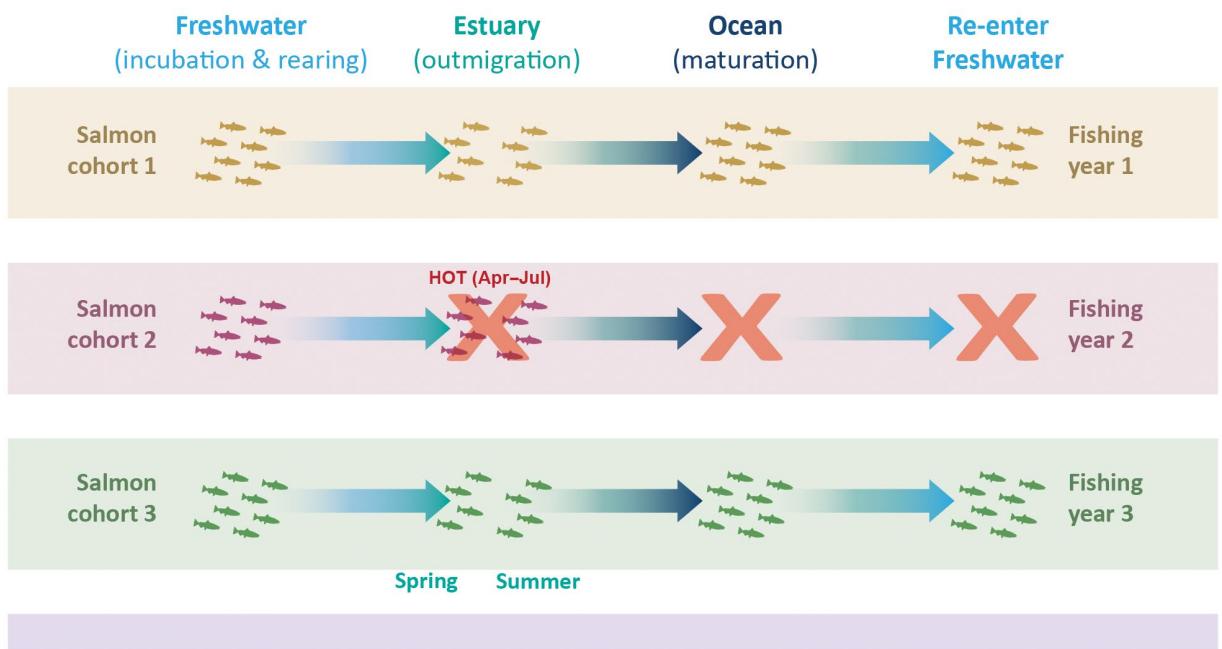
Against the backdrop of the Great Depression, the Dust Bowl, and World War II, people began industrializing the system's water supply. The Central Valley Project began in 1933 and over the following decades constructed dams and reservoirs on nearly all of the watershed's major rivers and tributaries (Madgic, 2013). This provided Californians, factories, and an agricultural industry that would become nationally significant (tens of billions of USD annually; USDA, 2017) with hydropower, flood protection, and year-round water despite the hydroclimate, but blocked salmon from an extensive network of high elevation habitats (Herbold et al., 2018, their Figure 5) where cool water is available, particularly during summer (FitzGerald et al., 2021). Winter and Spring Run life histories could no longer reach their spawning and rearing habitats and they declined catastrophically, including extirpation of the Spring Run from the San Joaquin basin (Yoshiyama et al., 1998). Winter and Spring Runs are now listed under the U.S. Endangered Species Act as endangered and threatened, respectively. In addition to water regulation, water extraction began to rise (Grantham & Viers, 2014; Reis et al., 2019). Consequently, less water overall reached salmon, flow regimes were seasonally flattened (Figure 2), and water could absorb more heat when it flowed more slowly through hot, unshaded regions (Daniels & Danner, 2020; Madgic, 2013).

Beginning in the 1940s, people implemented salmon hatcheries intended to mitigate dam impacts (Huber & Carlson, 2015; Madgic, 2013; Sturrock et al., 2019). Circa 1970-present, hatcheries released salmon over a narrowing range of calendar dates and life stages (Sturrock et al., 2019), presumably concentrating their climate experiences. Circa 1980-present, hatcheries also began trucking some juvenile salmon to sea to bypass stressful

## High life history diversity



## Low life history diversity



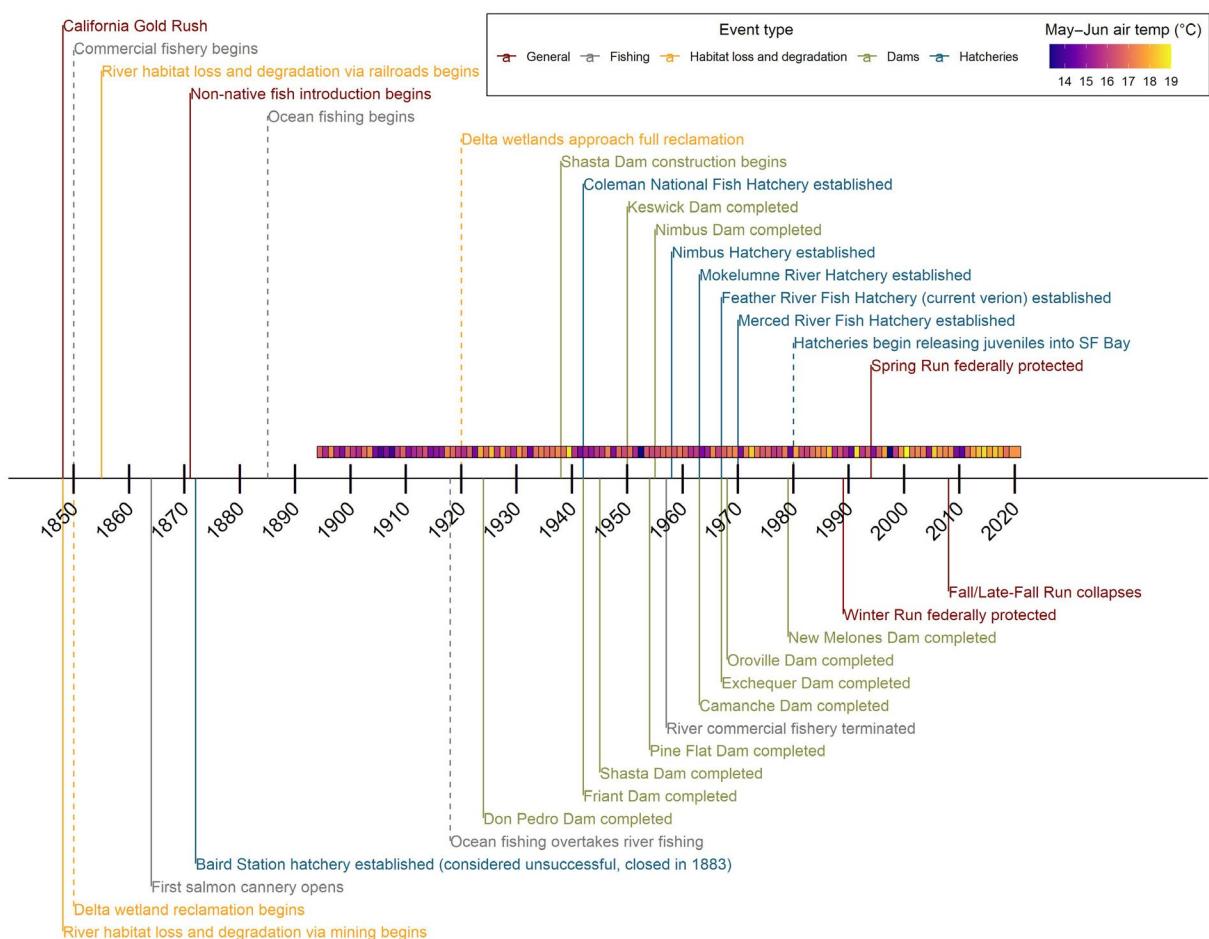
**FIGURE 3** Conceptual model of life history diversity imparting fishery climate resilience because some salmon avoid a disaster and the disaster's effects are diffused across multiple fishing years. Salmon colors indicate annual cohorts. Arrows indicate cohort movements across time and habitats. In one year, the spring-summer transition is hot, causing mortality (red Xs) in salmon using the lower watershed during those months. In the diverse stock, juveniles outmigrate across a wide range of dates, some juveniles rear in higher elevation habitats for a year, and adults return to spawn across a wide range of ages. In the simple stock, juveniles outmigrate across a narrow range of dates, all juveniles outmigrate the year they hatched, and all adults return to spawn 2 years after outmigrating. With high life history diversity, the disaster only impacts a portion of juveniles and these impacts on fishing are smoothed over many years, producing more reliable returns of adult salmon. This representation of stability emerging from life-history diversification across seasons and years is consistent with dynamics observed in other systems (e.g., Moore et al., 2014; Schroeder et al., 2016). Figure by Su Kim (NWFSC/NOAA) [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

freshwater environments, preventing juveniles from imprinting on navigational cues that guide adults to natal hatcheries (Sturrock et al., 2019). Consequently, hatchery-origin salmon increasingly strayed to natural spawning grounds, often in non-natal tributaries, homogenizing the stock's genetics across the watershed (Dedrick & Baskett, 2018; Williamson & May, 2005) and synchronizing the performance of its populations, presumably because the less diverse stock more universally responded to its regional environment (Carlson & Satterthwaite, 2011). The putative process of hatcheries homogenizing the population complex -- and therefore its relationship with climate -- culminated in fishery's unprecedented collapse from 2008 to 2009, hypothetically due to poor ocean conditions (Lindley et al., 2009), causing an economic loss of \$500 M-\$2B and 5000–23,000 jobs and keeping 1200 fishing boats in port when the fishery was closed (Huber & Carlson, 2015 and references therein, Madgic, 2013). Following the collapse, salmon productivity briefly rebounded but then fell again. This led to the fishery being declared overfished based upon 2015–2017 escapements, and the fishery did not meet rebuilt status criteria until satisfactory escapement over 2018–2020 (PFMC, 2021a).

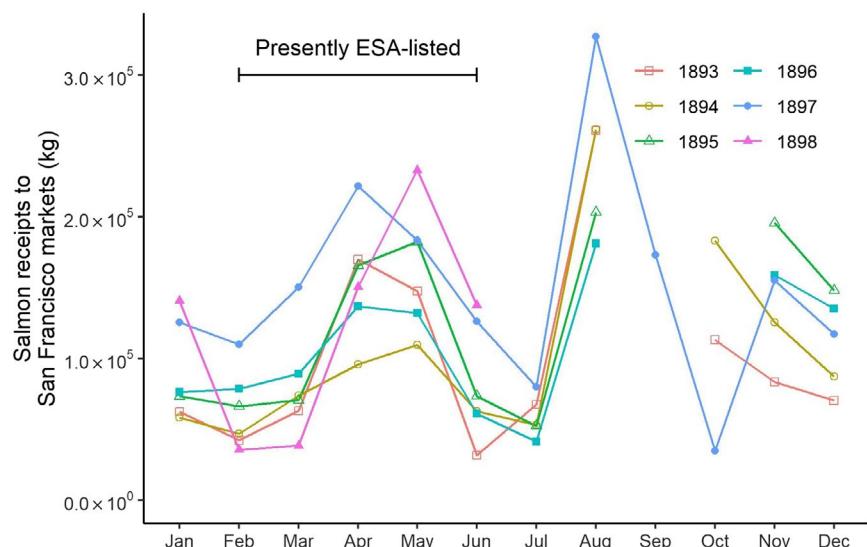
## 4 | HYPOTHESIZED INTERACTION BETWEEN CLIMATE STRESS AND A TRANSFORMED SALMON PRODUCTION SYSTEM

Thus, 170 years of stressors have transformed the Central Valley and its salmon. Layered upon these stressors, California is experiencing a warming trend (e.g., Cayan et al., 2008), including many warm spring-summer transitions in recent years (Figure 4). Here, we outline the hypothesis that stressors have eroded the fishery's climate resilience (Figure 3, bottom panel).

First, we hypothesized that the effects of climate forcing on Central Valley salmon production are more universal at present compared to the past. The current fishery is almost entirely reliant on the Fall Run, the remaining abundant life history that uses low elevations, was least impacted by dams (the Late-Fall Run was apparently always small), and includes a sizeable component of juveniles that migrate to sea during spring-summer transitions (Yoshiyama et al., 1998); thus, we predict that the suite of climate variables that act on this particular life history and its low-elevation habitats will determine the fishery's overall relationship



**FIGURE 4** Timeline of major events involving and impacting the Central Valley's salmon and time series of May-June air temperatures. Dashed lines indicate approximate dates. Sources: Yoshiyama and Fisher (2001), Whipple et al. (2012), Madgic (2013), Sturrock et al. (2019), and NOAA (2021) [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]



**FIGURE 5** Monthly sales of salmon caught in-river and sold in San Francisco in the late 1800s. Source: California Fish Commission (1900). Note that the Winter and Spring Runs that supplied the first annual peak in salmon catches have declined sharply, do not substantially contribute to the fishery, and are now listed under the U.S. Endangered Species Act (ESA) [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

with climate. Also, the historical watershed would have provided more heterogeneous and compartmentalized habitat experiences because its river network was more vast, diverse, sinuous, and dendritic (Herbold et al., 2018; Whipple et al., 2012). Furthermore, compression of outmigration timings by hatchery releases (Sturrock et al., 2019) and erosion of genetic differences among populations via hatchery-induced straying (Dedrick & Baskett, 2018; Williamson & May, 2005) homogenized the responses of salmon to their environments (Carlson & Satterthwaite, 2011). In addition, the combination of suppressed, seasonally flattened flow regimes, lack of rearing habitats, and warm summers is apparently compressing viable annual outmigration timings toward intermediate dates least impacted by these stressors (Sturrock et al., 2020). Finally, the loss of older fish and the potential loss of yearling outmigrants (Satterthwaite et al., 2017; Williams, 2006) probably concentrated the salmon stock's risk into climate conditions of fewer years. Altogether, transforming the stock's freshwater production system has concentrated its risk into fewer habitat use pathways, potentially causing the stock to respond more universally to relevant climate events.

Second, we hypothesized that the effects of spring-summer temperatures on Central Valley salmon production are more severe at present compared to the past. Dams confine salmon to the lower watershed where temperatures are generally highest (FitzGerald et al., 2021) and slower, regulated flows in warm, presently-unshaded areas can increase water temperatures (Daniels & Danner, 2020; Whipple et al., 2012). Nonnative predators now exert substantial predation pressure on juvenile salmon and consume more salmon in warmer waters (Michel et al., 2020), likely exacerbating the impacts of warm years on outmigrating salmon cohorts. Indeed, cool conditions promote salmon survival and landscape-scale habitat occupancy during spring-summer transitions in the contemporary watershed (e.g., Kjelson et al., 1982; Michel et al., 2020; Munsch et al., 2019). Juvenile salmon can thrive in localized patches of relatively warm waters within the Central Valley's remaining wetlands in late-winter/

early-spring because substantial prey availability enables prodigious, temperature-dependent growth (Sommer et al., 2001), and salmon, in general, can benefit from localized patches of relatively warm water to expedite digestion (Armstrong et al., 2013). However, such adaptations that may have historically offset some heat stress may go unrealized in much of the present Central Valley because productive, heterogeneous floodplain and delta wetland habitats have been destroyed and replaced with unproductive, homogeneous aqueducts (Herbold et al., 2018; Whipple et al., 2012). Altogether, transforming the Central Valley may have increased the sensitivity of its freshwater salmon production system to air temperature during spring-summer transitions.

## 5 | AN ANALYSIS OF EVOLVING CLIMATE CONSTRAINTS ON THE FISHERY

We examined empirical support for the hypothesis that a legacy of human stressors eroded the fishery's climate resilience. Specifically, we predicted that fishery performance was increasingly constrained by spring-summer temperatures and climate conditions in fewer cohort years. The former prediction reflects the fishery's increased reliance on life histories that outmigrate during spring-summer transitions that can be harmfully warm (e.g., Kjelson et al., 1982; Michel et al., 2020; Munsch et al., 2019). The latter reflects an increased reliance on a simplified age structure (Satterthwaite et al., 2017; Williams, 2006). To provide contrast against increasing temperature constraints, we also examined the relationship between the fishery and annual precipitation. This followed the logic that the benefits of precipitation (e.g., wintertime habitat inundation from rain, summertime high-elevation cold pools from snowmelt) probably transcended life histories, life stages, habitats, and the watershed's industrialization phases, whereas cool spring-summer transitions were hypothesized to be especially important for contemporary life histories and habitats (e.g., Kjelson et al., 1982; Michel et al., 2020; Munsch et al., 2019). That is, we expected to find evidence that wet



years benefitted the fishery across its history, but that cold spring-summer temperatures became more important in the contemporary era.

Our analyses used linear models across various time windows to detect the presence and evolution of fishery-climate relationships (see Data S1 for details). The response variable was "fishery performance," which described fishery landings prior to 1971 and expected returns in the absence of fishing thereafter when fishery-independent spawner surveys became available (*sensu* Hilborn et al., 2003). The explanatory variables were total annual precipitation and mean May–June air temperature (source: NOAA National Centers for Environmental Information). While instrumental records began in 1895, we were able to extend the precipitation time series to match the historical extent of the fishery's time series using tree growth chronologies that quantified streamflow (source: Meko et al., 2014) and were highly correlated with precipitation ( $r^2 = .77$  during overlapping periods). We lagged climate variables by two years and examined support for these variables based on either their single-year values or multi-year averages of up to 4 years, corresponding to effects of climate acting on an age structure of 3, 3–4, or 3–5-year-old salmon and, to some extent, their parents. We examined for patterns in variables that we differenced (i.e., values in time  $t$  minus values at time  $t - 1$ , denoted as  $\Delta$ ) to create stationary datasets intended to isolate dynamics between the fishery and climate that acted on an interannual timescale from other potential factors that may have influenced fishery landings but likely evolved more gradually or were punctuated (Figure S1). That is, we differenced variables so that our analysis was focused on relative fishery performance in proximate years because factors influencing historical landings other than salmon productivity were probably most similar in back-to-back years. Prior to differencing, we also separately z-scored the two time series describing fishery performance, altogether intending to place the response variable of fishery performance on a consistent scale across the fishery's history. Catch data must be interpreted cautiously, but we inferred that historical catch numbers from proximate years would track relative salmon abundances, especially because there was little restraint in historical fishing (McEvoy, 1986); indeed, the varied return timings of the different salmon runs were discernible from late-1800s monthly market sales (Figure 5).

To be clear, this study conceptualized climate constraints as acting on the overall productivity of the system, including hatchery returns. While some hatchery smolts have been trucked partially downstream or all the way to the ocean since the 1980s, and in recent drought years most hatchery smolts are trucked, in many years most hatchery smolts experience watershed habitats to some degree, particularly the delta and its temperature-sensitive predator field that is hypothesized to impact overall productivity (Michel et al., 2020 and references therein). Additionally, the dynamics of in-river and hatchery adult returns are positively coherent (Figure S2, note Fall run predominates total adult returns). Most of this coherence is probably attributable to hatchery-origin adult salmon straying into natural areas and there is noise added to these patterns by hatcheries not accepting returns after quotas are met (Sturrock et al., 2019).

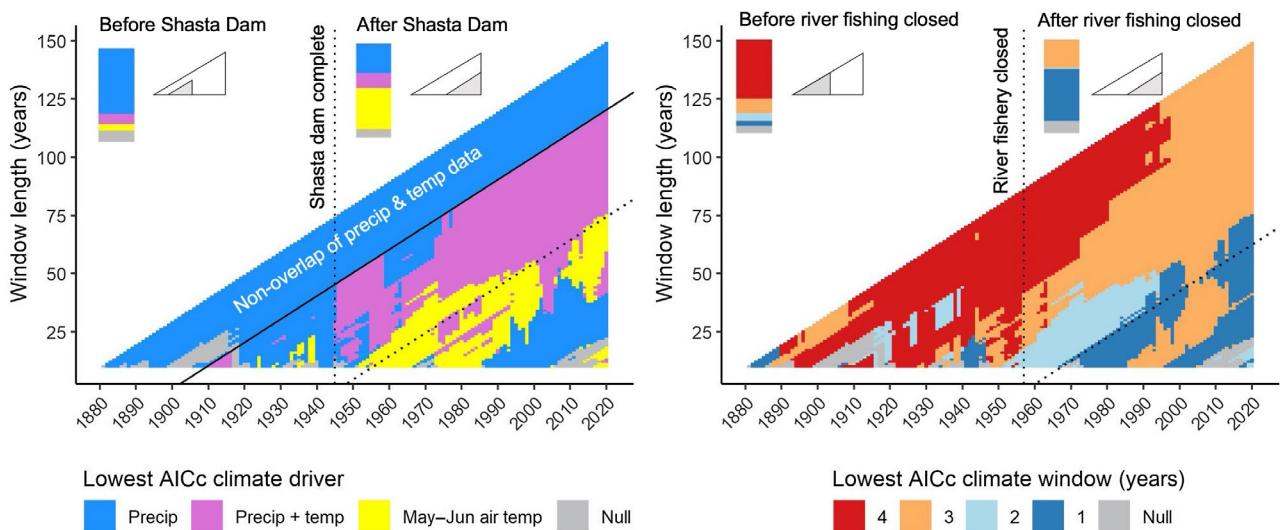
Acknowledging these caveats, we did not find overt evidence that hatchery recruitment was negatively impacting natural recruitment. As shown below, we also did not find a relationship between abundance of adult returns and hatchery releases in prior years.

We crafted an analysis that addressed two central challenges to distill evolving climate fishery-climate relationships from long-term datasets. First, when using data with one set of observations per year, we faced a trade-off of sample size (i.e., number of years considered) versus recency (i.e., detecting patterns soon after they emerged) to detect nonstationary relationships between the fishery and climate. Second, we could not precisely anticipate the timing of changes to fishery-climate relationships. For example, the fishery should have begun to track conditions of shorter climate periods roughly after ocean fishing became intense and the process of age truncation was underway. Both of these challenges raised the questions of what the appropriate time windows were to compare and how the determination of these time periods could influence the interpretation of the data's patterns. We, therefore, examined all combinations of time window lengths (i.e., the number of years into the past to include in data informing models; min.: 10 years) and end dates (i.e., the final year to include in data informing models) to appreciate the time periods over which climate effects and their changes were detectable, then distilled salient patterns that were consistent with the system's natural and industrial history.

## 6 | EMPIRICAL EVIDENCE THAT CLIMATE CONSTRAINTS ON THE FISHERY HAVE EVOLVED WITH STRESSORS

The historical fishery was constrained by climate but buffered interannual climate variation. To establish the existence of historical climate constraints, we examined relationships between fishery performance and precipitation because the precipitation time series completely extended through the early years of the fishery's history and because we expected precipitation to influence habitats regardless of the landscape's industrialization status. During the historical era -- reasonably delineated by the periods prior to construction of Shasta Dam in 1945 or the closure of the in-river fishery in 1957 -- fishery performance improved after wet periods and was typically best explained by average precipitation 2–5 years before fishing (i.e., a 4-year climate window; Figure 6). Visualizing historical time series revealed instances when precipitation varied substantially from year to year, but fishery performance tracked comparatively steady precipitation values averaged over 4 years (Figure 7, top two panels). We inferred from these patterns that the fishery always depended on California's unreliable precipitation but -- as in pristine systems today (e.g., Greene et al., 2010; Schindler et al., 2010) -- a complex salmon age structure expanded the number of years of climate conditions across which the fishery's stock integrated, stabilizing productivity against climate variation and promoting steady fishing.

Over time, the fishery increasingly relied on cold spring-summer transitions (Figures 6 and 8). Examining all combinations of time

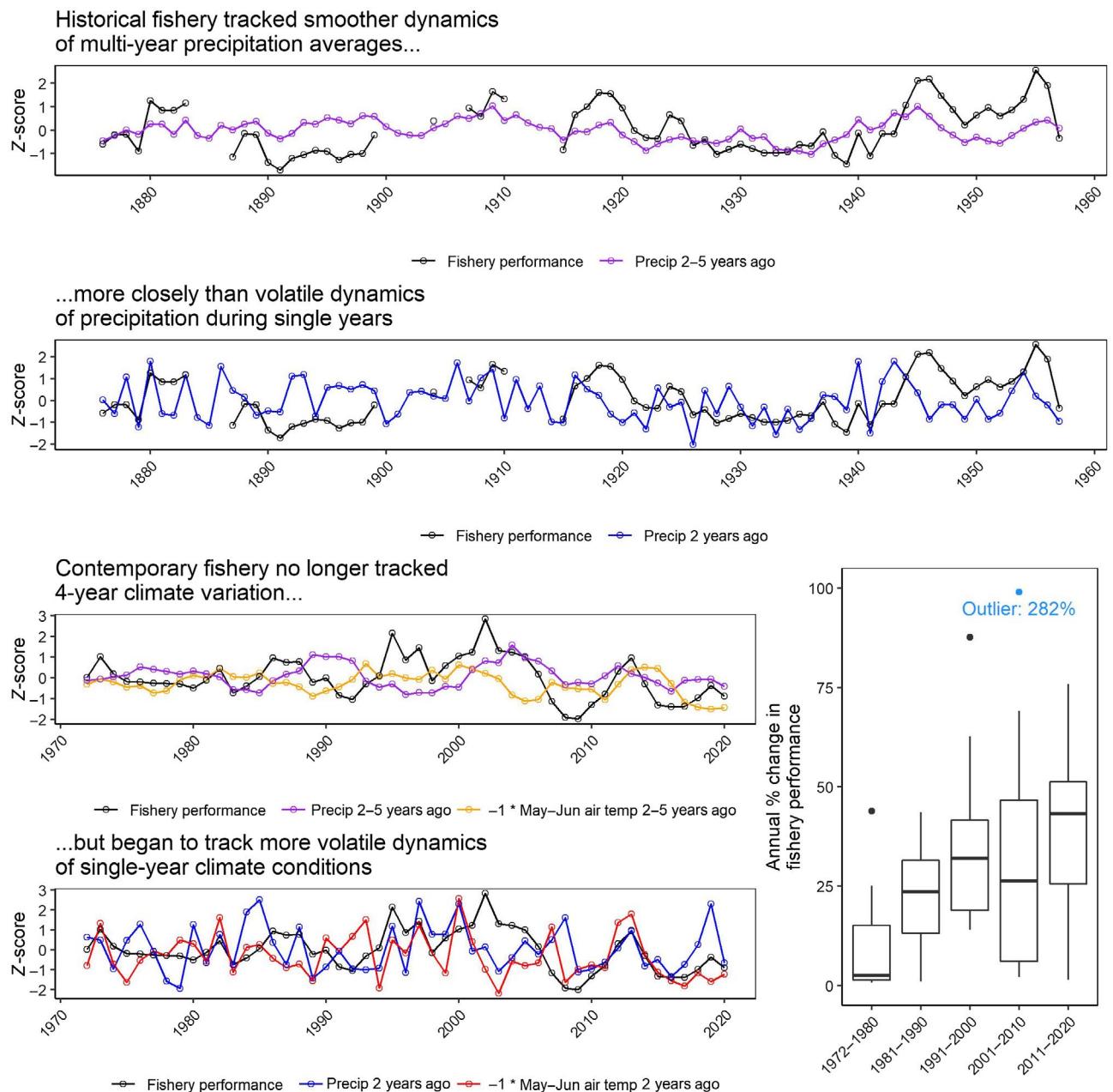


**FIGURE 6** Best performing (via AICc) linear models comparing  $\Delta$  fishery performance to  $\Delta$  climate drivers for all time window dates and lengths (min.: 10 years). The left and right panels refer to output from the same models, with the left shaded according to the climate driver that best-explained fishery performance and the right shaded according to the number of years of climate conditions that best explained fishery performance. Dates on x axes describe the final year of each time window. Dashed lines delineate time windows when groups of observations were entirely from before or after Shasta Dam construction was complete (left) or the in-river fishery was closed (right). Stacked bar plots indicate the total composition of best-performing climate drivers within the periods delineated by dashed lines. The solid line on the left panel delineates time windows when the availability of precipitation and temperature data overlap, thus allowing comparison between the two types of climate drivers in explaining fishery performance. Data: Table S1 [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

window lengths and end dates, fishery performance was related to climate variables across most of its history. However, instances of fishery performance being best explained solely by May–June air temperatures became more prevalent in the second half of the twentieth century. This transition coincided roughly with the 1945 completion of Shasta Dam, the system's largest dam and the first of many large dams built in the following decades (Madgic, 2013). That is, fishery performance was typically best explained by precipitation during time periods before dams were widespread, and fishery performance was often -- albeit not always -- best explained by air temperatures of spring–summer transitions during time periods after dams were becoming widespread. We inferred from these patterns that constraints of spring–summer temperature on fishery performance increased over time and that the impact of dams on the salmon and habitat portfolio was a major contributor to this transition, among other contributing stressors (e.g., wetland destruction, nonnative predators). Considering that contemporary flow requirements for salmon are evident from many previous studies (e.g., Michel, 2019; Michel et al., 2021; Munsch et al., 2020), the generally positive (albeit weaker) relationships between fishery performance and precipitation in the contemporary era (Figure 8), and recognizing that we employed a correlative analysis that evaluates model performance and parsimony, we interpreted the rise of temperature constraints as reducing the fishery's climate resilience by adding to -- rather than replacing -- the constraints of precipitation.

Over time, the number of years across which the fishery integrated climate conditions decreased (Figures 6 and 8). Examining

all combinations of time window lengths and end dates, a salient change was that the fishery transitioned from often to never tracking climate conditions averaged over four years. It was not straightforward to anticipate the exact timing of this process because there was only snapshot information on the stock's age structure across most of its history (Satterthwaite et al., 2017; Williams, 2006). However, while there was some variation in the number of years of climate conditions best-explaining fishery performance during earlier years, there was a general pattern that the fishery only tracked four-year climate windows during time periods that included years before the river fishery closed, and the loss of a 4-year climate signal roughly coincided with time periods when 5-year-old salmon changed from common (35%, 1919–1921) to scarce (3%–10%, 1947–1955) to vanishingly rare (0%–1%, 1973–present; Satterthwaite et al., 2017; Williams, 2006). Indeed, the 4-year climate signal appears to have dissipated over shorter time windows by the 1950s (Figure 6), when salmon had been primarily caught in the ocean for about four decades, and the river fishery that only captured fish that would have matured that year was terminated (McEvoy, 1986; Yoshiyama et al., 1998). There was also evidence that the fishery shifted to track the climate conditions of a single year. Examining only time periods after the closure of the in-river fishery, fishery performance was often best explained by climate conditions of a single year, coincident with the timing of 3-year-old salmon becoming increasingly prevalent (Satterthwaite et al., 2017). Examining the more recent time series showed the emergence of this potential shift: there were instances in the 1980s and 1990s

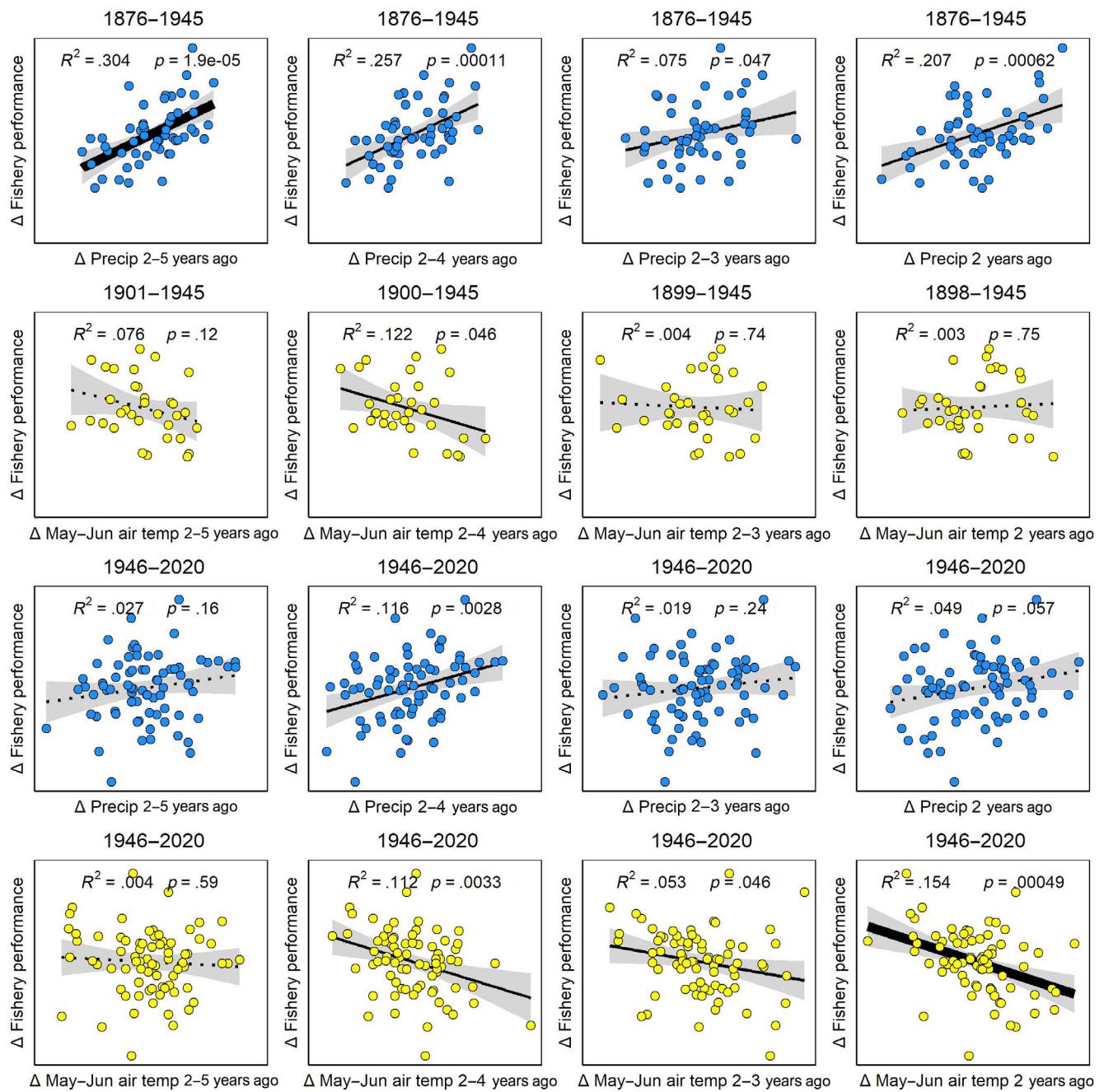


**FIGURE 7** Historical and contemporary fishery performance compared to climate variation. Top two panels: historical fishery performance relative to precipitation conditions of multiple years vs. singular years. Bottom panel: emergence of fishery tracking volatile conditions of singular years. The sign of temperature variables has been reversed so that decreasing (i.e., beneficial) temperatures tend to align with increasing fishery performance. Bottom right inset: Boxplots showing percent difference (positive or negative) in fishery performance between proximate years, grouped by decade, indicating increasing variation in proximate years over the past five decades. Data: Table S1 [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

when fishery performance tracked volatile year-to-year climate dynamics from 2 years prior, then, from the 2008–2009 stock collapse to 2020, fishery performance nearly mirrored single-year climate dynamics from 2 years prior (Figure 7, bottom left). We inferred from these patterns collectively that the fishery across its history shifted to integrate climate conditions over shorter periods due to a simplified age structure. Contributing stressors could have included ocean fishing that risked capturing fish that would not have matured that year, degrading and

blocking habitats that enabled extended juvenile rearing (e.g., over summer), hatchery effects through genetics and/or plastic responses to rearing conditions, and/or changes in ocean conditions (e.g., environment, predators, abundant hatchery salmon from other sources; Ohlberger et al., 2018; Williams, 2006).

Thus, across its history, the fishery shifted from typically tracking precipitation averaged over multiple years to often tracking spring-summer temperatures over fewer -- possibly singular -- years. These shifts coincided with the rise of a genetically



**FIGURE 8** Scatterplots comparing fishery-climate relationships before and after construction of Shasta Dam as a proxy for historical and contemporary eras. Lines and shaded areas show linear models and their 95% confidence intervals. Solid lines indicate statistically significant relationships ( $\alpha < 0.05$ ) and thick lines indicate the strongest relationships for each era. Both axes are unitless z-scores, but all y axis ranges are the same and x axis ranges are the same within columns. Historical fishery-temperature relationships begin in slightly different years because the temperature time series begins in 1895 (after the fishery time series begins); thus, the initial year for which a multi-year climate value can be calculated depends on the number of years in the climate window. Data: Table S1 [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

homogenized stock (Dedrick & Baskett, 2018; Sturrock et al., 2019; Williamson & May, 2005) and increasing year-to-year volatility in fishery performance (Figure 7, bottom right). Overall, we inferred the following: Historical and contemporary fishers both exploited salmon that relied on favorable weather in a dynamic climate. However, historical fishers exploited a diversified salmon production system that spread climate risk and enabled adaptive climate

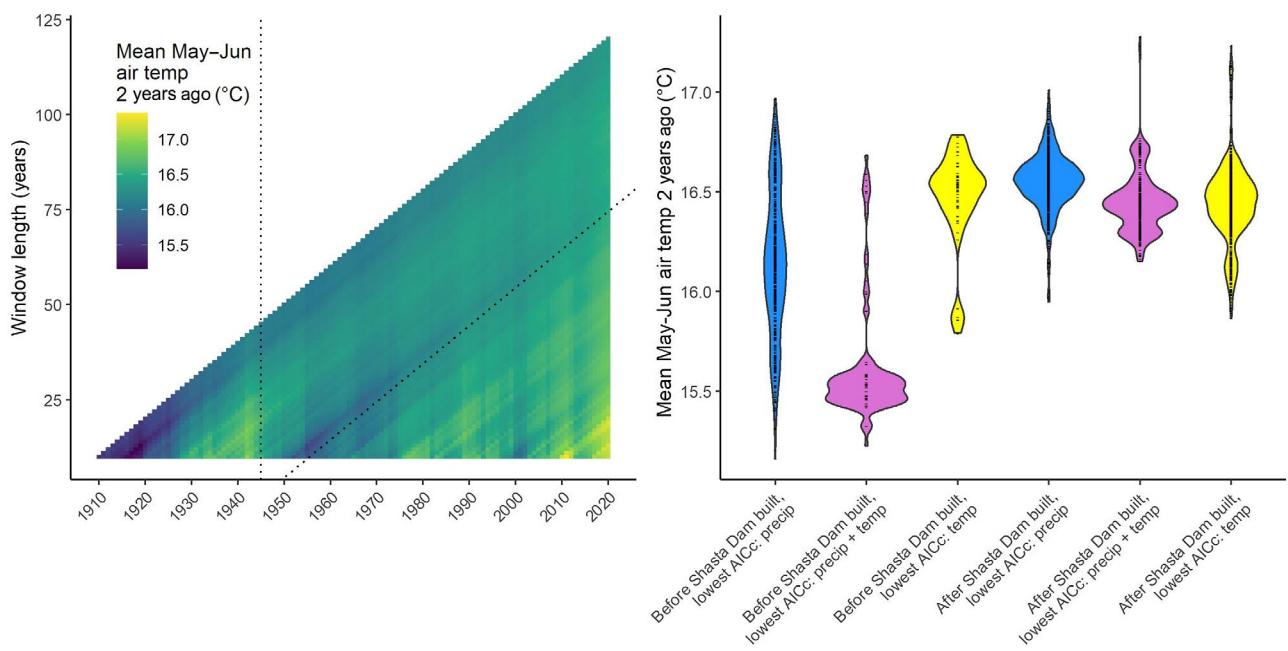
responses, whereas contemporary fishers exploited a homogenized, degraded, and constrained salmon production system that did not. This latter production system was less capable of buffering effects of poor climate years and depended more on cold spring-summer temperatures, priming the fishery for increased sensitivity to climate forcing as climate change decreased the frequency of cold spring-summer transitions.

## 7 | COMPLEXITIES OF HISTORICAL RECONSTRUCTION

An overarching challenge of this analysis was to distill a robust reconstruction from a complicated dataset, ecosystem, and history. We identified evidence for two shifts in the fishery's relationship with climate (i.e., increasing constraints of spring-summer temperatures and shorter climate windows relevant to fishery performance), but there were also time periods that appeared to break from these general patterns. There are many reasons why this may have happened. Ecologically, habitat mosaics and -- often linked -- salmon life histories are naturally dynamic (e.g., Brennan et al., 2019), which would cause the relative importance of climate drivers and climate window lengths on fishery performance to shift over time regardless of human stressors. Additionally, nonlinear ecological scenarios, such as regime changes in ocean conditions, could have differentially affected productivity across salmon life history types and, therefore, temporarily influenced the relative importance of climate conditions (e.g., cold weather vs. precipitation) for the stock complex on aggregate. Analytically, we used numerous linear models to illuminate nonstationary patterns in fishery-climate relationships, but making numerous comparisons risks introducing some models fit noise rather than signal. We attempted to mitigate this issue by presenting patterns that appeared to be robust to perspective (i.e., the choice of the time period and length examined), and by examining for patterns consistent with prior knowledge of salmon biology and this system's history. Nevertheless, a hazard of conceptualizing

complex human-ecological systems, especially from a historical perspective, is that some complexities will remain elusive.

Another important challenge was disentangling the effect of habitat stressors from that of long-term warming to explain increasing the constraints of spring-summer temperatures on fishery performance. Effects of temperature may be nonlinear (*sensu* Brett et al., 1969), and temperature effects could predominate after climate change increased the frequency of warm years. To accommodate the potential for fishery-climate relationships to reflect changes in temperature in addition to changes to the ecosystem, we compared the mean temperatures of time periods across the types of climate drivers best-explaining fishery performance before and after Shasta Dam was completed, focusing on years after temperature data became available (Figure 9). We indeed found that the pre-dam era included many cooler time periods when fishery performance was best explained by precipitation and that the post-dam era included some notably warm periods when fishery performance was best explained by temperature. However, there was also substantial overlap in temperatures across pre- and post-dam eras and time periods best explained by particular climate drivers, meaning that some of the time periods in the post-dam era when fishery performance was best explained by temperature were cooler than time periods in the pre-dam era when fishery performance was best explained by precipitation (and vice versa). We inferred from these patterns in light of a general understanding of temperature effects on salmon in this system and elsewhere (e.g., from the background presented above) that both phenomena probably occurred: Temperature



**FIGURE 9** Left: mean air temperatures during spring-summer transitions of all time windows for which fishery performance could be compared to air temperature and precipitation. As in Figure 6, dashed lines delineate time periods that only include groups of observations entirely before and after Shasta Dam was built. Right: violin plots showing mean air temperatures during spring-summer transitions compared across (1) whether fishery performance was best described by precipitation, spring-summer transitions, or both, and (2) the pre- and post-Shasta Dam periods (i.e., periods delineated by dashed lines on the left). Horizontal hashes indicate individual values to show replication. Data: Table S1 [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

effects probably became more common due to warming temperatures and due to stressors increasing the sensitivity of the salmon production system to temperature. We also acknowledge that such patterns in a correlative study should be interpreted cautiously and that without an unmodified replicate system to compare to, the relative influences of climate change and habitat degradation on temperature impacts remain uncertain.

During preliminary modeling exercises, we additionally considered potential explanatory variables of annual hatchery release abundances and indicators of ocean conditions describing springtime upwelling (March–May North Pacific High index) and temperature (March–May Northeast Pacific Arc sea surface temperature). These variables were not strongly related to fishery performance, especially in comparison to patterns in precipitation and annual temperature (Figure S3). Including these variables became impractical as our analysis expanded to include multiple permutations of explanatory variable combinations, explanatory variable window lengths, and time periods, especially because the time periods covered by these data differed from those of watershed climate indicators. Notably, hatcheries in recent decades released consistent numbers of juveniles (Sturrock et al., 2019) despite widely varying adult recruitment; thus little if any linear relationship between fishery performance and hatchery production might be expected despite hatchery production providing a major part of this system's harvest, and higher returns following colder, wetter years do not appear to be a simple artifact of hatcheries releasing more juveniles during colder, wetter years. Additionally, as discussed above, climate probably acts on hatchery-origin recruitment somewhat similarly to natural-origin recruitment and we did not find overt evidence of competition dynamics based on hatchery versus in-river returns. Furthermore, research tracking juvenile survival suggested an outsized effect of watershed rather than ocean climate conditions on salmon fitness in this system, although fish may be impacted by markedly poor ocean conditions (Michel, 2019) and they currently experience complex (e.g., multivariate, nonlinear) interactions at sea (e.g., Wells et al., 2017). We, therefore, leave analyses of evolving relationships between the fishery and hatcheries or ocean climate conditions for further work.

Finally, dams may have some influence on sensitivity to precipitation or influence the number of years of climate conditions most relevant to salmon. In preliminary analyses, we replaced the explanatory variable of precipitation with the total annual flow (USGS gage 11425500; Sacramento River in Verona, California), and still found a prevalence of spring-summer air temperature explaining fishery performance in the post-dam era. This was perhaps unsurprising because total annual flow and precipitation were highly correlated ( $R^2 = .86$ ), but water regulation may decouple habitat experiences from climate events in certain situations such as the first year of a drought when water storage is still available to supply flows above natural levels. However, effects of dams on relevant climate window lengths appeared to be minor because, while we would expect water regulation to increase the climate window relevant to salmon because water storage integrates across multiple years of precipitation, we nevertheless found that fishery performance was related to

a shorter number of climate years in the contemporary era compared to the historical era. In addition, the mode of precipitation benefits may have changed as people transformed the landscape and water supply. Historically, precipitation may have determined habitat capacity via the inundation of massive floodplains and wetlands. At present, precipitation may be important in overriding the effects of water regulation and extraction on the flow regime to determine whether flow within the simplified, channelized watershed does not drop below harmful thresholds as juveniles migrate to sea during the wet season (Michel et al., 2021; Munsch et al., 2020; Figure 2).

## 8 | STEERING TOWARD ROBUST RESOURCE FUTURES

Increasing climate constraints on the fishery as people simplified the Central Valley's salmon production system is consistent with fundamental ideas linking natural resource complexity to stability. Ecologists have long recognized that complex ecosystems appear stable despite volatile dynamics at fine scales (Levin, 1992) and more recently argued for management to protect processes that generate complexity so that asynchronous and redundant dynamics at finer scales impart stability at greater scales (Schindler et al., 2010, 2015). A pressing application of this concept is to promote ecosystem complexity to promote climate resilience; that is, the perception of stable population complexes despite unpredictable climate impacts on individuals, populations, life histories, or habitat components. Empirical studies and simulations suggest that protecting diverse habitat mosaics (Anderson et al., 2015; Hilborn et al., 2003; Walsworth et al., 2019) and complex age structures (Worden et al., 2010) may promote resilience of fish stocks to climate stress. Our study is consistent with these findings, suggesting that losing habitat and biological complexity risks diminishing resilience to climate and highlighting the importance of prioritizing distinct habitats and biologies that spread risk, enable adaptive responses, and fill voids created by disturbance to their counterparts (Levin & Lubchenko, 2008).

The challenge to promote climate-resilient salmon fisheries is emblematic of widespread ecological crises. On the one end of the spectrum, the Central Valley supports a massive human population and agricultural economy via a highly engineered landscape, but requires substantial intervention to generate even a fishery substantially constrained by climate. On the other end, relatively pristine landscapes support salmon-based economies via natural, climate-resilient productivity (Hilborn et al., 2003; Schindler et al., 2010). People worldwide rely on natural resources from transformed ecosystems (e.g., Jackson et al., 2001; Kess et al., 2019; Lotze et al., 2006) experiencing climate change (e.g., Free et al., 2019; Jones et al., 2020; Oremus, 2019; Pinsky et al., 2013) and, as shown here, impacts of human legacies can go beyond the system in which they occurred (e.g., watershed legacies impacting ocean harvest; Alvarez-Romero et al., 2011). Furthermore, fishing legacies have truncated the age structures of many fish

populations (Barnett et al., 2017). However, people are increasingly mindful of stressor impacts on long-term resource reliability (e.g., Duponchelle et al., 2016; Sabo et al., 2017). Indeed, volatile resources can be just as unacceptable as chronically scarce resources because people depend not only on resource abundance but stability (Oremus, 2019), a requirement they share with non-human consumers (Schindler et al., 2015).

In human-dominated landscapes some ecological change is inevitable, but a long-term vision to enable climate-resilient resources could emphasize promoting life history diversity in ways that are compatible with human activities. Options include restoring floodplain or coastal ecosystems that prevent property damage from flooding (FloodplainsByDesign.org, Temmerman et al., 2013), replicating natural features in developed landscapes to simultaneously enhance species' habitat and aesthetic, recreational spaces for people (Munsch et al., 2017; Toft et al., 2013), removing low-value dams (e.g., San Clemente Dam; Harrison et al., 2018), providing ecologically functional flows in regulated rivers (Poff et al., 1997), and -- as a terrestrial example -- reconnecting landscapes via wildlife highway overpasses that prevent collisions. In the case of fish, fisheries can be closed when very low abundances are forecasted (Lindley et al., 2009; Richerson et al., 2018), harvest regimes can be crafted that reduce impacts on recovering populations (e.g., Satterthwaite et al., 2018) or immature fish (e.g., size limits, terminal fisheries), and lost life histories can be "re-awakened" by restoring lost habitat niches, including in salmonids via dam removal (McMillan et al., 2019; Quinn et al., 2017). As natural resource outcomes are often the product of multiple management arenas, coordinating across these arenas may synergize recovery efforts (Threlfall et al., 2021). For example, the extent to which natural-origin juvenile salmon occupy restored habitats in the Central Valley likely depends on fisheries and flow management (Munsch et al., 2020). Munsch et al. (2020) also show that fry occupancy in natural rearing areas has a strong dependence on both winter flow and natural-area spawner escapement up to levels that are ~2.5 times the existing escapement goal (PFMC, 2021b). Taking full advantage of gains possible through improving one aspect of management likely requires concomitant improvement in other aspects.

History suggests many civilizations transformed their landscapes to support inherently narrow pathways of artificial production systems only for those systems to fail during periods of climate change (Diamond, 2005). In contrast, civilizations that exploited natural productivity or bolstered artificial propagation with intensive conservation, monitoring, and harvest regulations tended to experience more reliable resources (Diamond, 2005). A similar scenario appears to be unfolding for species that derive stability from complex, functional habitats, whereby people's excessive reliance on artificial propagation programs is problematic because economies of scale constrain programs from actualizing diverse life histories and habitat experiences that spread climate risk (Lichatowich, 1999). Moving forward, for systems like the Central Valley, there is a considerable risk that species will

go extinct with climate change unless stressors are alleviated to enable latent resilience (Crozier et al., 2019). Fruitful areas for further work could include examining how stressors may be most efficiently alleviated to restore diversity and the long-term fundamental (e.g., cultural, outdoor recreation) and economic (e.g., employment, local tax revenue, tourism) values of production systems that are sustainable and reliable because people protect the processes that give rise to ecological complexity.

Following the logic of the shifting baseline syndrome (Pauly, 1995) and recognizing that baselines of ecosystem attributes are rarely formulated under pristine conditions (Dayton et al., 1998), our findings broadly suggest that climate forcing on natural resources at present may often reflect a novel state manifested by recent climate conditions *and* systemic anthropogenic change. Indeed, climate disturbance in modified systems should not be attributed solely to climate, which lies outside localized management influence, but also the consequences of human legacies and current management actions. The Central Valley's 170-year transformation reflected the culture and constraints of the U.S.'s frontier era, which valued landscape settlement, wealth extraction from assumedly inexhaustible landmasses, and a desire for fundamental security in a landscape prone to droughts and floods. The culture and technologies of human generations during the Anthropocene will continue to evolve, potentially enabling the recovery of ecosystem attributes that confer climate resilience in California and elsewhere. For example, demands for ecologically stressful activities may be lower if future generations prioritize ecosystem services over human-engineered solutions or advanced technologies that sequester water, energy, and food with less environmental impacts. Optimistically, there may be potential to rehabilitate ecosystems to states that are more resilient than has been observed in living memory if people invest in the processes promoting ecological complexity. Whether such approaches actually restore or mitigate the loss of resource reliability in the face of climate shocks will likely depend on many factors, including the magnitude of long-term climate change and the species interactions of particular ecosystems.

In conclusion, our findings provide empirical, longitudinal weight to the argument that stressors can reduce climate resilience across landscapes, human generations, and ecosystem boundaries (e.g., land/sea). In an era of climate change and widespread ecological simplification and degradation, it is crucially important to promote diverse habitats and biologies to steer toward resilient ecosystem services (Levin, 1992; Schindler et al., 2010) and thriving human populations that depend on them.

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## AUTHOR CONTRIBUTIONS

Stuart H. Munsch conceived a study relating historical catches to climate indices, led the data explorations and analysis, and led the writing. Correigh M. Greene, Nathan J. Mantua, William H. Satterthwaite provided additional intellectual content, suggested further analyses, advanced the interpretation of the results, and contributed revisions.

## DATA AVAILABILITY STATEMENT

Data used in this study are in the Supplement.

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