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RESEARCH

Climate Change Effects on San Francisco Estuary Aquatic Ecosystems: A Review

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ABSTRACT

Climate change is intensifying the effects of multiple interacting stressors on aquatic ecosystems worldwide. In the San Francisco Estuary, signals of climate change are apparent in the long-term monitoring record. Here we synthesize current and potential future climate change effects on three main ecosystems (floodplain, tidal marsh, and open water) in the upper estuary and two representative native fishes that commonly occur in these ecosystems (anadromous Chinook Salmon, *Oncorhynchus tshawytscha* and estuarine resident Sacramento Splittail, *Pogonichthys macrolepidotus*). Based on our review, we found that the estuary is experiencing shifting baseline environmental conditions, amplification of extremes, and restructuring of physical habitats and biological communities. We present priority topics for research and monitoring, and a conceptual model of how the estuary currently functions in relation to climate variables. In addition, we discuss four tools for management of climate change effects: regulatory, water infrastructure, habitat development, and biological measures. We conclude that adapting to climate change requires fundamental changes in management.

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KEY WORDS

Chinook Salmon, Sacramento Splittail, tidal marsh, floodplain, open water, drought, flood

INTRODUCTION

Climate change is reshaping biological communities worldwide and estuaries are no exception (Cloern et al. 2016; Lauchlan and Nagelkerken 2020). The San Francisco Estuary (estuary) is subjected to extreme seasonal and annual variation from regional and global atmospheric and oceanic forcing (Cloern and Jassby 2012) that contribute to difficult problems for management (Luoma et al. 2015). Increasing trends in climate-related variables (e.g., water temperature, sea level, drought duration) and climatic extremes (e.g., strong atmospheric rivers, record heat waves), are creating estuarine conditions outside the historic range of conditions (Cloern et al. 2011). As a result, understanding the ecology of the estuary is now inextricably linked to understanding the cumulative effect of multiple interacting stressors (Orr et al. 2020)—resulting from both climate change and management—on environmental and biological processes.

Environmental conditions have been monitored in the estuary since the early 20th century, and consistent monitoring of fishes goes back to the 1950s. These data show that since the 1980s:

1. Peak flows and floodplain inundations occur earlier in the year, are shorter in duration, and are more intense than historically (Cloern et al. 2011; Wang et al. 2018; He et al. 2019).

2. An uptrend in salinity intrusion is greater in the Spring than in the Summer–Fall (July–October vs. February–June; Hutton et al. 2021).

3. Water temperature is rising, primarily during the late Fall to Winter and mid-Spring (Bashevkin et al. 2022).

4. Changes in environmental conditions are concordant with a decline in many native species and an increase in many alien species (Cloern 2007; Winder and Jassby 2011).

To identify the effects of these changes on ecosystems and species in the estuary, we reviewed the literature and the environmental data for climate and climate-related effects. We focused the review on two representative fish species—the anadromous Chinook Salmon (*Oncorhynchus tshawytscha*) and the resident Sacramento Splittail (*Pogonichthys macrolepidotus*)—and on three aquatic ecosystems in the upper estuary that are used by those species: floodplain, tidal marsh, and open water. This work builds on an extensive literature review of climate effects on the estuary by the Interagency Ecological Program (IEP) Climate Change Team (CC MAST 2022). We also build on recent climate-related discussions about effects and adaptation (Ghalambor et al. 2021; Norgaard et al. 2021). Our goal is to identify priority topics for research and monitoring that can facilitate sound management of the estuary under climate change.

FINDINGS

Effects of Climate Change

Global warming significantly increased air temperature in California during the 20th century (Figure 1A and 1B), a trend expected to increase by an additional 1.5 °C to 4.5 °C by 2100 (Cayan et al. 2008; Knowles et al. 2018; Pierce et al. 2018; IPCC 2021). In the estuary, air temperature is a key driver of water temperature, which has increased by approximately 0.85 °C in the past 50 years (Bashevkin et al. 2022). However, the rate of temperature change exhibits considerable seasonal and regional variability, with the highest rates detected during winter and spring and in the northern Sacramento–San Joaquin Delta (Delta) (Bashevkin et al. 2022). Warmer temperature not only directly affects organisms by altering physiological processes but can interact with other environmental factors, such as contaminants, to increase effects on aquatic organisms (Brooks et al. 2012; DeCourten et al. 2017, 2019; Kolomijeca 2020).

The Mediterranean climate of California consists of an extremely variable wet season from October through March, and a dry season the rest of the year (Knowles et al. 2018). Warming air temperature in the winter increases the amount of precipitation arriving as rain rather than snow (Stewart et al. 2005; Reich et al. 2018; Knowles et al. 2018) and leads to a decrease in the snowpack (Knowles et al. 2006; Mote et al. 2018). Warmer air temperatures reduce the moisture content of the snowpack (Cayan et al. 2008), shift the timing of snowmelt to earlier in the year, and decrease its duration (Huang et al. 2020).

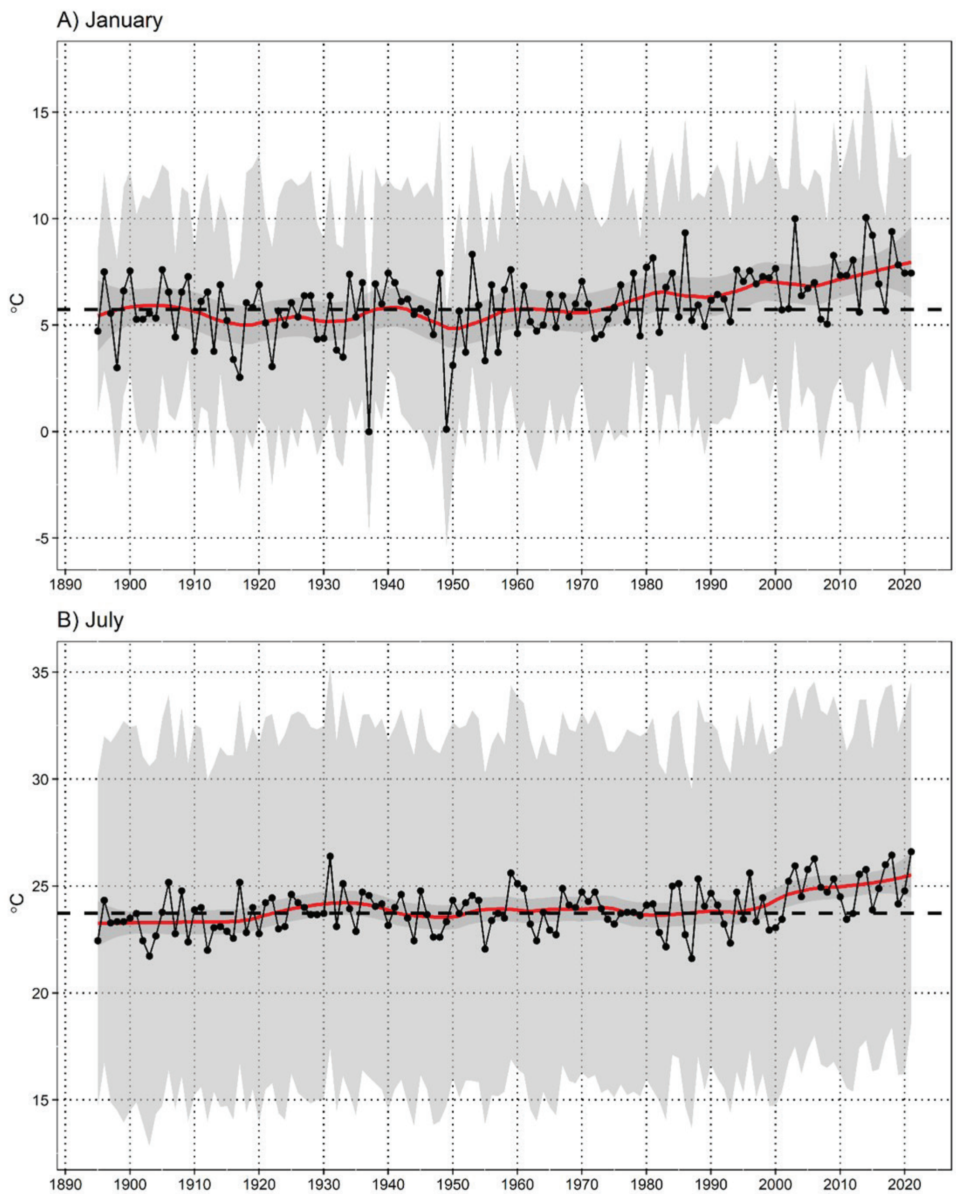

Figure 1 California statewide air temperature time series from US Climate Divisional Database (*https://www.ncdc.noaa.gov/cag/statewide/time-series)* for January (i.e., the coldest month of the year) and July (i.e., the warmest month of the year). *Points* represent average temperature for the month and year, *black dashed line* represents the average temperature for the month between 1901 and 2000, and *outer grey shading* represents the maximum and minimum temperatures. The *red line* and *darker grey shading* represent the LOESS smooth line for average temperature points and the 95% confidence intervals, respectively (fraction of points used to fit local regression = 0.25).

Winter precipitation as rain, reduced retention of precipitation as snow, and low moisture content of the snowpack (Dettinger et al. 2016; Luković et al. 2021)—in combination with an increase in the frequency and intensity of severe storms (Das et al. 2013; Knowles et al. 2018; Swain et al. 2018)—creates a new hydrologic regime. Daily rainfall totals are projected to increase by 5% to 20% (Pierce et al. 2018). This increase in storm frequency and intensity leads to record floods in California, where storms are already more variable and extreme than in the rest of the United States (Ralph and Dettinger 2012). Patterns of freshwater flow from 1906 to 2020, the longest record available in the estuary, show strong seasonal and annual variation driven by winter and spring precipitation and wet and dry regimes (Figure 2A and 2B). Consecutive wet years have not occurred in the estuary since 1996-1999, while consecutive dry and critical years have occurred three times. Overall, rising regional temperatures are expected to further intensify changes in the timing and magnitude of freshwater flow into the estuary, including "weather whiplash" scenarios characterized by rapid transitions between

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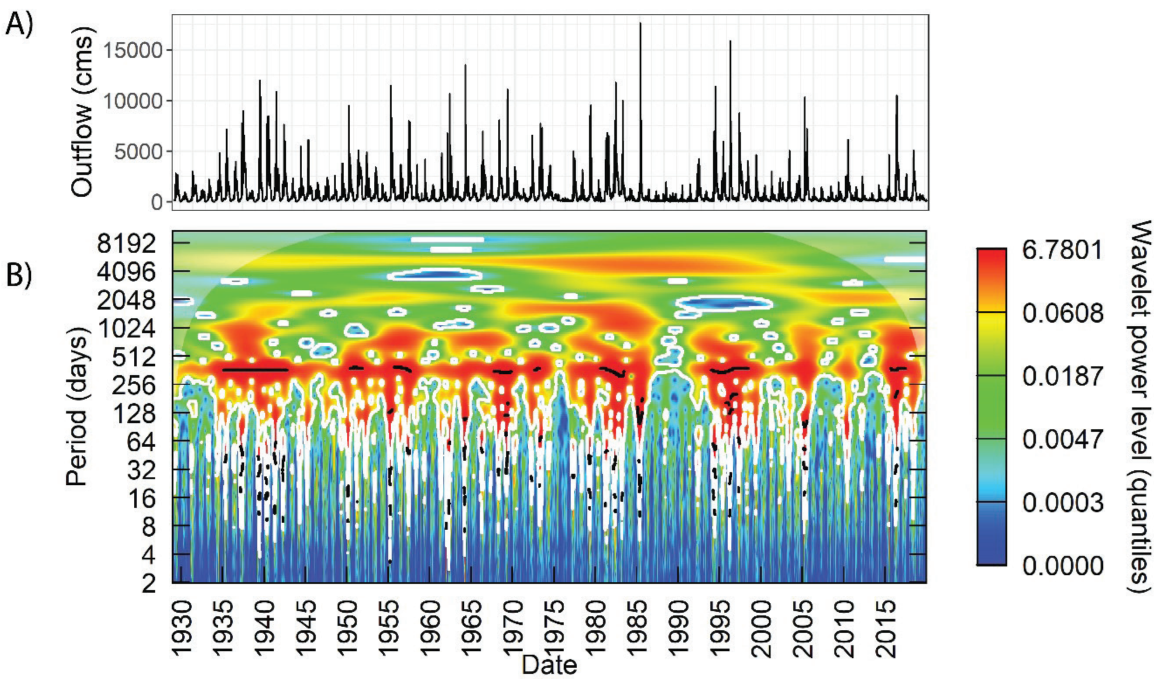

Figure 2 (**A**) Daily net Delta outflow (m^3s^{-1}) estimated for Chipps Island from 1929 to 2020. (**B**) A wavelet plot for estuary outflow (Roesch and Schmidbauer 2018). Wavelet power levels (*color scale*) represent the strength (amplitude) of periodicity in outflow across the different scales (y-axis, in days) and over the years (x-axis). For example, the annual scale (period = ~ 365 days) shows variation in wavelet power that was often strong (*color = red*; *line = black*), reflecting annual fluctuations in flow that are characteristic of California's Mediterranean climate. Transitions from *red* to *non-red* areas represent hydrologic regime shifts (e.g., a shift to extreme drought in the late 1980s and early 1990s). Data source: CDWR 2021.

extreme wet and dry conditions (Swain et al. 2018).

The high decadal-scale variability that has characterized climate in the eastern Pacific over the past 4 centuries (Biondi et al. 2001) also includes drought. Drought is not new to California (Stahle et al. 2011), but increasing temperatures increase the likelihood of precipitation deficits co-occurring with warm conditions (Diffenbaugh et al. 2015). Drought is three to four times more likely today than in pre-industrial times in California (Swain et al. 2018), and anthropogenic warming intensifies recent droughts (Williams et al. 2020). Future droughts are likely to be longer, warmer, and drier than the recent extreme drought of 2012-2016 (Meko et al. 2014; Dettinger et al. 2016). Extreme drought will further influence ecosystems in the estuary through the effect of salinity intrusion (Ghalambor et al. 2021). Sea level rose 20 cm over the 20th century, and conservative estimates indicate it will rise by another 20 to 170 cm by 2100 (Flick et al. 2003; NRC 2012). Paleoclimatic data, when combined with climate change projections, suggest a sea level rise of several meters over 50 to 150 years is possible (Hansen et al. 2016). Modeling studies suggest a sea level rise of 140 cm could shift the estuary's salinity field landward by 7 km (MacWilliams and Gross 2010).

Human activities have transformed the estuary landscape over the last 150 years, eliminating most of the natural habitats and drastically altering the hydrodynamics (Whipple et al. 2012). Upstream dams, infrastructure, water diversion, and land use substantially alter the hydrograph, water quality, and the distribution and abundance of native species (Brown et al. 2010; Moyle et al. 2010). For example, in low-precipitation years, upstream and Delta diversions take a large proportion of available water, which increases salinity intrusion (Moyle et al. 2010; Castillo et al. 2018). In high-precipitation years after droughts, replenishing water in depleted reservoirs becomes a priority, which can reduce the amount of water released downstream from dams (Reis et al. 2019). The increased frequency of drought under climate change is likely to enhance other stressors with a variety of synergistic interactions (Bennett and Moyle 1996; Brook et al. 2008; Castillo 2019). As climate change progresses, untangling and anticipating these multiple interacting stressors will be essential to management (Orr et al. 2020; Carrier-Belleau et al. 2021).

In addition to the direct effect of environmental stressors on species, climate change also affects species interactions and foodweb structure. The estuary has been invaded by hundreds of non-native species at every trophic level (Cohen and Carlton 1998), resulting in an unprecedented combination of species and fundamentally altered food-web dynamics (Winder and Jassby 2011; Moyle 2014). Many of these non-native species have had unpredictable, usually harmful, consequences to Delta fish communities and ecosystems described as the "Frankenstein effect" (Moyle 1999). Climate change may continue to favor invaders that are highly tolerant of warm temperatures (Moyle et al. 2013), such as Largemouth Bass (*Micropterus salmoides*), Inland Silverside (*Menidia beryllina*), and Brazilian waterweed (*Egeria densa*) (Brown and Michniuk 2007; Conrad et al. 2016; Mahardja et al. 2016, 2017). In addition, more non-native species are expected to invade the estuary, with uncertain consequences to ecosystem function and native species persistence (Moyle et al. 2013).

The effects of climate change on the estuary thus occur within an array of interacting anthropogenic and natural factors. We do not address the likely, but indeterminate, effects of climate change on levee stability and water project operations. The linkages in the estuary between global climate change and regional physical effects and local ecosystem processes are illustrated in Figure 3.

Biota of Interest

We focus on two management-relevant and ecologically distinct native fish species that can be found in all three ecosystems: the anadromous Chinook Salmon and the estuarine resident Sacramento Splittail. Anadromous species migrate from rivers to the ocean and back and are thus only exposed to estuarine conditions for part of the year. Variation in their overall abundance may be partially determined by conditions elsewhere. Resident species are exposed to environmental conditions in the estuary year-round so fluctuations in their abundance reflect conditions in the estuary.

Chinook Salmon

The Central Valley contains the southernmost populations of Chinook Salmon, which were exceptionally abundant before the mid-20th Century. Fish would mature in the ocean for up to 5 years before migrating into rivers of the Central Valley to spawn and die in the cold water their eggs require. Young grow in their natal streams for weeks, or as much as a year before migrating through the Delta to the ocean. Dams blocked access to most traditional spawning grounds, and agriculture and urban development eliminated much of the habitat used by growing and migrating young fish (Moyle 2002). All runs are now seriously depleted.

Four different runs of Chinook Salmon are found in the Central Valley, named for the season when the adults migrate from the ocean though the Delta on their way to riverine spawning grounds (Moyle 2002; Yoshiyama et al. 2011). Fall-run and late-fall-run fish spawn shortly after their upstream migration, and the young move out during the subsequent spring. Spring-run and winter-run adults hold for various lengths of time after migrating to their spawning grounds, and their young hold for various lengths of time before outmigrating (Moyle 2002). Spring run and winter run are currently listed as threatened and endangered (81 FR 33468 and 70 FR 37160), respectively, under the federal Endangered Species Act (USFWS 2003). As climate change continues, the decline of Chinook Salmon abundance is accelerating (Munsch et al. 2019;

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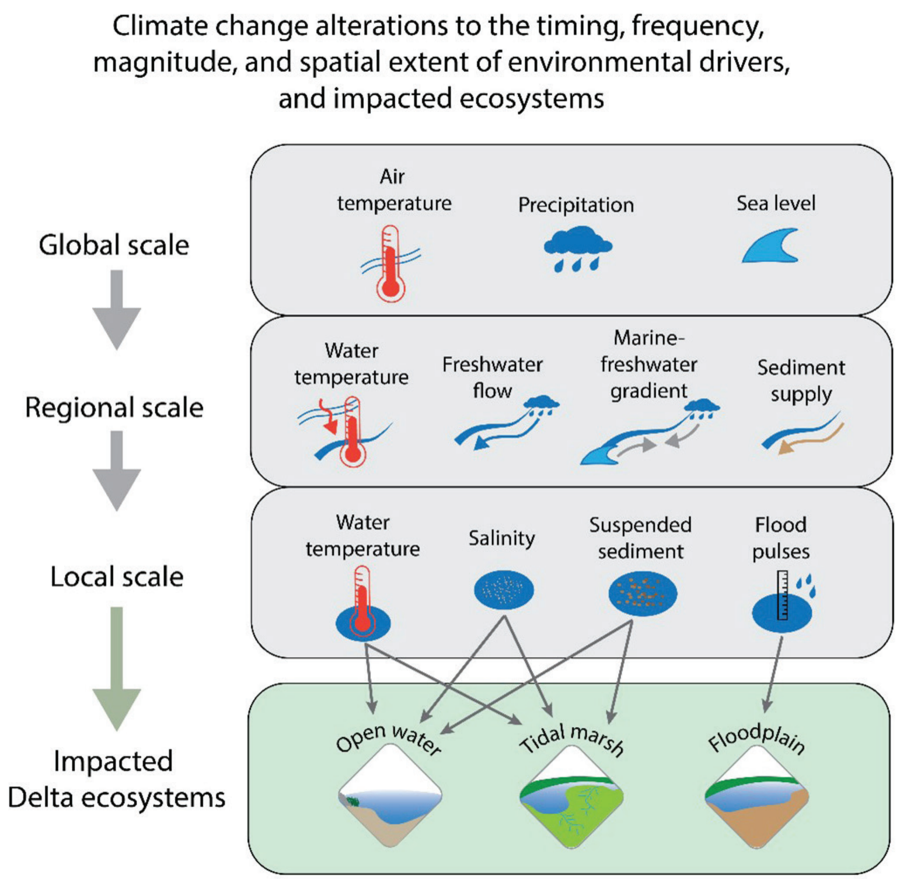

Figure 3 Schematic of the key climate change impacts on Delta ecosystems. Spatial down-scaling is represented with *arrows* from global, regional, and local scales (*grey arrows and panels*) to open water, tidal marsh, and floodplain ecosystems (*green arrow and panel*).

Cordoleani et al. 2021), as predicted in climate change vulnerability assessments nearly a decade ago (Katz et al. 2013; Moyle et al. 2013; Quiñones and Moyle 2014).

Sacramento Splittail

Sacramento Splittail is a large, long-lived, cyprinid fish that is endemic to the estuary although some movement upstream is common; years in which the bypasses flood are associated with large production of young (Moyle et al. 2004). Splittail consist of two genetically distinct populations: one that spawns in the Central Valley and another that spawns in the Petaluma and Napa rivers around San Pablo Bay (Baerwald et al. 2007). Although the two populations are largely reproductively isolated from one another, spatial overlap occurs during wetter years when salinity is low throughout the upper estuary (Feyrer et al. 2015; Mahardja et al. 2015). Sacramento Splittail is a California Species of Special Concern (Moyle et al. 2015) and was listed as a threatened species by the U.S. Fish and Wildlife Service from 1995 to 2003 (USFWS 2003; Sommer et al. 2007). More recently, climate change vulnerability assessments determined that Splittail populations are vulnerable to extinction from climate change effects on the estuary (Moyle et al. 2013).

Aquatic Ecosystems of Interest

We examine three contrasting ecosystems—floodplains, tidal marshes, and open water—to provide insights into effects of climate change. Historically, the upper estuary was an expansive habitat mosaic featuring rivers, floodplains, tidal sloughs, tidal marshes, and deep and shallow bays (Whipple et al. 2012). Starting with the California Gold Rush and the annexation of California by the United States in 1850, rapid development via urbanization, agriculture, commerce, and water conveyance transformed the estuary into an open-water-dominated system (Nichols et al. 1986). Currently, there is a large emphasis on improving the ecological conditions of the upper estuary

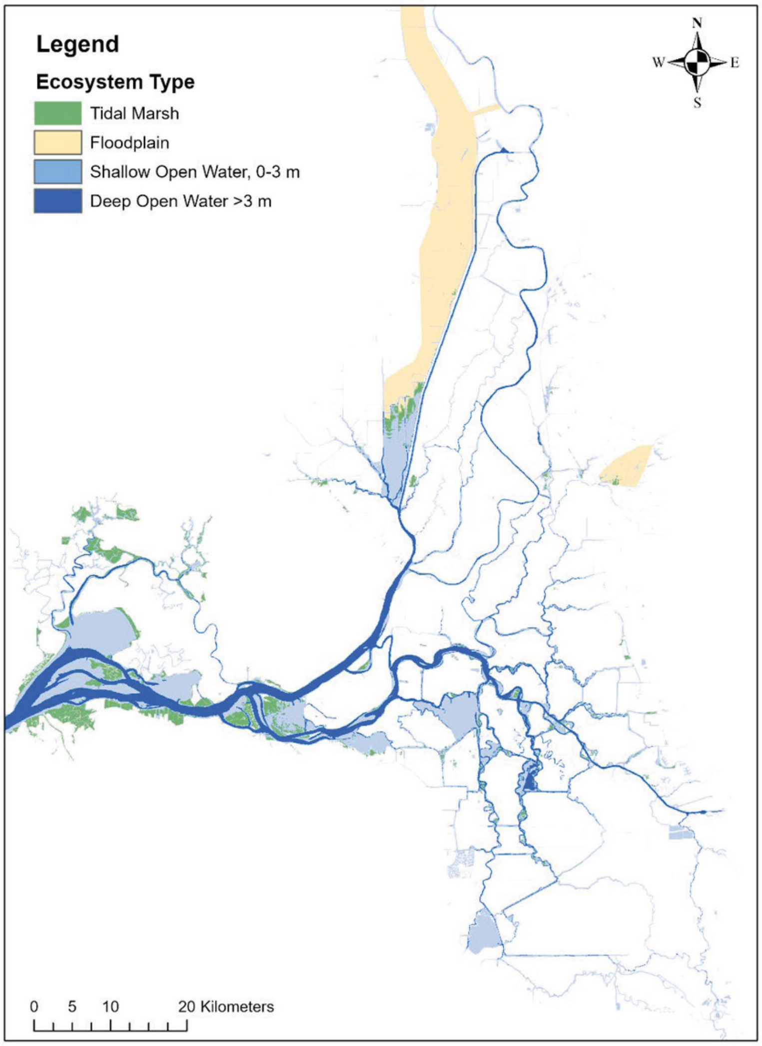

Figure 4 Map of three aquatic ecosystem types in the upper San Francisco Estuary: floodplain (*yellow*), tidal marsh (*green*), and open water (*blue*). Data sources: SFEI 2017, 2020; Fregoso et al. 2017.

by restoring habitat complexity and variability (Moyle et al. 2010; EcoRestore 2021; Sherman et al. 2017; Young et al. 2018; Cloern et al. 2021). However, the extent to which climate change affects floodplains, tidal marshes, and open-water ecosystems and their current distribution (Figure 4) warrants further investigation because each is the target of major management actions.

Floodplain

Levees and water management block inundation of much of the historic floodplain habitat in the upper estuary and Central Valley (Opperman et al. 2017). However, remnant floodplains such as the Yolo Bypass and Cosumnes River floodplains provide benefits to a variety of native aquatic species (Sommer, Harrell, and Nobriga et al. 2001; Sommer, Nobriga, Harrell et al. 2001; Crain et al. 2004). The magnitude, frequency, duration, and seasonal timing of floodplain inundation is changing with climate. Floods are more likely to occur in the winter months (December through February) than in the spring (March through April), as precipitation from local rainfall—rather than snowmelt from the mountains—becomes the source of water (Dettinger et al. 2016). Although the magnitude and frequency of floods will increase, the duration of floods will decrease (DSC 2021). A decrease in the duration of floods can lead to an increase in flood intensity, making extreme flood events like the "Great Flood of 1862" more common (Swain et al. 2018). Extreme flood events larger than those in recent history are possible based on tree-ring chronologies

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that date back 2,000 years (Meko et al. 2014) in the western region, and 1,000 years in the San Francisco Estuary (Hutton et al. 2021).

Floodplains and the species dependent on them are sensitive to the frequency, timing, duration, and intensity of floods (e.g., Takata et al. 2017; Zischg and Bermúdez 2020). Climate change alters the timing and duration of inundation. Inundation in the late winter and early spring enhances production at the base of the food web by stimulating the growth of phytoplankton, particularly diatoms (Lehman et al. 2008). Diatoms grow within a few days in the low light and cooler conditions of late winter and thrive in the high-flow conditions that promote vertical mixing in the floodplain (Lehman et al. 2008; Glibert et al. 2014). In contrast, insect larvae such as chironomids, an important macroinvertebrate food for juvenile fish, require 2 weeks or more of inundation to achieve maximum abundance (Benigno and Sommer 2008). Co-occurrence of the lower food-web production with fish abundance is essential to fish production in the floodplain (Grosholz and Gallo 2006; Moyle et al. 2007). As a result, shifts in the timing of seasonal flooding may pose a problem for energy transfer through the food web (Jardine et al. 2012).

The frequency and severity of droughts may also affect the resilience of the floodplain ecosystem. Severe or prolonged drought as we have seen in the last 20 years can damage the invertebrate egg bank on the floodplain, so that when inundation occurs, invertebrate populations are low (Bond et al. 2008). Few periods of inundation may limit the export of nutrients and phytoplankton that is needed to stimulate downstream food webs (Frantzich et al. 2018). In addition, fluctuation from drought to flood may affect the persistence of floodplain vegetation (Greet et al. 2011).

All four runs of outmigrating Chinook Salmon use floodplains in the estuary. In years when floodplains are inundated, juvenile salmon enter floodplains to feed on zooplankton and insect larvae, which are larger and more abundant than those in adjacent river channels (Jeffres et al. 2008; Limm and Marchetti 2009; Bellmore et al. 2013). As a result, juvenile Chinook Salmon that feed in floodplains during high-flow years have a high growth rate and enter the ocean at a larger size than those which only feed in river channels during low-flow years (Sommer, Nobriga, Harrell et al. 2001; Takata et al. 2017). Large fish tend to have high survival rates in the ocean, which can result in larger returns of spawning adults to rivers in subsequent years (Woodson et al. 2013; Willmes et al. 2018). Shorter durations of floodplain inundation from climate change may limit foraging opportunities for outmigrating juveniles or result in a temporal mismatch whereby flooding occurs too early for them to access floodplain resources (Jardine et al. 2012). Elevated air temperature can make the water in floodplains too warm for salmon; however, cooling of water with tide and evaporative cooling may contribute to the development of more favorable water temperature in the floodplain than in nearby sloughs (Enright et al. 2013; Aha et al. 2021).

Similar to Chinook Salmon, Splittail abundance is linked to floodplain inundation (Sommer et al. 1997), but climate-related effects on seasonal flooding can have a greater effect on Splittail populations. Adult Splittail migrate upstream into the floodplain during high-flow events in January and February (Sommer et al. 2014) and lay their eggs on flooded vegetation in March and April (Caywood 1974; Moyle et al. 2004). Early and/or short floodplain inundation periods adversely affect spawning success (Sommer et al. 1997; Sommer, Nobriga, Harrell et al. 2001]). Inundated floodplains also provide safe migration corridors between spawning and rearing habitats, as well as brackish-shallow-water rearing habitat (Moyle et al. 2004).

Tidal Marsh

Tidal marsh was a dominant landscape feature in the historic estuary; however, extensive diking, draining, and conversion to agriculture (e.g., farmland, pasture) in the 19th and 20th centuries eliminated up to 98% of tidal marsh area and nearly all associated aquatic primary production (Cloern et al. 2021). The remaining tidal marshes are sparsely distributed throughout the upper estuary and have received less attention from long-term aquatic monitoring programs (Brown 2003). Nevertheless, there is a growing recognition of the role that tidal marsh plays in the estuary food web and as key habitat for species of concern (Davis et al. 2019; Hammock et al. 2019; Colombano, Handley, O'Rear et al. 2021). Because of the various ecosystem services that tidal marsh can provide, extensive marsh restoration planning and implementation throughout the estuary is now underway (Herbold et al. 2014; Sherman et al. 2017).

Tidal marsh ecosystems face multiple interacting stressors from climate change (Colombano, Litvin, Ziegler et al. 2021), including rising sea level (Stralberg et al. 2011; Schile et al. 2014), shifting sediment dynamics (Barnard et al. 2013), and elevated temperature and salinity (Ghalambor et al. 2021; Bashevkin et al. 2022). While shading and evapotranspiration, nighttime flooding of the marsh plain, and Delta breezes may help maintain cool water temperatures in tidal marshes (Enright et al. 2013), the extent to which marshes can provide adequate thermal refugia and thus ameliorate the effects of warming on thermally sensitive fish species remains unclear.

Rising sea level increases the duration of tidal inundation of the marsh plain and, thus, the rates of sediment and organic matter accumulation. The capacity for marshes to resist and recover from disturbance (e.g., storm surges, drought) and to maintain elevation (i.e., relative position of the marsh surface with respect to tidal heights) depends on whether the annual rate of sediment and organic matter accumulation keeps pace with sea level rise (Cahoon and Guntenspergen 2010). How much sediment is delivered to marshes under different climate change scenarios remains uncertain. High flows as a result of strong atmospheric rivers in winter and spring may mobilize large amounts of sediment in pulses, which could increase the annual sediment supply to the estuary (Schoellhamer et al. 2018; Stern et al. 2020). Alternatively, sediment capture and flow regulation by dams, dredging, and other human effects influences will continue to deprive the estuary of some of its upstream sediment supply (Wright and Schoellhamer 2004; Schoellhamer et al. 2013). Salinity intrusion and increased hydroperiod could further exacerbate physiological stress to freshwater and brackish vegetation (Ghalambor et al. 2021) and, with reduced sediment delivery, could ultimately result in marsh edge erosion, channel expansion, ponding, and drowning (e.g., sudden peat collapse and conversion to open water) (Cahoon et al. 2021). Under the latter scenario, marsh islands surrounded by water in the low-salinity zone (e.g., Sherman Island, Browns Island, Ryer Island) may be most vulnerable to sea level rise and drought. In contrast, interior marshes adjacent to upland transition zones (e.g., Rush Ranch in Suisun Marsh) may be able to migrate if there is sufficient upland connectivity and accommodation space (Kirwan et al. 2010; Knowles 2010; Buffington et al. 2021).

Marsh restoration and managed retreat are considered the primary mechanisms for marsh persistence in the estuary under climate change (Goals Project 2015). However, uncertainties surround tidal amplification vs. attenuation, and different areas will likely respond differently. Where shorelines remain armored with levees for flood control, sea level rise may increase tidal amplitude; however, if widespread marsh restoration occurs and/or low-lying areas flood with tidal waters, then tidal amplitude may decrease (Holleman and Stacey 2014). Because tidal forcing is critical to site-level marsh geomorphology, habitat availability, and food production and transport, changes in tidal amplitude have profound ecological implications (Ganju et al. 2013; Lehman et al. 2015), particularly whether freshwater tidal marshes in the interior Delta are at risk of drowning (Swanson et al. 2015).

Despite their limited areal extent, tidal marshes provide critical refuge, foraging, and rearing habitat for resident and transient fishes (Brown 2003; Colombano et al. 2020). Juvenile Splittail rely on tidal marshes upon arrival to the low-salinity zone in late spring and early summer (Moyle et al. 2004). Shallow, dendritic tidal channels lined with

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emergent vegetation support seasonally diverse food webs (e.g., detrital and algal pathways; Feyrer et al. 2003; Schroeter et al. 2015; Young et al. 2021) and provide ample cover for young fish seeking refuge from predators (Colombano, Handley, O'Rear et al. 2021). Widespread loss of tidal marsh via drowning would likely create a bottleneck for Splittail recruitment to adult populations by reducing optimal nursery habitat.

In contrast, the degree to which juvenile Chinook Salmon use tidal marshes in this estuary is poorly understood. Outmigrating Chinook Salmon are commonly found in near-shore areas adjacent to emergent marsh, including tidal slough complexes in the North Delta (McLain and Castillo 2009; Takata et al. 2017). Similarly, they are regularly captured in springtime beach seine samples in Montezuma Slough, a migratory corridor that connects the Sacramento River to Suisun Marsh (O'Rear et al. 2020). However, the frequency and extent to which outmigrants rear in tidal marshes (as is commonly observed in the Pacific Northwest; e.g. Roegner et al. 2010; Davis et al. 2016), remains unknown (Aha et al. 2021), in part from the challenge of capturing them in existing sampling programs (Perry et al. 2016). At the very least, tidal marsh may enhance juvenile salmon survival by providing vegetated cover, velocity refuge, and foraging habitat along migration corridors from the Delta to the ocean. Overall, as climate change progresses, the capacity for remnant and restored tidal marshes to provide refuge and rearing habitat depends on their capacity to either keep pace with sea level rise or to migrate into upland transition zones.

Open Water

Currently, the upper estuary is primarily a sub-tidal, open-water ecosystem (Whipple et al. 2012). While much of the tidal marshes and floodplains in the estuary have been lost since the mid-19th century, the open-water area has more than doubled (Cloern et al. 2021). In the Delta, the open-water ecosystem now consists mostly of straightened, web-like channels with shallow-water-edge habitat at levee margins. Large expanses of shallow-water habitat (i.e., tidal lakes) are also present because of unrepaired levee failures that flooded agricultural tracts. More westerly open waters (e.g., Suisun Bay, Suisun Marsh, and San Pablo Bay) typically have a mix of embayments and channels that experience a wide range of salinity (e.g., freshwater and brackish) as a result of increased ocean influence (Hutton et al. 2016).

The deep open-water areas of the estuary have received the most monitoring and research attention over the past 60 years (Stompe et al. 2020). Here, freshwater flow interacts with tidal currents and wind, producing a dynamic environment that changes considerably across hours, days, seasons, years, and decades (Figure 4). Before the late 20th century, the estuary's open waters were sparsely vegetated (e.g., with native *Stuckenia* spp.; Whipple et al. 2012) and therefore dependent on *in situ* production of photosynthetic microplankton to provide new organic matter to the food web. However, proliferation of the filter-feeding overbite clam (*Potamocorbula amurensis*), which was introduced in 1987, has reduced the abundance of many photosynthetic microplankton and zooplankton species (Kimmerer et al. 1994; Lehman 2004; Winder and Jassby 2011). Another large shift occurred in the early 2000s, when several native and introduced species of fish and invertebrates experienced sharp population declines (e.g., the endemic Delta Smelt, *Hypomesus transpacificus*; Sommer et al. 2007; Mac Nally et al. 2010; Thomson et al. 2010). While pelagic productivity has declined in the estuary's bays and channels over the years (Kimmerer et al. 1994; Mac Nally et al. 2010; Thomson et al. 2010), productivity in the shallow littoral areas (e.g., near-shore habitats such as levee margins) within the Delta appears to have increased. Submerged and floating aquatic vegetation have become more widely distributed over the past few decades, and the abundances of non-native fishes associated with this vegetations have also increased (Brown and Michniuk 2007; Conrad et al. 2016; Mahardja et al. 2017; Ta et al. 2017).

Reduced outflow and warmer temperatures in late-spring and early summer months produce favorable habitat for many invasive fish, invertebrates, and aquatic vegetation (Mac Nally et al. 2010; Kimmerer et al. 2019; Michel et al. 2021). Harmful algal blooms also thrive under conditions of warm water and high residence times (Lehman, Kurobe, and Teh 2022). These same conditions are detrimental to most, though not all, native fishes (Brown et al. 2016; Young et al. 2018; Munsch et al. 2019). Intervening years of high outflow reset the salinity regime, but the increased frequency of drought conditions may not allow adequate time for native fish populations to recover (Mahardja et al. 2021).

Salinity intrusion from sea level rise, in combination with reduction in snowpack, is expected to shift species' phenology and increase the prevalence of salt-tolerant species in the upper estuary. More saline conditions may favor some native fishes and aquatic vegetation over their invasive counterparts, though it may come at the cost of freshwater-associated species (Moyle et al. 2010; CC MAST 2022). These changes may incur management responses such as reconfigurations of the Delta, as seen in the emergency drought barriers of 2015 and 2021 (Kimmerer et al. 2019), as well as the proposed Franks Tract redesign, which would reduce salinity intrusion permanently (CDFW 2020; see "Management Options").

Chinook Salmon are at the warmest end of their natural range in California. Rising temperatures will pose additional challenges to up-migrating adults and outmigrating juveniles in the estuary's open water (Herbold et al. 2018). Higher water temperature increases the metabolic demand of salmon as they migrate and increases their susceptibility to diseases (Richter and Kolmes 2005; Rhodes et al. 2011; Lehman et al. 2020). Juvenile mortality may increase with higher temperature and can be exacerbated by the likely further spread of invasive aquatic vegetation and the piscivorous predators associated with such habitat (Nobriga et al. 2021; Zeug et al. 2021).

The higher frequency of extreme floods and droughts affect Chinook Salmon in diverse ways. Chinook Salmon typically benefit from wetter years and suffer in drought years (Munsch et al. 2019, 2020). However, Chinook Salmon demonstrate high life-history diversity and phenotypic plasticity (e.g., Crozier et al. 2008; Goertler et al. 2018), which buffer the species from various detrimental conditions (Cordoleani et al. 2021). Nevertheless, human actions have weakened the overall complexity of Chinook Salmon populations in the Central Valley, though efforts are underway to mitigate such effects (Carlson and Satterthwaite 2011).

Splittail adults are often found near the bottom where they predominantly feed (Caywood 1974; Meng and Moyle 1995; Sommer et al. 1997). Adult Splittail have broad thermal and salinity tolerances that may buffer them from the dominant effects of climate change in the open-water ecosystem (Moyle 2002). The largest direct climate change effect on Splittail in the open water may be on the connectivity between the species' two distinct geographic populations (Baerwald et al. 2007). Because Splittail reside mostly in low- to moderate-salinity waters, salinity intrusion may compress their distribution and possibly lead to less frequent interactions between the two populations (Ghalambor et al. 2021). Extreme flood years may lead to higher overlap between the two populations, while more numerous and intense drought years may more effectively isolate the populations (and likely also of individuals within each population, such as those in Petaluma and Napa rivers) (Feyrer et al. 2015; Mahardja et al. 2015). Because of the lack of access to floodplain in dry years and the projected increase in the frequency of droughts, Splittail spawning at river margins may become more common.

Summary

The estuary is rapidly changing in response to changes in climate-related variables (Cloern et al. 2011; Dettinger et al. 2016). Multiple interacting stressors are shifting baseline environmental conditions, amplifying extremes, restructuring physical habitats and biological communities, and, ultimately, causing scientists and managers to rethink conservation strategies. From the ocean, climate change will affect the estuary

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primarily through salinity intrusion and sea level rise, which will inundate low-elevation habitats, facilitating levee breaches, and changing salinity distributions. From the terrestrial side, increased temperatures and altered hydrologic conditions affect both the quantity and quality of aquatic habitat. The total amount of Delta inflow may not change radically on a decadal scale, but an increase in the frequency of extreme wet and dry years will amplify the already high hydrologic variability in the system (Dettinger et al. 2016). Rising salinities (Ghalambor et al. 2021), warmer temperatures (Bashevkin et al. 2022), and newly inundated areas will shift suitable habitat for some species (CC MAST 2022).

Major environmental changes force species to "*adapt, move*, or *die*" (e.g., Habary et al. 2017; Johansen et al. 2017). *Adaptation* for species depends on the rate of environmental change and the ability of species to change in response. *Moving* may be an option for mobile species at the expense of range contractions both within the estuary or through regional range contraction (e.g., non-endemic anadromous or semi-anadromous fish shifting to northern marine and estuarine habitats). *Dying* (extinction) is not a desirable outcome in most cases. Therefore, we expect that *adaptation* by humans and aquatic organisms will be necessary.

Management options in the context of climate change can be viewed as "*resist, adapt*, or *direct*" (Thompson et al. 2021; Rahel 2022). We can *resist* change and attempt to keep our familiar and desirable ecosystems, we can *adapt* our management to accommodate climate change effects while maintaining desirable ecosystem services, or we can *direct* expected changes into more desirable configurations. Our management activities, our institutions, and our science enterprise face unprecedented challenges, making innovation vital to cope with these extreme changes.

Management in the face of climate change requires a fundamental re-thinking of how we manage and study the estuary. Climate change interacts with other stressors, further complicating monitoring and management (Lauchlan and Nagelkerken 2020; Orr et al. 2020). We have described some of the major effects of climate change on key estuarine ecosystems and identified some of the needed management and science approaches. At the very least, we need to consider our science and management in the context of environmental extremes as the new normal.

To help understand the breadth of change, we recap how climate change will affect three major ecosystems in the Delta: floodplain, tidal marsh, and open water. While each of the three has very different responses to climate change, these responses are likely to scale up to significant population-level effects on resident and migratory fishes that rely on the estuary.

- **Floodplain** ecosystem dynamics vary with the frequency, timing, duration, and intensity of floods, which are all affected by climate change. Extended dry periods between inundation events are increasing, which in turn influences environmental conditions and food webs. Flood characteristics control floodplain access for Chinook Salmon rearing and for Splittail spawning and rearing.

- **Tidal marshes** are threatened by rising sea level and altered upstream sediment inputs. Tidal marshes with insufficient elevation will not be able to keep pace with sea level rise and will ultimately drown and transition to open-water habitats. Sacramento Splittail (and possibly Chinook Salmon) will likely be severely affected by widespread loss of this productive nursery habitat.

- **Open-water ecosystems** are particularly vulnerable to the short-term effects of extreme warming and salinity intrusion. These changes, combined with uncertainty of whether the estuary will experience increased or decreased turbidity, are expected to greatly alter habitat suitability for Chinook Salmon and Sacramento Splittail during dispersal and migration, particularly for more sensitive juvenile life stages.

MANAGEMENT OPTIONS

Given the extreme conditions that can occur with climate change, there is an urgent need to consider what management options are available to reduce effects on the estuary. On the positive side, the estuary has an unusually broad suite of aquatic management tools that have been used both at the pilot scale and for routine management (Sommer 2020). However, application of these tools so far has not prevented sharp declines for many species (e.g., Quiñones and Moyle 2014; Hobbs et al. 2017). At least four general categories of tools can be used to address habitat management: regulatory; water infrastructure; habitat; and other biological measures. Below, we summarize some of the potential management tools that could be used to mitigate the effects of climate change. For each of these actions, we recommend strong science support to guide management, based on sound adaptive management and precautionary principles (e.g., Allen and Gunderson 2011; Dark and Burgin 2017).

This evolving environment is characterized by greater extremes than seen historically. As a result, management tools used in the past will likely have reduced efficacy in the future. We therefore agree with Norgaard et al. (2021) that policy and management likely need to move into a forward-looking mode of scenario planning and rely less on historical conditions to address the rapidly evolving issue of climate change. Below, we briefly describe some of the ways that these management tools might be implemented.

Regulatory

Since the 1990s, environmental regulations such as water rights decisions and endangered species laws have played an increasing role in the management of the estuary, although not as much as depicted in public forums (Reis et al. 2019). Hence, agencies such as the State Water Resources Control Board, California Department of Fish and Wildlife, National Marine Fisheries Service, US Fish and Wildlife Service, and Army Corps of Engineers have a major role in the regulatory response to climate change. However, many of these agencies rely on historical conditions to evaluate the need for remedial actions. The Clean Water Act (1973; §131.12) requires that all the beneficial uses of all bodies of water must be protected and not be degraded further than they were when the act was adopted in 1973. Listing of endangered species requires identification of the habitat critical to survival of every taxon, often defined by historical data (ESA 1973; §4). Climate change may require changes in the beneficial uses associated with water bodies and the nature and location of habitats that support listed species.

Water Infrastructure

Water infrastructure—including dams, gates, barriers, and diversions—was designed around historical hydrology and landscapes. A primary use of dam releases has been to control salinity in the estuary; rising sea level will make this task more difficult. Historical dam operation strategies may not be sustainable as hydrology vacillates between extreme flood and drought. This, in turn, affects Delta inflow and corresponding salinity intrusion, influencing a broad suite of habitats. Improved weather forecasting combined with better hydrologic models may improve efficiency of operation.

One of the highest-profile issues will be sustainable water diversion for urban and agricultural uses, which is vulnerable to salinity intrusion from levee collapse because of high tide and flood, earthquake, and/or sea level rise (Lund et al. 2010). Alteration in the timing and location of diversions will likely require adaptations to reduce fish entrainment and to offset reductions in habitat quality associated with water diversion (e.g., Grimaldo et al. 2009; Moyle et. al. 2010).

Infrastructure such as dams and weirs could be tools to respond to climate-induced changes. One recent example is the novel use of the Suisun Marsh Salinity Control Gates to limit salinity intrusion and improve habitat conditions for Delta Smelt and other species in Suisun Marsh (Sommer, Hartman, Koller 2020; Beakes et al. 2021). Infrastructure such as the proposed Fremont Weir Notch project (USBR and CDWR 2019; see "Habitat") can enable floodplain inundation at lower river stages to support floodplain ecosystem processes.

Habitat

Habitat restoration is perhaps the single most important management tool to mitigate some of the effects of climate change. Restoration can buffer climate effects by expanding the area of suitable habitat, supporting broader species distribution (e.g., "bet hedging"), and increasing food production. The three ecosystems support very different values for species and provide strikingly different management options.

Floodplains are of great importance for Sacramento Splittail and Chinook Salmon, and they provide food-web subsidies for downstream regions (Sommer, Harrell, and Nobriga et al. 2001; Feyrer et al. 2006a, 2006b; Jeffries et al. 2007). The Yolo Bypass has been well-studied over the past 2 decades, resulting in a robust understanding of some of the necessary habitat improvements (USBR and CDWR 2019). The single most important modification is the construction of a notch in Fremont Weir at the north end of Yolo Bypass to improve connectivity with the Sacramento River. This notch has the potential to substantially buffer some of the expected changes in flood timing, frequency, and duration. Moreover, greater access to food-rich floodplain habitats can help species such as Chinook Salmon deal with the increased bioenergetic costs of warmer temperatures (unless temperatures exceed acute or lethal levels). A related management approach is to make better use of existing floodplain habitats (Katz et al. 2017; Sommer, Schreier, Conrad et al. 2020). As an example, agricultural areas could be modified in several ways to improve their value for juvenile salmon rearing (e.g., Herbold et al. 2018). Managed flooding has also been examined on a pilot scale for other species such as Sacramento Splittail (Sommer et al. 2002, 2008).

In addition to the targeted fish-management improvements above, major changes in the flood-management system are likely (CDWR 2017). Specifically, to deal with increased frequency and intensity of extreme floods, there is a clear need to increase the area of floodplain. Enlarged floodplains provide a unique and major opportunity to increase ecological value, while simultaneously helping to mitigate the higher flood risk. As a recent example, the planned Lookout Slough project will substantially increase the size of Yolo Bypass, providing more floodplain habitat as well as expanded flood conveyance (CDWR 2020).

Tidal marsh restoration represents a similar and critical complement to floodplain management. The science behind this activity is expanding rapidly, with an increased understanding of the potential benefits of restoration to at-risk species (Sherman et al. 2017). As summarized in previous sections, this habitat type could provide resilience to climate change in several ways. A major focus of ecosystem management is to increase the amount of tidal marsh habitat, with much of the effort in the upper estuary concentrated in the North Delta and Suisun Marsh (USFWS 2019). A key challenge for these habitats is that sea level rise may inundate low-elevation projects; still, new marsh habitats, especially those with the potential for upland transgression, could provide an important buffer for planned retreat under sea level rise.

The concept of habitat restoration is much more complicated for open-water regions, which are more expansive than under historical conditions (Whipple et al. 2012). Climate change will likely mediate the creation of large new areas of open-water habitat that may have benefits for some species (Moyle et al. 2013; Young et al. 2018). Management of these areas must focus more on the quality—rather than quantity—of habitats. For example, aquatic weed management could help maintain suitable open-water areas for target species (Ta et al. 2018). Moreover, efforts such as the Franks Tract project could generate benefits for fish habitat, water quality, and recreation in this large, flooded island (CDFW 2020). Planning a response to flooded island based on aquatic community patterns (e.g., Young et al. 2018) and levee maintenance costs (Suddeth et al. 2010) could greatly ameliorate the environmental and economic effects of levee breaches because of climate change.

Other Biological Measures

Example tools in this category include population supplementation and predator control (Sommer 2020). Predation will increase under climate change as warmer temperatures increase the metabolic needs of some consumers, increasing mortality rates of prey. Unfortunately, predator removal remains largely conceptual; pilot evaluations have not shown sustained, measurable benefits (e.g., Cavallo et al. 2012; Michel et al. 2020). Numerous predator "hot spots" occur throughout the Delta (Lehman et al. 2020; Grossman 2016), so some targeted efforts may be useful. However, unintended consequences of predator control on predator-prey dynamics are not uncommon (Pine et al. 2009; Shephard et al. 2019) and are more likely under climate change (e.g., Grossman 2016; Davis et al. 2019).

Supplementation of desirable species has historically been an important tool to sustain salmonid populations, particularly Chinook Salmon and Steelhead Trout (*Oncorhynchus mykiss*), whose populations are particularly sensitive to raised temperatures throughout their ranges and the loss of upstream habitats via dam construction. Hatchery populations will, therefore, continue to be a critical part of salmonid management in the Central Valley. Major changes may be necessary in response to climate extremes. For example, transporting juvenile Chinook Salmon for release past the Delta instead of in their natal stream has been used as tool during extreme low-flow conditions (e.g., Sturrock et al. 2019). Increasing the use of hatcheries to maintain refuge populations of salmonids as well as a variety of other species may also be needed. Supplementation of Splittail seems unlikely in the foreseeable future because better management of floodplain inundation, via the notch and reservoir reoperations, more directly addresses the needs of the species. However, a new fish refuge and research center has been proposed to help house other at-risk species such as Delta Smelt and Longfin Smelt (*Spirinchus thaleichthys*) (CDWR and USFWS 2017). To be useful, however, supplementation must be integrated with effective flow- and non-flow habitat-restoration actions (e.g., Moyle et al. 2010; Hobbs et al. 2017).

In addition, these management actions should consider the amount of toxins present in the environment in which they are done. Global warming has increased the abundance of harmful blooms in the estuary, particularly cyanobacteria (Lehman et al. 2017, 2021). Through the production of hepatotoxins and neurotoxins, these blooms affect the survival of species from bacteria to fish (Ger et al. 2018; Acuña et al. 2020; Lehman et al. 2021). The blooms can also decrease the dissolved oxygen concentration in the water column (Sutula et al. 2017). Management actions are needed to control the major nutrients, water temperature, and residence time that enable large blooms to develop (Paerl and Otten 2013).

SCIENCE NEEDS

Beyond the suite of management approaches described above, science support is needed to monitor and diagnose climate effects. The central pillar of science support is maintaining core long-term monitoring programs to evaluate changes in ecological processes (Stompe et al. 2020; Cloern et al. 2021). These long-term changes are different from the current priorities that focus more on daily operational issues such as fish entrainment into water export facilities (Grimaldo et al. 2009; USFWS 2019). Consequently, monitoring may need to change to address some aspects of climate change. Below, we note two urgent areas.

Marsh Habitat

Tidal marshes are historically under-sampled yet are some of the habitats most vulnerable to sea level rise and salinity intrusion. As more tidal marsh habitats are constructed and mature, their value to target species must be assessed to guide restoration designs. More robust and coordinated tidal marsh monitoring and research is a top priority for science support (Sherman et al. 2017; Hartman et al. 2019).

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Extreme Events

Major floods, sustained drought, record heat waves, major levee breaks, and harmful blooms are all examples of climate-related events that can have major effects on the estuary. Long-term monitoring provides a good baseline of information but evaluating the effect of extreme events will require more focused sampling and habitat management. For example, levee breaks can create entirely new open-water habitats. Advanced planning for monitoring such extreme events can provide valuable and timely information.

CONCLUSIONS

Climate change is the gravest threat facing humans and ecosystems over the coming decades. We review relevant literature for the estuary to give insight into the current and potential effects of climate change on three estuarine ecosystems and processes affecting two native fish species with very different life-history strategies. Global warming is changing hydrodynamics in California by altering the timing and magnitude of streamflow, particularly during the late winter and spring. Altered streamflow will affect the migration and feeding success of the two very different fish species we considered. Through its effects on water temperature and the salinity field, climate change will also significantly affect most aquatic species of conservation concern. We identify some of the management and science approaches needed to adapt to these changes in the estuary and conclude that a fundamental rethinking of how we manage and study the estuary is needed.

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