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RESEARCH

Managing for Salmon Resilience in California's Variable and Changing Climate

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ABSTRACT

California's salmonids are at the southern limits of their individual species' ranges, and display a wide diversity of strategies to survive in California's highly variable climate. Land use changes after statehood in 1850 eliminated important habitats, or blocked access to them, and reduced the abundance, productivity, and distribution of California's salmon. Habitat simplification, fishing, hatchery impacts, and other stressors led to the loss of genetic and phenotypic (life history, morphological, behavioral, and physiological) diversity in salmonids. Limited diversity and habitat loss left California salmon with reduced capacity to cope with a variable and changing climate. Since 1976, California has experienced frequent droughts, as were common in the paleo-climatological record, but rare in the peak dam-building era of 1936–1976. Increasing temperatures and decreasing snowpacks have produced harsher conditions for California's salmon in their current habitats than they experienced historically. The most likely way to promote salmon productivity and persistence in California is to restore habitat diversity, reconnect migratory corridors to spawning and rearing habitats, and refocus management to replenish the genetic and phenotypic diversity of these southernmost populations.

INTRODUCTION

Chinook Salmon, Coho Salmon, and Steelhead populations in California have declined precipitously since the mid-1800s (Ricker 1981; Yoshiyama et al. 1998, 2001; NMFS 2009; Williams et al. 2006, 2012). Many of California's salmonid populations are either extirpated or at risk of extinction. How to manage salmon and Steelhead populations in California's variable and changing climate was the topic of a workshop held at the University of California, Davis, in September 2015. (A video recording of the entire workshop is available at: *https://cmsi.ucdavis.edu/events/salmon-and-climate-symposium.html*.) We explore issues raised at that workshop, with emphasis on possible management approaches to improve salmon resilience in California.

Salmon resilience is based on habitat heterogeneity. Salmon in California had access to diverse freshwater and estuarine habitats, and display an array of life history and physiological adaptations to the challenges posed by the dynamic climate. Diverse habitats support genetic and phenotypic diversity among populations, providing opportunities to optimize growth and survival at early life stages (Figure 1). Climate variations included multi-year and multi-decadal droughts, including the so-called mega-droughts of the medieval warm period from 800 CE to 1300 CE (Stein 1994). Salmon also face varying ocean conditions such as year-to-year El Niño/La Niña cycles (Fiedler and Mantua 2017), and the multi-decadal patterns of the Pacific Decadal Oscillation (Mantua et al. 1997) and the North Pacific Gyre Oscillation (Di Lorenzo et al. 2008). Diverse habitats for diverse genotypes and phenotypes can provide a portfolio of options to support sustainable salmon populations in challenging climates (Hilborn et al. 2003; Figge 2004; Koellner and Schmitz 2006; Schindler et al. 2010, 2015).

Salmon adaptations to earlier conditions in California are mismatched with current habitats. Dams, water management, logging, levees, and land use changes have simplified California's mosaic of aquatic environments. Populations of naturally-spawning Chinook Salmon are at historically low levels despite regulatory and management efforts, restoration work, and large hatchery programs. In addition, the genotypic and phenotypic traits expressed by California's salmon have become less diverse because of the cumulative effects of hatcheries, harvest, and altered habitats. Restoration of diverse habitats, genotypes, and phenotypes may permit salmonids to adapt to new and changing conditions in freshwater and the ocean.

Climatic Effects on Salmon Habitat

The habitat-forming processes that affect salmon in freshwater are driven by California's Mediterranean climate interacting with the state's diverse topography and geology. Paleoclimate reconstructions show much longer droughts before California became a state in 1850, but such droughts

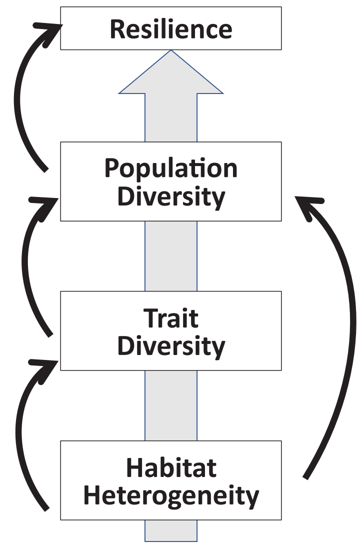

Figure 1 Conceptual model of how habitat heterogeneity creates trait and phenotypic diversity to promote population resilience. Source: S.M. Carlson.

were periods of more frequent moderately dry years with fewer moderately wet years (Stein 1994; Ingram and Malamud–Roam 2013). The mega-droughts were often followed by floods greater than any seen since (Biondi et al. 2000; Ingram and Malamud–Roam 2013). Thus, the climatic extremes to which California salmonids were exposed before 1850 were greater than those since.

Central Valley watersheds include high-elevation catchment areas (to 4,421 m) with often-persistent snowpacks that extend the runoff season. In the Central Valley, salmon distribution was always limited by hot, dry summers and sub-freezing temperatures in winter at high elevations. Eight widely-separated major rivers drain into a catchment area 720 km long and averaging 62 km wide, culminating in a common delta that enters San Francisco Bay.

California's coastal-zone climate features moderate temperatures. The Coast Range is lower (max elevation 2,268 m) and seldom develops a persistent snowpack. From December to March, the many isolated coastal watersheds have "flashy" hydrographs with frequent overbank flows. In late summer and fall, flows are extremely low, even dry in many reaches. Large coastal basins like the Klamath/Trinity have substantial catchment areas at both high and low elevations. This produces a "transitional" hydrograph with high runoff from fall and winter rains, and snowmelt runoff in spring to early summer. Coastal fog from April to September improves stream habitat by cooling streams and reducing evaporation (Johnstone and Dawson 2010).

Variability in annual precipitation (Figure 2) is higher in California than in any other state in the continental US (Dettinger 2011). This variability rests entirely on November–May precipitation, producing extreme fluctuations in freshwater salmon habitat quality and quantity. Precipitation from June through October is negligible. Years of high snowfall have high runoff from May through July. In other years, warm "atmospheric river" storms generate rapid runoff that leads to overbank flows in November–March (Ralph and Dettinger 2012). In extreme drought years, like 1976–1977, 1987–1992, and 2013–2016, stream flows remain low year-round.

Almost all California rivers are impounded. Reservoirs provide flood control in wet winters, and water delivery to cities and irrigated agriculture during drier times. As a result, reservoir operations flatten the natural hydrograph. Reservoir storage volume and release patterns have large effects on temperature and flow conditions downstream, often controlling salmon habitat quality, location, and quantity.

Annual variability in water supply, water management actions, and habitat alteration drive estuarine conditions for Central Valley fish. Wet years inundate flood-control bypasses that provide habitat beneficial to the growth of outmigrating young salmon (Sommer et al. 2001, 2004, 2005). Wet years extend freshwater conditions down to Suisun and San Pablo bays, where most remaining or restored tidal wetlands occur. Wet years provide pulses of freshwater that help guide salmon adults back to spawning grounds. Lower river flows produce fewer of these benefits. Coastal estuaries vary less because there are reduced effects of snowpack, water management activities change less from year to year, and wetland habitats are available in all years (Hayes et al. 2006).

Ocean habitat and food web productivity vary dramatically within and between years and across decades, causing salmon survival and return rates to vary greatly. Changes in Pacific physical patterns associated with El Niño conditions have further destabilized salmon survival rates (Kilduff et al. 2015). Seasonal shifts in surface wind patterns produce a strong seasonal pattern in temperature, currents, and nutrient suspension. Upwelling within this California Current System controls near-shore productivity (Checkley and Barth 2010). In winter months, consistent southerly and southwesterly winds typically produce onshore and northerly movement of relatively warm and nutrient-poor surface waters and coastal downwelling. In spring and summer, variable northwesterly winds move surface waters southward and offshore; these surface waters are replaced by cooler, nutrient-rich water from lower depths and higher latitudes. These cooler, nutrient-rich waters support a lipid-rich food web beyond the continental shelf from Vancouver Island to Pt. Conception (Checkley and Barth 2009).

As juvenile salmon leave the estuary, they experience the most direct effects of ocean conditions (Beamish and Mahnken 2001; Satterthwaite et al. 2014). Warmer-than-average periods in the California Current System reduce food quality and production, shift salmon predator distributions and diets, and reduce early marine survival for Coho and Chinook Salmon (Peterson and Schwing 2003; Wells et al. 2016, 2017). Higher survival rates occur in years during which salmon enter the ocean when food is plentiful (Duffy and Beauchamp 2011; Wells et al. 2012; Dale et al. 2016). When food is scarce, early marine survival is low, and only the fish that grow the fastest in the freshwater survive to adulthood (Woodson et al. 2013).

Historic Habitat Heterogeneity in California

The Central Valley, formed by the San Joaquin and Sacramento rivers and their tributaries, is a highly diverse and dynamic landscape. Consistent flows from volcanic springs from Mt. Lassen and Mt. Shasta, with variable snowmelt from the Sierra Nevada, fed the Sacramento River through 2,400 km of steep, cold streams and meandering mid- elevation rivers, to support 46,620 sq km of lowland floodplains, wetlands, and water bodies (Yoshiyama et al. 2001). The San Joaquin River arises from snows on the southern, higher peaks of the Sierra Nevada, and formerly cascaded through

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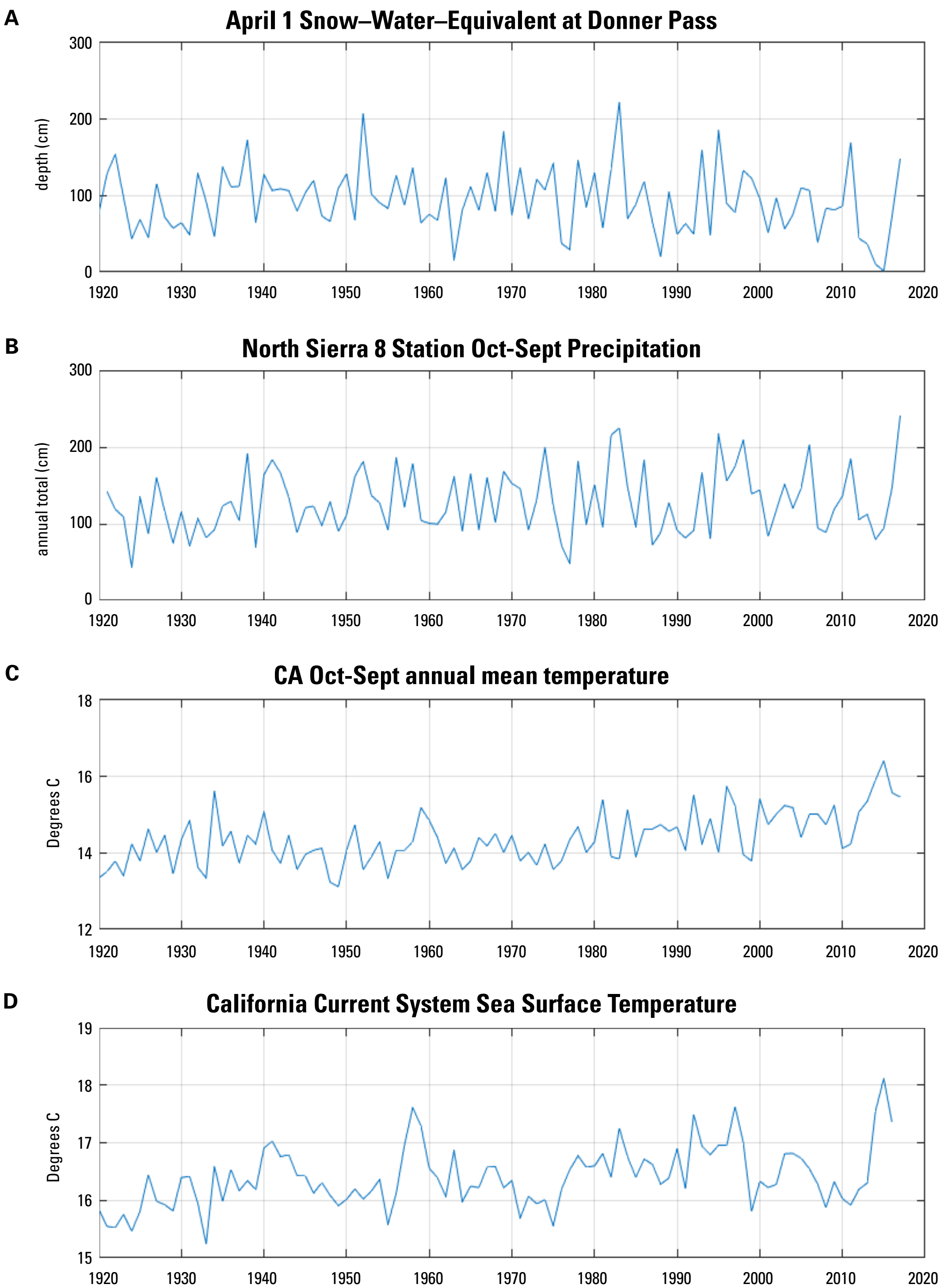

Figure 2 Time-series for key climate drivers of California's salmon habitat from long-term monitoring stations. End-of-season snow–water equivalent, amount of water in the snowpack at Donner Pass near Tahoe (**A**) changes sharply from year to year. The snowpack was zero in 2015 for the first time on record. Runoff from the Northern Sierra (**B**) shows wide year-to-year variation but little trend. Statewide average (Oct–Sept) temperatures (**C**) show a warming trend since the 1970s in addition to high year-to-year variation. Prominent peaks and valleys in annual mean Sea Surface Temperatures in the California Current System (**D**), correspond with those in the statewide terrestrial air temperature record (**C**)

Sources: Snow–water equivalent data for Donner Pass and North Sierra 8 Station Precipitation Index data obtained from the California Department of Water Resources (*http://cdec.water.ca.gov*). Statewide-average water year precipitation and air temperature data were obtained from the National Climate Data Center's U.S. Climate Division Data (*http://www.ncdc.noaa.gov/cag/time-series/us*) granite and glacial outwash into vast marshes and seasonal inland swamplands (The Bay Institute 1998). These river systems converged in expansive tidal wetlands and joined smaller tributaries to flow into San Francisco Bay and the Pacific Ocean (Whipple et al. 2012). Northern California's coastal tributaries are shorter, rain-dominated systems; many supported oversummering habitat of deep pools formed around downed redwoods, beaver dams, or bedrock. Salmonids found winter rearing habitat on flood benches, complex side channels, and intermittent tributaries. Estuaries, floodplains, and tidal marshes provided productive rearing habitat for outmigrant salmon and Steelhead before they entered the Pacific Ocean (Healey 1982; Simenstad et al. 1982).

California's salmonids adapted to the diversity and dynamism of the state's habitats and climate. Some are migratory and some are resident, some are semelparous and others iteroparous, some spend substantial portions of their lives in freshwater and others move quickly to the ocean (Kendall et al. 2014; Moyle et al. 2017). These multiple life- history strategies allowed them to exploit freshwater and estuarine habitats that varied from year to year in location, amount, and quality. Diverse phenotypes allowed adaptation to local conditions and produced populations resilient to fire, flood, earthquake, landslide, and drought. This diversity is exemplified by the Central Valley Chinook Salmon complex, comprising four distinct runs named for their respective seasons of adult migration (Fry 1961) (Figure 3). Although each run is named for the time of adult return, all life stages of Chinook Salmon are present in the system year-round. Both wild spring-run and hatchery-reared late-fall-run Chinook Salmon migrate more quickly and survive better in wetter years (Michel et al. 2013, 2015; Cordoleani et al. 2017). Distinct, naturally-spawning populations of Coho and Chinook Salmon occur in large coastal systems such as the Klamath and Eel rivers. Steelhead and resident Rainbow Trout also occupy many rivers year-round as far south as the Tijuana River. Salmonid life-history variation in response to California's heterogeneous landscape and variable climate suggests a broad capacity to withstand and adapt to climate variability and change if diverse habitats are available.

California's salmon-bearing rivers formerly supported a suite of ecosystem processes that drove biological productivity. Interconnections among aquatic habitat types distributed production across the landscape. Pacific salmon played complex and critical roles in ecological productivity. Eggs and spawned-out carcasses provided ocean nutrients to nutrient-limited, montane streams. These imported nutrients nourished everything from invertebrates to birds, deer to coyotes, and redwood trees to wine grapes (Merz and Moyle 2006). In the valleys, flood flows created productive habitat for outmigrating juvenile salmon, diversified their size and migration timing, and conveyed prey and nutrients downstream. Estuaries, with ocean and freshwater inputs of nutrients and food, provided a highly productive zone for rearing and smoltification (Sommer et al. 2001, 2004, 2005). Materials from upstream also provided flow and

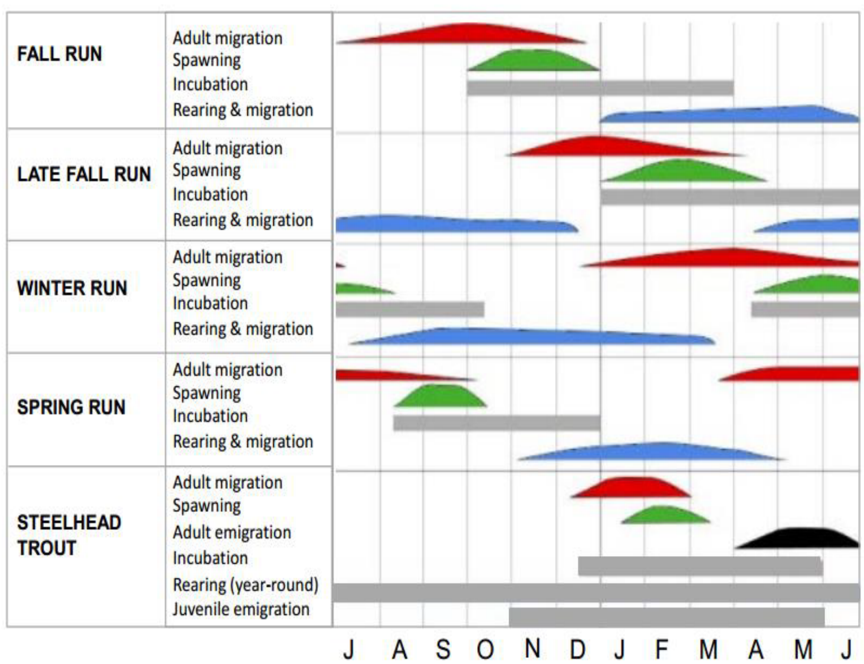

Figure 3 Central Valley salmon with multiple life stages of all four runs of salmon and steelhead in the freshwater landscape year-round. This variation spreads extinction risk within populations, across evolutionarily significant units, and brings resilience to populations. Source: CH2M Hill for the California Rice Promotion Board.

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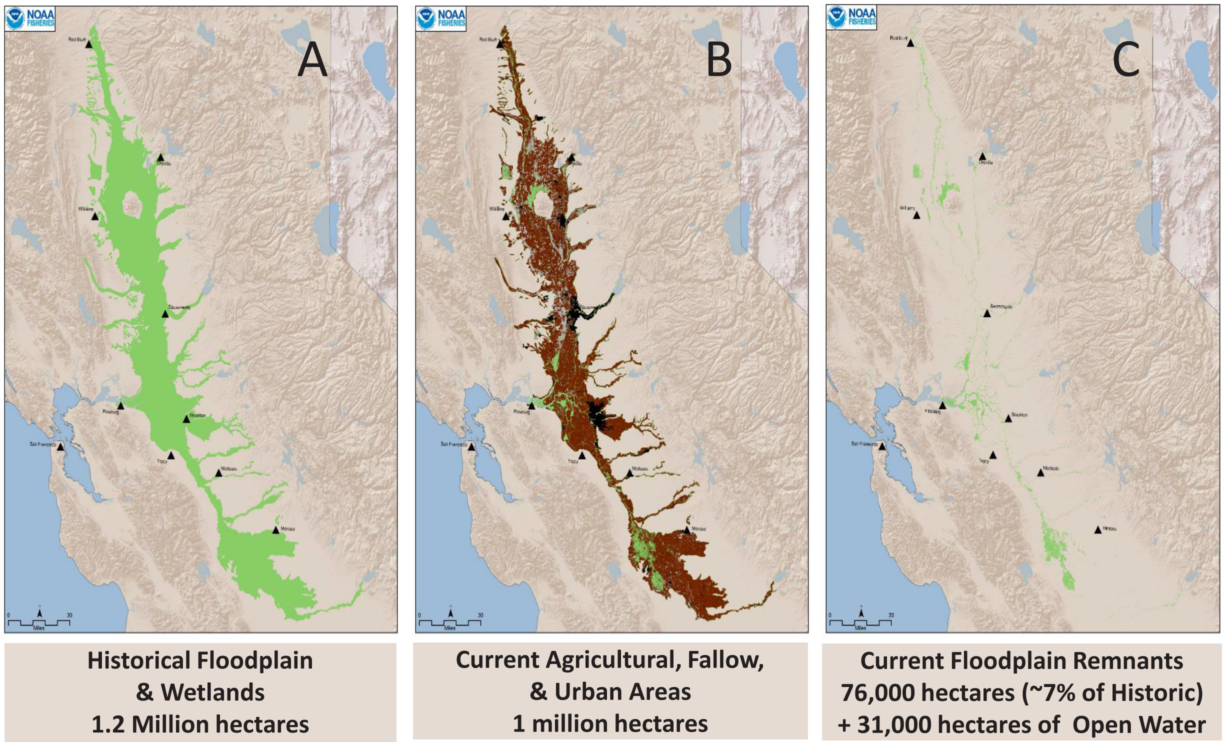

Figure 4 (**A**) Historical floodplain and Delta wetlands habitat; (**B**) remnant floodplain and wetland habitat currently in agricultural lands, fallow lands, or urban areas; and (**C**) floodplain and wetland remnants. Sources: The Bay Institute the Sierra of the Sea GIS maps and USDA 2014 Cropland Data Layer.

chemical cues to guide adults back to their natal streams. California's extremely productive salmonid assemblage supported Native American fisheries for thousands of years (McEvoy 1986).

The Modern Salmonid Landscape

Since statehood, watersheds of the Central Valley and Coast Range have undergone radical transformations. Less than 5% of the native wetland, riparian, and floodplain habitats remain in the Central Valley (Whipple et al. 2012). Hydraulic mining and logging produced dammed, denuded, and channelized headwater streams, and sent massive sediment and contaminant loads downstream (The Bay Institute 1998). Coastal streams were straightened, and pond-forming redwoods and beaver were removed. Thus, much of the quantity and complexity of salmonid habitat was lost, and the remaining habitat was often greatly simplified and impaired.

Dams and diversions disconnected rivers from their upstream reaches and reshaped hydrodynamic processes. State and federal water projects now control river flows throughout the Central Valley in all but the most extreme floods and droughts. Coordinated operation of reservoirs, pumps, and canals removes as much as 7.4 billion cubic meters of freshwater from the San Francisco Bay–Delta estuary each year. Timing and volumes of reservoir releases control much of salmon survival downstream (Zeug et al 2014). Native landscapes have been almost entirely supplanted by urban and agricultural landscapes (Figure 4). Dams and levees block access to more than 70% of anadromous salmonid spawning and rearing habitats (Figure 5; Yoshiyama et al. 1998) and limit the diversity of habitats that salmon can access (McClure et al. 2008). Along the coast, road construction, channel alteration, dams, and diversions impede migration, disrupt physical processes in streams, and reduce estuarine and tidal marsh habitat.

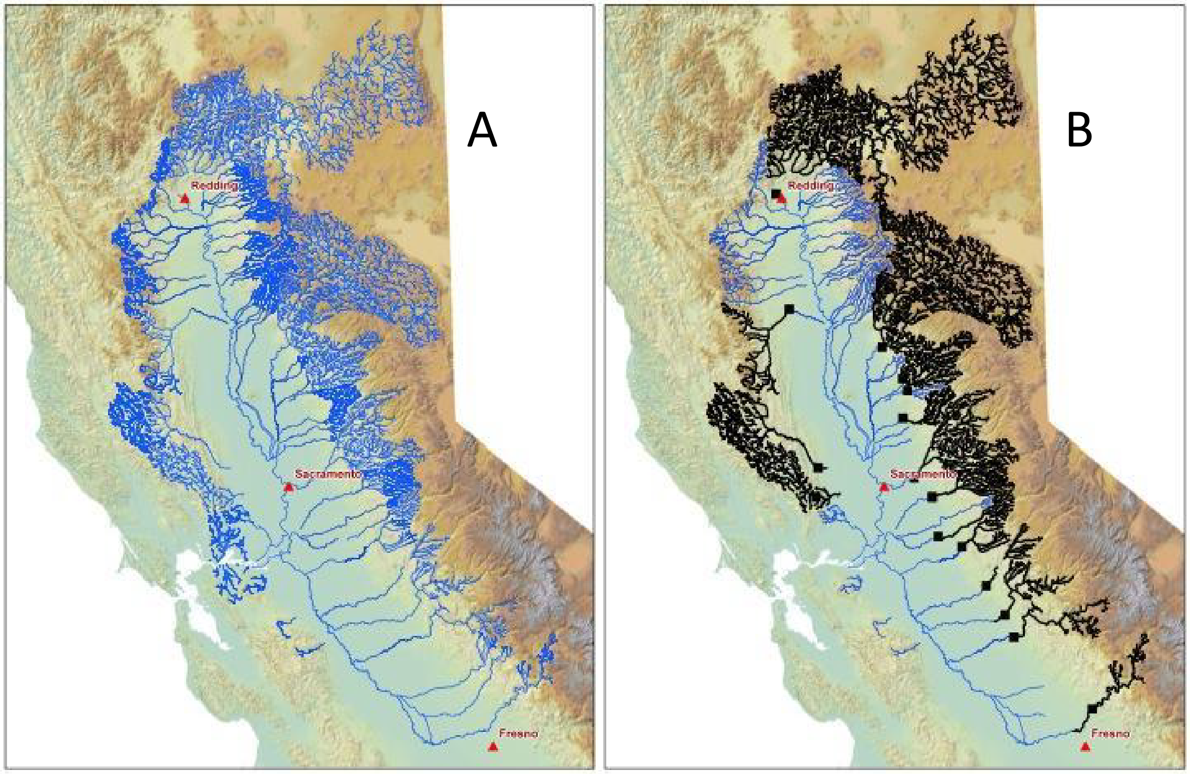

Figure 5 Historical habitat accessible to salmonids (**A**, in blue) and lost upstream habitat (**B**, in black) from construction of impassible dams (black squares). (**B**, in blue) Remaining anadromous habitat for multiple life stages of salmon is largely confined to the valley floor. Modified from Lindley et al. (2016).

Climatic Effects on Salmon in the Modern Landscape

Decadal-scale climate variations, combined with physical degradation and loss of freshwater and estuarine habitats, have driven down salmon abundance. California's salmon populations have suffered rapid declines under recent simultaneous extremes in freshwater and marine conditions. These sharp population declines are followed by persistent periods of low-productivity for natural populations, leading to weak recovery (Willmes et al. 2018). Subsequent extreme events then affect smaller populations, leading to lower and slower recoveries (Lindley et al. 2009). Consecutive years of drought and exceptionally high air, stream, and sea surface temperatures have had widespread negative effects on the freshwater, estuary, and marine phases of Chinook and Coho Salmon and Steelhead from 2012–2016 (Williams et al. 2016).

The drought of 2012–2016 contained several features consistent with climate change effects generally, especially exceptionally high temperatures and the low percentage of precipitation as snow. Responses of salmon and their ecosystem to this drought may foreshadow future trends. Much of the northeast Pacific Ocean, including areas typically used by California salmon and Steelhead, experienced record high sea surface temperatures from 2014 to 2016 (Jacox et al. 2017). A "warm blob" formed offshore of the Pacific Northwest region in fall 2013 (Bond et al. 2015). Off the coast of southern and Baja California, upper ocean temperatures became anomalously warm in spring 2014, and this warming spread to the central California coast in summer 2014. In fall 2014, a shift in wind and ocean current patterns caused the entire northeast Pacific to experience unusually warm sea surface temperatures from the West Coast offshore for several hundred kilometers (Swain et al. 2017). The California Current System overall experienced its warmest 3-year average temperatures

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on record from 2014–2016, with 2015 having the record warmest year going back to at least 1920 (Jacox et al. 2017). These extraordinarily warm conditions presented salmon with a combination of physiological stress and reduced food availability.

California had well-below-average precipitation in water years 2012–2015, record high surface air temperatures in 2014 and 2015, and record low snowpack in 2015. Anomalously high air temperatures made this a "hot drought," in which high surface temperatures substantially amplified annual water deficits during the period of below-average precipitation (Williams et al. 2015). The combination of heat and dryness may be the most extreme in the past 500 or more years (Diffenbaugh et al. 2015), and is likely to become more extreme (Singh et al. 2016). Further, droughts and floods are both expected to become more frequent, producing greater volatility in conditions from year to year (Swain et al. 2018). Thus, although floods and droughts in the last 250 years are not as great as those in the paleo-climatological record, California salmon in their present landscape now encounter more stressful climatic conditions than those in which they evolved.

In 2014 and 2015, low reservoir storage, low precipitation, and high air temperatures elevated stream temperatures to historic extremes in many watersheds. The lack of cold water behind Shasta Dam led to a loss of suitable stream temperature in winter-run Chinook spawning grounds in September 2014. Stream temperatures exceeded the 56°F (13°C) target in 2014 and 2015, and contributed to 95% mortality of eggs and fry in those years (Johnson et al. 2017). There were similar concerns in the Klamath Basin in the summers of 2014 and 2015 because high stream temperatures elevated the effect of pathogens. These concerns prompted emergency reservoir releases that aimed to lower downstream temperatures and reduce risks to salmon. Thus, the freshwater environment was harsh for salmonid populations throughout California during the recent drought, and led to changes to water operations in attempts to mitigate for low precipitation, stream flow, and water storage.

Changes in Salmon as a Result of Current Conditions

Lost Genetic Independence

Genetic diversity is greatly reduced in Central Valley Chinook Salmon (Meek et al. 2014; 2016). Reduced numbers of populations and reduced population sizes, combined with the loss of genetic and demographic independence, make remaining salmon populations more vulnerable to extinction (Lindley et al. 2007).

Financial analysts use the "Sharpe Ratio" (performance divided by variability; Sharpe 1994) to estimate risk-based performance. The same approach can describe fish dynamics (Moore et al. 2010). Salmon and steelhead sub-populations that vary more independently produce larger and more stable yields (Hilborn et al. 2003; Schindler et al. 2010; Moore et al. 2014). The greater stability and performance of populations when sub-populations vary independently—the portfolio effect—has been quantified in several salmon systems, e.g., in the Snake River (Figure 6). Extirpation of several Central Valley salmon sub-populations and increased synchrony among the remaining sub-populations

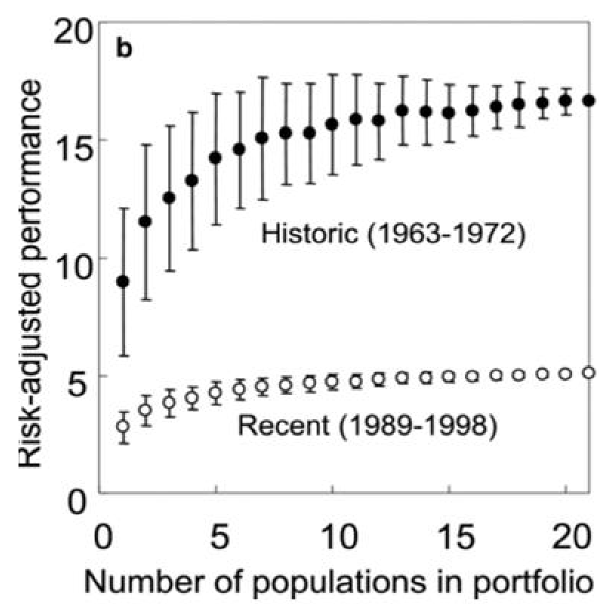

Figure 6 Modeled salmon resilience from historical data on 21 Snake River salmon populations in 10 early years when populations varied more independently vs. 10 later years when they varied more in synchrony . Modified from Moore et al. (2010).

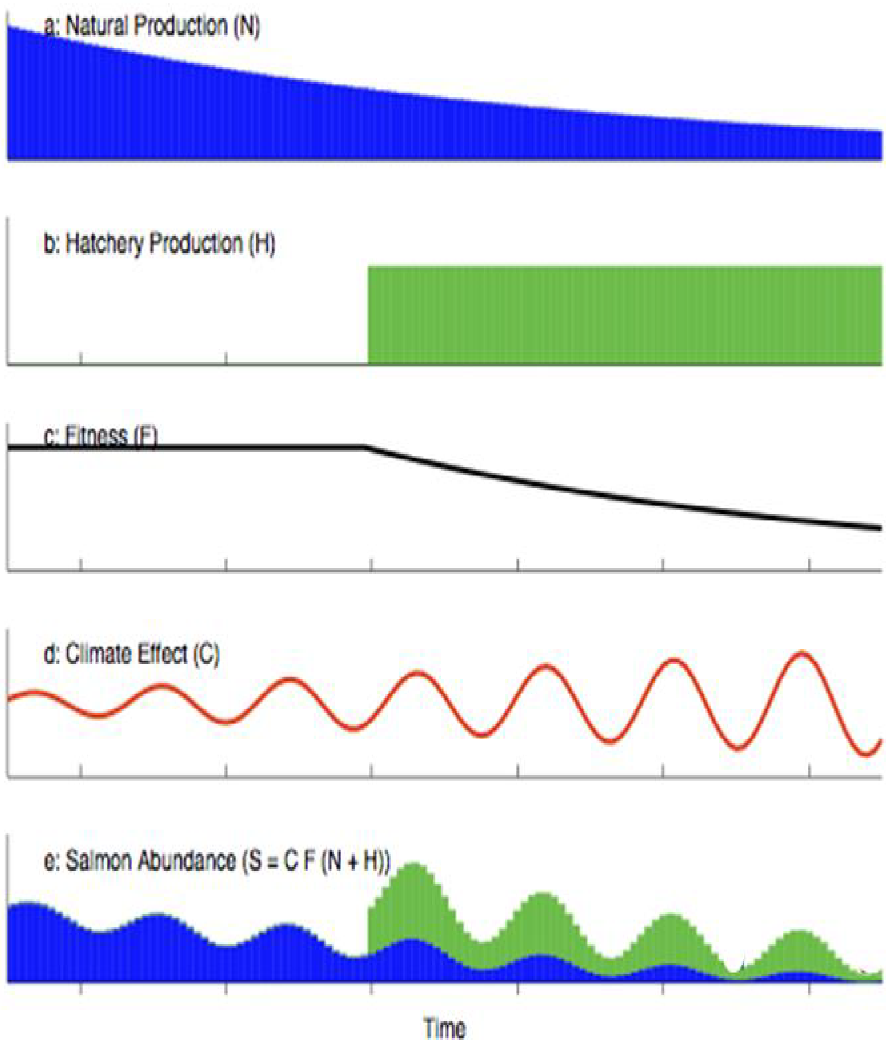

Figure 7 Interactive effects of reduced natural production of salmon (N) with more stable production of less-fit hatchery fish (H) lowers fitness (F) overall. With no variability in population response, climatic trends (C) ratchet all abundances downward, but the proportion of hatchery fish increases Source: S Lindley, NMFS.

greatly reduces their risk-adjusted performance and bodes ill for long-term resilience of the Central Valley's salmon production system (Figure 7) (Lindley et al. 2007; Carlson and Satterthwaite 2011; Satterthwaite and Carlson 2015; Franks and Lackey 2015).

Lost Habitat

Important salmon habitats have become unavailable, eliminated, or simplified, resulting in extirpation of some populations and a fundamental shift in the dominant life histories within and among sub-populations. Spring-run Chinook Salmon were formerly the basis of the commercial and recreational salmon fishery. Their success was the result of the quantity, quality, and reliability of accessible high-elevation habitat for adult holding, spawning, and juvenile rearing (Fisher 1994; Yoshiyama et al. 1998, 2000). Spring-run spent variable lengths of time growing in streams, floodplains, and rivers before migrating to the ocean, so they were often large, and entered the ocean over a broad window of time. This diversity in timing and size likely buffered them from many stressors.

Impassable dams on all major Central Valley rivers have shifted the advantage to fall-run salmon that use valley-floor habitats. California's climate is expected to continue warming, and precipitation events are expected to become more extreme. This warming is likely to cause higher snowlines and widespread declines in California's snowpack, more precipitation as rain, and warmer stream, estuary, and coastal ocean water temperatures (Cloern et al. 2011). Summer and fall water temperatures on

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the valley floor may rise more sharply than winter temperatures and become even more challenging for cold-water fish (Cloern et al. 2011). The windows of appropriate conditions for Central Valley Chinook Salmon to complete the freshwater part of their life cycle are likely to narrow even more, in both time and space. Winter-run are blocked from the reliable cold-water spawning grounds coming off Mt. Shasta, and spring-run are blocked from most reliably cold water habitat in the upper reaches of Sierra Nevada streams. These US Endangered Species Act (ESA)-listed runs—winter-run and spring-run—already require substantial habitat, harvest, and hatchery management to reduce their extinction risks. Without significant alleviation of existing stressors, climate change will make survival difficult for fall-run and late-fall-run Chinook Salmon, as well (Moyle et al. 2017).

The loss of access to reliable good conditions in the freshwater environment means that the proximate cause of low return rates is often ascribed to poor ocean conditions (Lindley et al. 2009). This emphasis on the role of the ocean in year-to-year variance in abundance masks the larger problem of persistently poor conditions in freshwater (Table 1). Occasionally, freshwater conditions can become extraordinarily bad, as for winter-run Chinook Salmon in 2014–2015 (Figure 8; SWRCB 2016; Kratville 2016, unreferenced, see "Notes"). Winter-run Chinook Salmon are especially vulnerable because they only have one spawning ground, now limited to the tailwaters below Keswick Dam. In 2013, ocean conditions were supportive while the drought produced mildly stressful conditions on the spawning grounds. Then, in 2014 and 2015, conditions were extremely stressful in both the ocean and freshwater. As the drought was nearing its end in 2016, conditions became more moderate in both habitats (Figure 8). Thus, oceanic habitat conditions vary from good to poor, and have a greater influence than freshwater conditions on year-to-year variability in salmon numbers. However, climate variability has an amplified effect on freshwater production in California because there is so little freshwater habitat now available to salmon. Increased variability in northeast Pacific Ocean conditions is likely to make conditions more frequently stressful for salmon in the ocean (DiLorenzo and Mantua 2016; Jacox et al. 2017). However, if more numerous and more diverse juvenile salmon arrived at the ocean at different times and at different sizes, it is likely that adult returns would be less sensitive to inter-annual variation in ocean conditions.

In freshwater, floodplain habitat use has been a focus of research for the past 15 years; seasonally-inundated floodplains provide foraging habitat and more food (Sommer et al. 2001; Sommer et al. 2004; Corline et al. 2017). Such habitat and food supply enhance juvenile salmon growth, compared to the nearby mainstem Sacramento River (Figure 9) (Sommer et al. 2001; Jeffres et al. 2008; Henery et al. 2010). Ephemeral and intermittent streams show a seasonality similar to floodplains and may also be important habitats for California salmon and trout (Limm and Marchetti 2009; Hwan et al. 2017; Phillis et al. 2018).

Access to spatially-diverse habitats influences fish growth rates, movement, and phenotypic diversity (Hilborn et al. 2003; Schindler et al. 2015; Lisi et al.

Table 1 Environmental conditions (poor, moderate, or good) in freshwater and marine aquatic ecosystems influence predicted salmon population sizes and limiting factors on the populations. Consistently poor freshwater conditions result in only moderate or small population sizes, depending on the variable quality of ocean conditions (highlighted in grey boxes).

Ocean conditions	Freshwater conditions	Population size	Limiting factors	Example year
Good	Good	Large	Competition/Predation Habitat	
Poor	Good	Moderate	Ocean conditions Food	
Good	Poor	Moderate	Spawning habitat Rearing habitat	2013, 2016
Poor	Poor	Small	Food and space -> Extinction spiral	2014, 2015

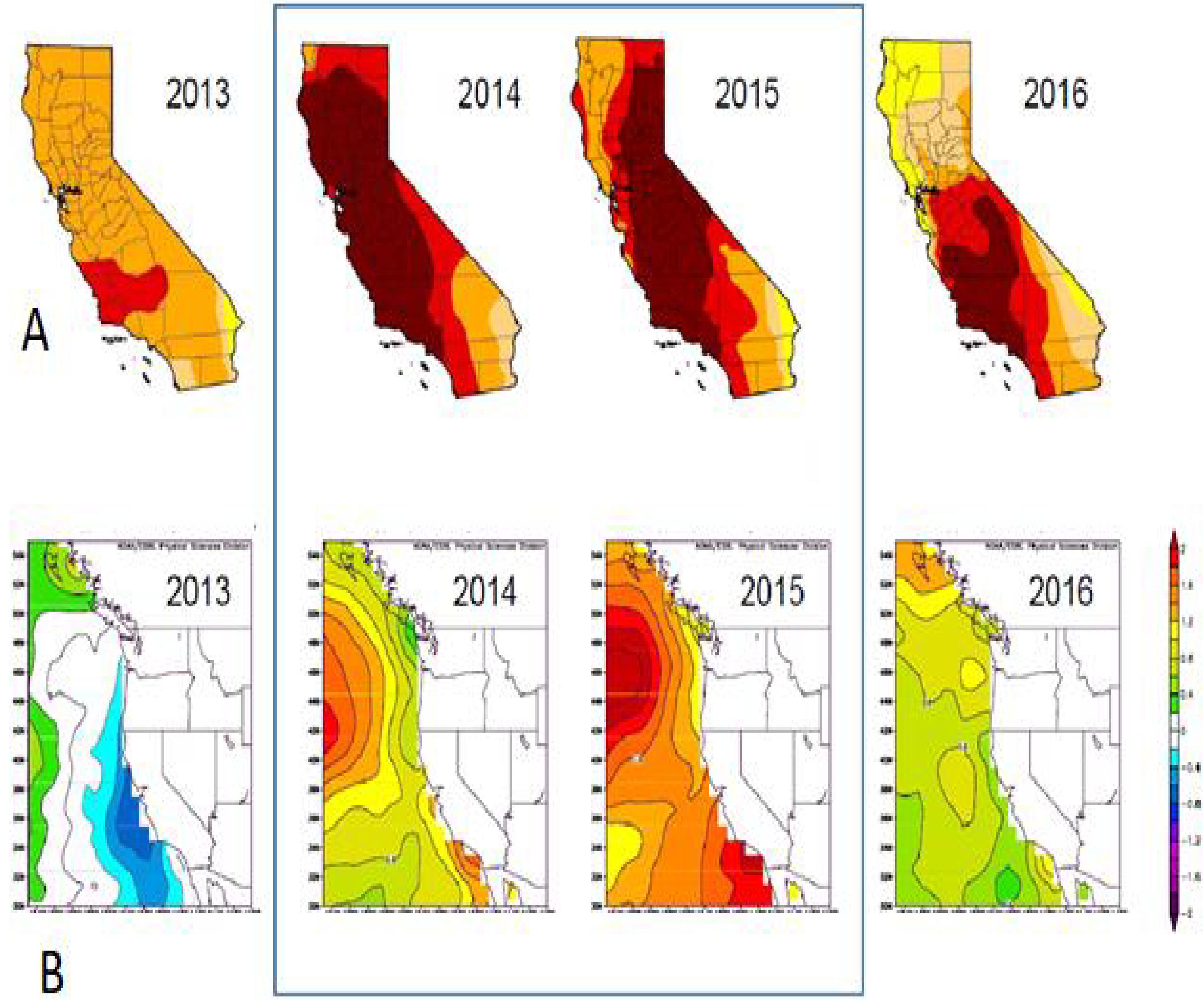

Figure 8 Salmon experienced years of extreme temperatures in the freshwater and ocean life stages in 2013–2016. (**A**) Severity of drought conditions from abnormally dry (yellow) to exceptional drought (dark red) measured in August each year. (**B**) Observed annual mean ocean temperature anomalies with colder than normal (blues) and warmer than normal (yellows/reds) relative to the 1981–2010 average. Note the extreme conditions experienced in 2014–2015 (boxed) in both aquatic habitats in the salmon life cycle indicating the cumulative effects of warming Sources: *http://www.droughtmonitor.unl.edu*; bottom-row images provided by the NOAA/ESRL Physical Sciences Division, Boulder Colorado from their website at *http://www.esrl.noaa.gov/psd/*.

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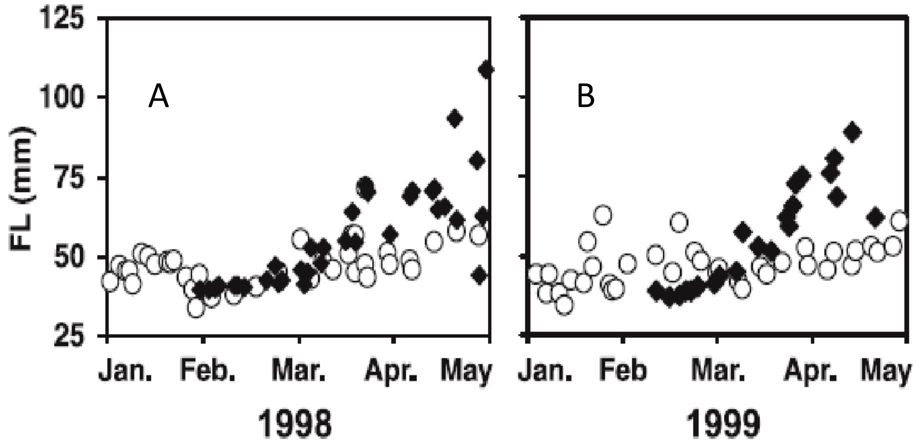

Figure 9 Two years (A and B) of data of juvenile Chinook Salmon size from the Yolo Bypass (black diamonds) and in the adjacent Sacramento River mainstem (open circles) that demonstrate the role of habitat mosaics in creating phenotypic diversity and potential differences in outmigration timing. Modified from Sommer et al. (2001).

2013). Such diversity stabilizes inter-annual variation in juvenile production (Thorson et al. 2014). Variation in size and timing of outmigration increases the likelihood that some individuals experience optimal arrival timing in variable riverine, estuarine, and early ocean conditions (Satterthwaite et al. 2014; Huber and Carlson 2015). In some years, juvenile salmon that leave their natal rivers as small fry (<55 mm) and rear for several months downstream become a large proportion of adult returns (Miller et al. 2010; Sturrock et al. 2015). Rearing in estuarine habitat substantially improves Chinook Salmon survival rates (Magnusson and Hilborn 2003). Thus, for salmon in a variable climate, different habitats may be of different importance in different years.

Hatchery Impacts

The first North American commercial salmon cannery opened in Sacramento in 1864, and the industry rapidly spread north (NWPC 2011). Sharp declines in salmon abundance as a result of habitat degradation and overfishing led in 1870 to the establishment of hatcheries, or "breederies" (Stone 1874; Leitritz 1970). Fall-run fish migrate, spawn, and outmigrate quickly, and so they became the primary stock for hatchery propagation (Hallock 1978). Currently, five hatcheries propagate fall and late-fall-run Chinook in the Central Valley: four state-operated hatcheries (Feather River Hatchery, Nimbus Fish Hatchery on the American River, Mokelumne River Hatchery, and Merced River Fish Facility) and one federally-operated hatchery (Coleman National Fish Hatchery on Battle Creek). Together, these hatcheries typically release >30 million juvenile Chinook Salmon each year (Huber and Carlson 2015). These hatcheries, and the remaining natural spawning areas, support culturally and economically important tribal, sport, and commercial fisheries. For instance, in 2013, 297,409 Chinook Salmon were harvested commercially, and 175,307 were recreationally caught, for economic benefits of $244 million and $105 million, respectively (PFMC 2014).

Hatchery fish create conservation challenges when they mingle with wild fish and use shared resources. Salmon hatcheries produce many more smolts from a small number of spawners than would be produced in nature. Large numbers of hatchery salmon can bolster predator populations that then prey more heavily on wild salmon (CALFED 2000). During the 2012–16 drought, the percentage of wild fish fell disproportionately, and led to greater dominance by hatchery-based fish (Willmes et al. 2018). For many years, hatchery effects were a concern largely in freshwater because of concerns about the limited carrying capacity of freshwater habitats. However, the ocean's carrying capacity has become better understood, and hatchery salmon can influence growth and survival of wild salmon stocks and other species in the ocean (Ruggerone et al. 2010; Ruggerone and Irving 2018). Thus, the release of millions of hatchery fish from one river system can have broad effects. The degree and mechanisms of competition between hatchery and wild fish requires further research into spawning dynamics, rearing habitat, and food limitations in both freshwater and the ocean.

Hatchery managers make several logistical decisions that influence diversity and resilience of wild stocks:

the number of each sex to use, the number of fish to produce, the size and stage to release, and where and when to release the fish. The number, size, location, and timing of release of artificially-propagated fall-run Chinook have become more standardized across hatcheries in the Central Valley. These practices result in relatively similar-sized juveniles entering the ocean within a narrow temporal window (Huber and Carlson 2015). Because Central Valley fall-run Chinook Salmon populations are dominated by hatchery-produced fish, this homogenization of release strategies has presumably weakened the portfolio effect (Barnett–Johnson et al. 2007; Carlson and Satterthwaite 2011; Satterthwaite and Carlson 2015).

Trucking hatchery fish for release has influenced the dynamics and resilience of both hatchery and wild fish. Currently, about 40% of the Chinook Salmon produced in Central Valley hatcheries are trucked to San Pablo Bay for release (Huber and Carlson 2015). Trucking is used to circumvent the mortality associated with down-river migration. However, the trucking program has consequences that erode the resilience of the stocks.

1. Trucking decreases variation in ocean arrival timing relative to fish migrating downstream volitionally. Downstream-migrating fish use diverse corridors and rearing habitats that vary outmigration timing and fish condition. For example, salmon in the Yolo Bypass slow their migration, presumably to take advantage of feeding opportunities in the Bypass (Sommer et al. 2001). Larger body size is known to improve early-marine survival, and delayed migration might contribute to more variable ocean arrival timing. Variable timing of ocean entry influences salmon survival via match–mismatch dynamics (Satterthwaite et al. 2014)—individuals that arrive when prey resources are plentiful grow quickly and survive. Variable timing within and among populations buffers populations from uncertain ocean conditions.

2. Trucked salmon do not imprint to the characteristics of their natal stream. Consequently, when trucked smolts return as adults, many stray into rivers more frequently than fish that outmigrated volitionally (Palmer–Zwahlen and Kormos 2015; Keefer and Caudill 2014). Straying of trucked hatchery fish, especially into streams without hatcheries, reduces local adaptation in the recipient population and degrades local adaptations. Indeed, the trucking program is a likely cause of the genetic homogenization of Central Valley fall-run Chinook Salmon (Williamson and May 2005; Meek et al. 2014, 2016); this homogenization is unusual for such a large salmon stock complex. Moreover, unmarked hatchery fish on the spawning grounds mask declines in the abundance of wild fish (Johnson et al. 2012). Finally, elevated straying leads to more similar dynamics among all populations, which weakens portfolio performance (Satterthwaite and Carlson 2015).

Actions to Facilitate Salmon Resilience to Climate Variability

The highly variable genetic and phenotypic characteristics of salmon promoted their resilience and abundance in the variable landscape of historical California. The modern California landscape challenges salmon with: lack of access to reliable cold water for spawning, lack of nursery habitat for all young life stages, and simplified migratory corridors occupied by invasive predators and competitors (Sabal et al. 2016; Lehman et al. 2017). In general, the simplified and shrunken area to which salmon have access leads to smaller, simpler, and less diverse salmon populations. Restoring habitat complexity is essential to restore salmon resilience to stress.

Salmon have four responses to environmental stress:

1. **Adapt.** Depending on the degree and pace of change, salmonids can adapt to shifting conditions. Such local adaptation to high temperature has likely occurred in some California trout (Verhille et al. 2015). The process is complicated by temperature effects on other stressors, such as disease organisms and their vectors (Schaff et al. 2017). Increased genetic and phenotypic diversity is fodder for selection and adaptive evolution; however, there are also clear physiological limits on the ability of salmon

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to adapt to temperature increases (Muñoz et al. 2015).

2. **Hunker Down.** Individuals find thermal refuges in groundwater springs or shaded habitats and wait for the stressor to pass (i.e., a resistance strategy). Increased habitat diversity increases the chance that members of a population will find suitable refuges.
3. **Move.** Individuals or populations may move to new, more suitable locations. Insurmountable barriers and habitat fragmentation have greatly limited the ability of salmon populations to move long distances in most California rivers.
4. **Extinction or Extirpation.** If individuals are unable to move, acclimate, or adapt, then populations are likely to die out.

Humans have greatly reduced the ability of salmon to exercise the first three options while increasing the likelihood and rate of the fourth. Management can facilitate salmon recovery and resilience by enhancing their ability to adapt, hunker down, or move (Beechie et al. 2013; Mantua et al. 2016; NMFS 2014). Management actions that build on historical adaptations of salmon to California's climate are most likely to yield positive outcomes.

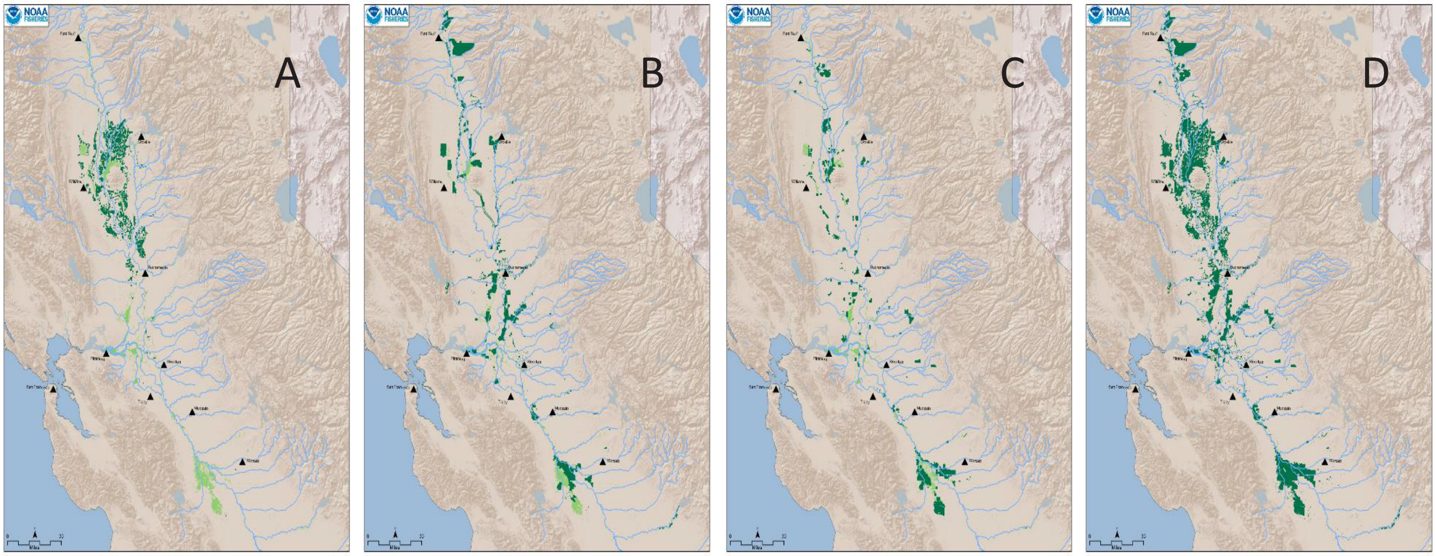
Four approaches are likely to improve the ability of salmon to persist in a changing climate.

1. **Improve Upstream Access.** Blocked access to cold-water habitat can be addressed in several ways. Removal of barriers is a near-term option where the political will exists and socio-economic considerations allow. Some dams are unlikely to be removed, although fish passage structures are possible at some (e.g., NMFS 2009). The value of such work has been shown in smaller streams such as Butte Creek, with substantial improvements in naturally-spawning spring-run Chinook Salmon escapement (Johnson and Lindley 2016). Because of the complexities, and lack of proven success to facilitate volitional passage around large dams, interest has focused on the feasibility of using trap-and-transport methods. Substantial engineering, biological, and societal issues are associated with this approach. However, for winter-run and spring-run Chinook Salmon, trap-and-transport is an important option to consider because they are most vulnerable to climate effects in their current habitats (Lindley et al. 2007; NMFS 2009; Lusardi and Moyle 2017).
2. Improve Bioenergetic Conditions. Higher temperatures increase bioenergetic stress and susceptibility to disease (Schaff et al. 2017). Warmer water increases the amount of food needed to meet the higher metabolic demands. Salmon, therefore, have greater resilience if warm-season water temperatures can be reduced, or prey availability can be increased, or both.

   Existing infrastructure can sometimes mitigate water-temperature stress. Specifically, increased hypolimnetic releases from reservoirs maintains cold-water habitat below dams. This is a key strategy for winter-run Chinook Salmon, where summer releases from Keswick and Shasta dams help sustain developing eggs (NMFS 2009). Similarly, releases from Oroville Dam are managed to provide cooler temperatures for steelhead downstream. The effect is geographically limited to waters below major dams, and is more difficult or less effective when reservoir storage is low. Coordinated operations can conserve cold water supplies for the most at-risk populations.

   Habitat restoration is broadly expected to create spatial and temporal refuges and options for salmon and trout. For example, tidal inundation in Suisun Marsh generates warming and cooling patterns (Enright et al. 2013) that may provide thermal refuges for fish. Similarly, on the Yolo Bypass, wind and topography generate different patterns of temperature variability than the adjacent Sacramento River (Sommer et al. 2001; Goertler et al. 2017). However, little of the targeted restoration in the Delta has yet been completed, and so results are lacking.

   Enhanced food supply is the other key tool to improve salmon bioenergetics. The bioenergetic benefits of improved food availability in seasonally-inundated floodplain habitat are amplified by higher consumption rates at lower activity levels (Sommer et al. 2001). Hence, a major goal of habitat restoration efforts is



Rice Fields 114,000 hectares	Wildlife Areas 106,000 hectares	Conservation Easements 110,000 hectares	Potential Areas for Wetlands Restoration 407,000 hectares

Figure 10 Opportunities for recovery of Central Valley wetland habitat extent and function through the reoperation of seasonally-inundated areas including: (**A**) rice fields, (**B**) existing wildlife areas and preserves, and (**C**) conservation easement lands. (**D**) These opportunities comprise over 35% of the historical habitat extent. Sources: (**A**)–(**C**) 2014 USDA Cropland Data Layer; (**D**) 2014 Protected Area Database.

to improve connectivity between river and floodplain habitat (NMFS 2009).

Increased duration of inundation enhances the benefit of floodplain habitat to more individuals of each population and to more populations (Katz et al. 2017). Long-term data from the Yolo Bypass reveal that increasing the duration of flooding enhances use of off-channel habitat and increases fish size at migration (Takata et al. 2017). In the Central Valley, many seasonally-inundated habitats in the form of rice fields, wildlife refuges, and duck clubs continue to support wildlife. Salmon recovery efforts on these lands can include restoration of access—either temporary access by season, or access in different areas in different years. For inundated areas without direct fish access, production and release of invertebrates can subsidize food supply in accessible habitat. Preliminary analysis suggests that re-operation of these lands to provide salmon habitat could recover as much as 35% of historic floodplain habitat (Figure 10).

Seasonally-flowing streams may be another important habitat for refuge and food supply for young salmon in some years (Maslin et al. 1996, 1998, unreferenced, see "Notes"; Limm and Marchetti 2009; Phillis et al. 2018). There is substantial evidence from the Pacific Northwest that restoration of tidal marsh in the estuary could also generate major food-web benefits (Shreffler et al. 1990; Miller and Simenstad 1997; Bottom et al. 2005). Moreover, restoration of tidal marsh and floodplain habitat is likely to benefit other native fishes (Sommer et al. 1997; Brown LR. 2003; Feyrer et al. 2006; Sherman et al. 2017).

3. **Restore Life-History Diversity.** Different life stages of salmon require different habitats; in different years, they require those habitats in different geographic areas. Within a watershed, habitat diversity allows access to a broader spatial and temporal range of suitable refuges. Diverse refuges allow individuals to pursue diverse strategies with varying degrees of success, thereby distributing risk. Across watersheds, habitat diversity—coupled with the fidelity of salmon

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returning to spawn in their natal rivers— allows populations to diverge genetically, and to adapt to different stressors in different watersheds. Salmon from floodplain versus riverine habitats show the large phenotypic differences that can result from using different habitats (Goertler et al. 2017). Given the significant loss of historical salmon habitat, a mosaic of aquatic habitats to support all stages would better allow California salmon stocks to withstand stochastic events and a changing climate.

Bottlenecks in survival can occur in all three major habitats: freshwater streams, estuaries, and the ocean. Diverse types of high-capacity habitats permit salmon to avoid poor habitat and reduce inter-specific competition—but only if phenotypes and/or timing of habitat use are different. California's climate was remarkably variable historically, and in all modeled future climate scenarios; diverse, accessible, high-quality habitat will contribute to variable growth rates and variability in phenotypes, including outmigrant behaviors and timing. This life-history diversity is thought to create diverse sub-populations with more reliable overall population growth rates. Performance will vary across watersheds and through time with this diversification, and, much like a stock portfolio's diversification, can thereby reduce overall risk. The effects of ocean fishing will likely change with climate change and require new considerations for sustainable harvest management (Worden et al. 2010). In years when both ocean and freshwater habitats are poor, diverse populations of sufficient size can better rebound.

4. **Artificial Propagation.** Hatcheries can be important parts of a conservation strategy for imperiled stocks, despite substantial issues with some traditional practices (see above). Modern hatcheries can involve any part of the salmon life cycle and, as a result, they shape demographic and genetic components of salmon populations. Reliance on hatchery production has been a tool to sustain salmon populations by promoting increased juvenile survival to adulthood during poor ocean and freshwater conditions. Hatcheries can provide temporary refuge under the most extreme conditions. During the recent drought, hatchery propagation compensated for extremely low egg-to-fry survival in rivers, while trucking hatchery juveniles probably boosted survival of juveniles at the cost of increased straying rates of adults. For imperiled stocks (particularly winter-run Chinook Salmon) considerable effort is routinely invested in reducing the effects of hatchery production on genetic integrity. For viable salmon populations, hatchery practices that assist in short-term protection of stocks must support the longer-term genetic and demographic needs of natural-spawning salmon (Johnson and Lindley 2016). Efforts to reduce straying and to reduce significant gene flow between hatchery and natural-origin salmon are essential to allow the maintenance or re-emergence of locally-adapted populations (Araki et al. 2008; Christie et al. 2016).

Newly-developed analytical tools provide ways to assess which of these various actions—or combination of actions—provide the greatest benefits to the portfolios of different runs and populations to promote recovery in a changing climate (Hendrix et al. 2014; Yamane et al. 2018).

CONCLUSIONS

Improving upstream and floodplain access as well as bioenergetic conditions, restoring life-history diversity, and careful consideration of artificial propagation practices provide a suite of process-based management objectives that could collectively strengthen the salmon portfolio. Over the last 170 years, California's aquatic habitats, and the salmon that rely upon them, have lost much of their complexity. To successfully deal with California's variable and warming climate, California's salmon and steelhead need more habitat options than they have now. Access to diverse habitats will allow salmon to express the genetic and phenotypic diversity that gave them the portfolio to thrive in California's historical climate. Re-investing in that portfolio is the most likely way to bolster the persistence of salmonids in California.

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