

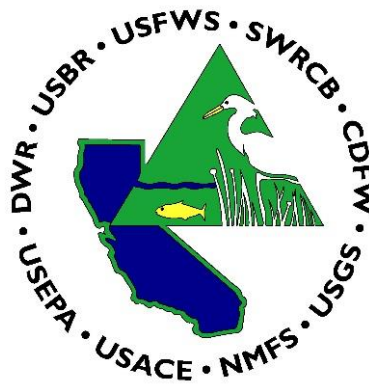
Interagency Ecological Program

**Synthesis of data and studies related to the effect of
climate change on the ecosystems and biota of the
Upper San Francisco Estuary**

Year 2022

By the Climate Change - Management, Analysis and Synthesis Team (CC-MAST)

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Ecological Program**

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Executive Summary

Management strategies for ecological values in the face of climate change require reliable and focused information. In this technical report, our focus is on the Upper San Francisco Estuary which contains the Sacramento-San Joaquin Delta and Suisun Bay. This area is home to three interconnected ecosystems: open water, floodplain, and tidal marsh.

Starting with a conceptual model, we focus our analyses on the likely impacts of climate change on these aquatic habitats. We illustrate how changes in habitats are likely to affect diverse species. We describe ecological trends attributable to climate change and likely future impacts.

The amount of open-water habitat has essentially doubled since the mid-19th century and today it is the dominant aquatic habitat in the estuary. Climate change impacts will alter the dynamics of the open water habitat in the Estuary and impact the organisms that inhabit it in both direct and indirect manners. The multivariate and interacting nature of these environmental drivers result in much uncertainty regarding the trajectory of this habitat; however, some larger overarching trends were evident from our literature review. For all functional groups, we expect a shift in phenology and increased prevalence of brackish-water or salinity tolerant assemblage in the upper estuary. A considerable number of non-native and cosmopolitan species tolerant of high temperatures are predicted to be resistant to or benefit from climate change consistent with their upward trends in the estuary. In contrast, climate change impacts are expected to be detrimental to some fish species of conservation concern in the estuary that utilize the open waters while other native species may become more prevalent.

Tidal marshes of the estuary have declined in area by over 95% in the last 150 years. The future of these habitats is unclear – with enough sediment supply, low-to-moderate sea level rise, and an increased emphasis on restoration, tidal marshes could become an important part of the future ecosystem, providing increased productivity, nursery habitat, and thermal refuges. However, the assemblage of species in the marshes will almost certainly be different due to changes in temperature and salinity. If sediment supply is insufficient, and development continues to encroach on the shores of the estuary, existing marshes may drown with sea level rise and the estuary will continue to lose this important habitat and many marsh-obligate species.

Floodplains in the Sacramento-San Joaquin Delta are highly diminished and disturbed. For natural floodplains like the Cosumnes River floodplain, the largest climate-change effect will come from changing patterns of river flows resulting in changing patterns of floodplain inundation. While inundation patterns of managed floodplains like the Yolo Bypass may also be affected by changing river flow patterns, management actions can have a stronger effect on inundation patterns. The combination of higher temperatures, longer, more severe droughts, and increased frequency of high-magnitude floods is expected to reduce native species

diversity, facilitate invasion of non-native species, and result in simplified, less distinctive, and fragmented riparian floodplain ecosystems. However, climate change is likely to not harm and may even benefit some native floodplain spawners. Some native and non-native floodplain foragers are less vulnerable to climate change and may even benefit from higher temperatures and changes in the inundation regime. Larger, more catastrophic storms could cause levee failures that could change the landscape, reworking the local topography and resetting succession. Restoring the natural flooding regimes will likely have a greater effect on the biota in the Cosumnes River floodplain than climate change. Improved floodplain connectivity to rivers will restore the ability of floodplains to absorb flood flows and recharge groundwater levels to increase resiliency of both wildlife and people to withstand droughts.

The three ecosystems in our synthesis are driven by different aspects of climate change and will have very different time scales of response. Marshes will change gradually, largely with trends in increasing sea level and salinity, as well as with shifts in sediment dynamics. Open water habitats will change greatly in temperature, flow, and salinity on short time scales, especially droughts and heatwaves. While the mobility of pelagic species buffers them from the effects of short-term changes, sessile benthic species such as clams must endure them. Floodplains are an episodic ecosystem isolated from some climate change impacts and affected mostly by extreme flood events. Management and restoration of these ecosystems and the species that live in them will require an awareness of their different sensitivities and a better understanding of ecosystem processes.

Chapter 1: General Conceptual Model for Climate Change in the Upper San Francisco Estuary

Date: 08-01-2022

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Notes:

* While Dr. Larry Brown worked on the conceptual framework early drafts of this report, he passed away before this manuscript was finalized and was unable to see its final version.

Introduction

This report is a collaboration by many state and federal agencies working in the Upper San Francisco Estuary to analyze the potential impacts of climate change to different ecosystems found here. Management strategies for ecological values in the face of climate change require reliable and focused information. In this technical report, our focus is on the Upper San Francisco Estuary (SFE), which contains the Sacramento-San Joaquin Delta and Suisun Bay. This area is home to three interconnected ecosystems: open water, floodplain, and tidal marsh. For this geographical area, we have decades of in-depth monitoring information and scientific investigations that have been successfully used to address a number of management needs. In 2019, the Interagency Ecological Program established a diverse work team to improve our ability to anticipate and respond to climate change impacts. The charge to the group was to:

- synthesize science relevant to climate change,
- determine important knowledge gaps, and
- identify ecosystem metrics for climate change.

We focus our analyses on the likely impacts of climate change on interconnected aquatic habitats. We illustrate how changes in habitats are likely to affect diverse species.

In this report we describe ecological trends attributable to climate change and likely future impacts. We address four principal questions:

1. How have the habitats and biotic communities changed due to climatic trends and events?
2. How are estuarine habitats, flora, and fauna likely to change as climate change trends continue?
3. What are key metrics to document ecosystem change as a result of climate change?
4. How should our monitoring change to improve information value?

Our work builds on the similar work of the San Francisco Baylands Goals Project (Goals Project 2015), which addressed climate change impacts to wetlands downstream of the confluence of the Sacramento and San Joaquin Rivers. We aim to contribute to an integrated baseline understanding of climate change impacts for the entire San Francisco Estuary.

Scope

We limit our review to the potentially most significant ecological impacts of climate change on aquatic habitats in the Sacramento-San Joaquin Delta and Suisun Marsh (henceforth the Delta). Similar ecological impacts in the brackish lower parts of the estuary were addressed in depth in 2015 (Goals Project 2015), and a number of ongoing efforts continue to pursue anticipation and

adaption to climate change in San Francisco Bay (e.g., Ackerly et al. 2018, SFEI and SPUR 2019). We are attempting to coordinate with, and not duplicate, those efforts.

Substantial developed areas in the Delta are protected by levees that are at risk because of climate change and other stressors. We do not address levee failure and the likely habitats it will produce because those topics are being addressed by other groups (i.e., Delta Stewardship Council 2018, 2021). We focus on the contiguous waterways of the Delta and therefore do not include isolated wetland habitats. Similarly, numerous exotic species have become established in the estuary and have disrupted ecological communities; we expect such disruptions to continue, but we do not attempt to identify which new species may invade. Climate change will facilitate invasions of some types of species, and we discuss those patterns.

Although floodplain and marsh were the dominant habitat types in the mid-1800s, land reclamation and leveeing have made the open water habitat dominant today (Robinson et al. 2014). Considerable effort and resources are being invested to reconstruct tidal wetlands and increase the frequency and extent of floodplain inundation, but little has been completed to date (USFWS 2019, NMFS 2019, CDFW 2020, EcoRestore 2021).

This report is focused on how climate change will affect the characteristics of our three ecosystems. We recognize that climate change will, through various possible scenarios, cause these habitats to change in size and location. We do not attempt to anticipate what the Delta will look like.

Approach

Increasing severity and frequency of drought are predicted impacts of climate change in California (Diffenbaugh et al. 2015) that will have major impacts on human health and economic vigor, as well as on diverse terrestrial and aquatic resources. The drought of 2012-2016 was the warmest and driest on record and was widely seen as a harbinger of further climate change impacts. Several aspects have a high degree of certainty (see Dettinger et al. 2016):

1. Air temperatures will increase by about 2°C by mid-century and by 4°C by 2100, if greenhouse gas emissions continue their accelerating trajectory.
2. Precipitation will arrive as more intense storms within periods of longer, warmer droughts. Warmer air temperatures leading to less snow increase the probability of extreme flood risk and drought risk (i.e., extreme events).
3. Sea level rise (SLR) was approximately 0.2 m during the previous century and is estimated to continue to rise an additional 0.2 m -1.7 m by the end of the current century, resulting in increased inundation and saltwater intrusion.

In addition to this combination of SLR, reduced snowpack, earlier snowmelt, and more intense

storms, water temperatures will rise (Brown et al. 2016a). These changes will challenge both water operations infrastructure and management of aquatic resources in the SFE. Climate-induced changes in sea level rise and air temperature will substantially affect SFE aquatic habitats and species of concern (Cloern et al. 2011, Brown et al. 2013, 2016, Feyrer et al. 2015). The extent and location of abiotic habitat (salinity, turbidity, and water temperature) suitable for estuarine species, including Delta Smelt (*Hypomesus transpacificus*), will likely change (Cloern et al. 2011, Brown et al. 2013, 2016, Swanson et al. 2015, Feyrer et al. 2015). Changes in seasonal water temperatures may affect the duration of important life stages for many species. For example, Brown et al. (2016a) estimated future water temperatures using climate models downscaled to the watershed predicted that the Delta Smelt reproductive maturation window could be shortened by 18-85 days as water temperatures rise.

Climate change has been documented as an ongoing process in California for 120 years (Cloern et al. 2011). All modeling projections suggest an increase in the rate of change, but with substantial differences between different models and different assumptions, such as emission scenarios, rate of sea level rise, etc. From an ecological perspective, we focus on two types of climate change impacts (see Harris et al. 2018):

1. Trends through time, appearing as changes of multi-year averages. These impacts represent an increasing pressure on the physiology of organisms and on the functional ecological groups to which they belong. Such impacts include increasing temperatures that increase growth, metabolic rate, and physiological stress.
2. Events, appearing as new maxima or minima in environmental conditions within a year or shorter time frame that represent extreme weather and climate that immediately impact the survival of a substantial percentage of the population of organisms. Examples include the hot drought of 2014-2015 (NMFS 2019) and the detrimental water quality impacts of the massive fires in California and the Central Valley watershed (Uzun et al. 2020, Rust et al. 2018, Stein et al. 2012).

Trends and events are neither functionally nor statistically separable; the increased impacts due to increasing stressful conditions heighten the impacts of events, and the new maxima and minima within years contribute to the long-term trends.

We organized our thinking about climate change according to a graphic conceptual model derived from the Goals Project (2015) developed by consensus after multiple discussions (Figure 1). The graphic conceptual model flows from global climate change impacts to the ecosystem outcomes that affect our ecosystems of interest. This process is shown by the downward pointing arrows. The species found in our ecosystems of interest are the result of ecological responses to the physical template from the individual species to the ecosystem

level. We discuss the outcomes of these processes as impacts on functional groups and give examples for individual species.

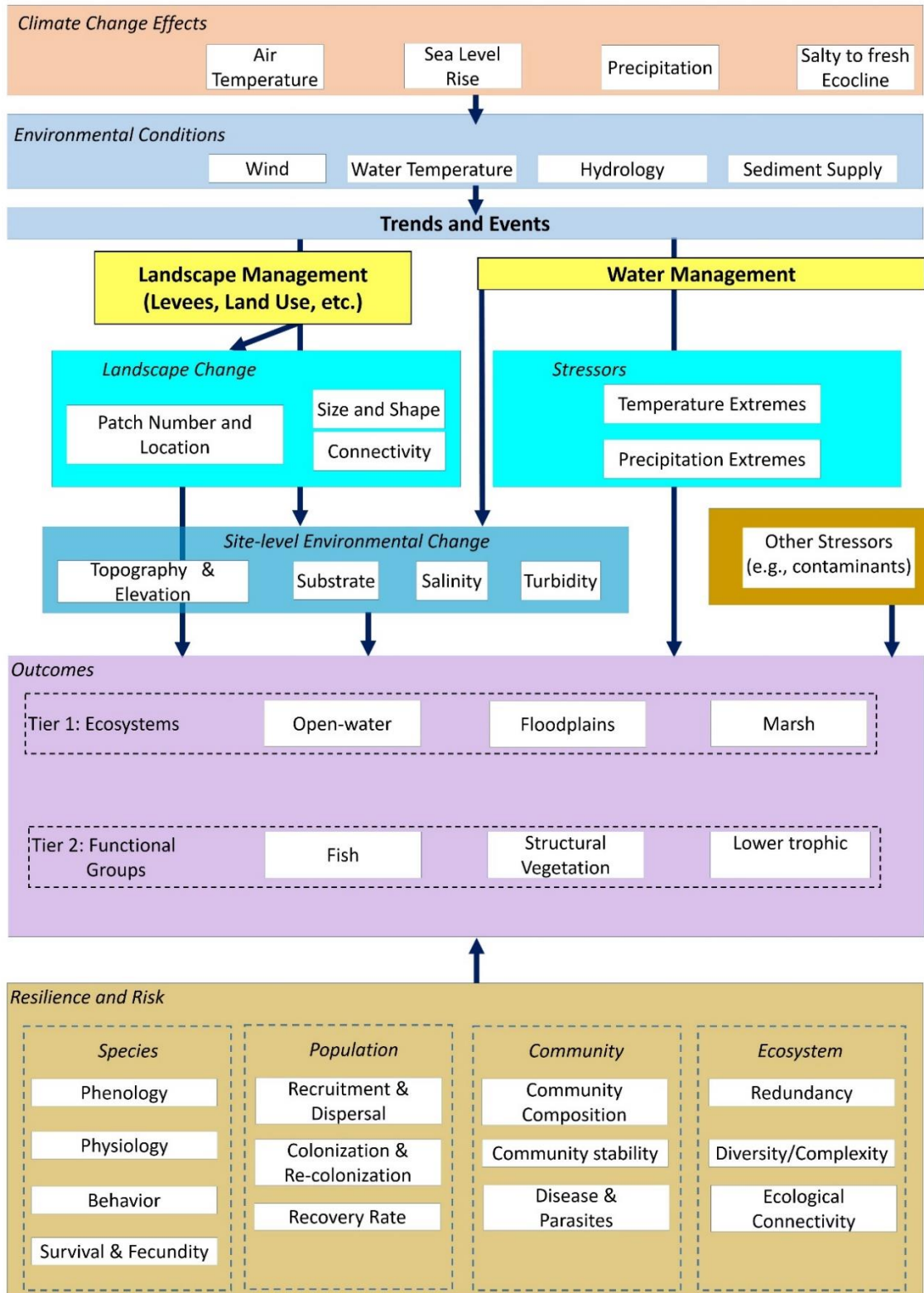


Figure 1. Conceptual model diagram for climate change impacts on estuaries

We start with aspects of global climate change, selecting the factors we believe will have the most effect on Delta conditions, and review available data. We then assess the environmental conditions most important for aquatic organisms and review available data regarding the likely effects of climate change. Those environmental conditions are then viewed through a number of filters, including human management activities, to assess how the altered conditions are likely to affect the landscape, site-level characteristics, and environmental stressors affecting organisms within our habitats of interest.

We recognize a broad influence of ‘other stressors’ that we do not address in detail. This category includes three large subcategories:

1. Stressors where there are insufficient data or understanding to project how the stressor might change with climate change. An example would be how contaminant loads of herbicides will change with changes in growing seasons, both for agriculture and aquatic weed control.
2. Stressors that affect species of interest but are outside our geographic limits. For example, ocean conditions will have an important influence on anadromous species that rear in the ocean. Similarly, fire effects on upstream areas may strongly affect habitats the anadromous species rely upon.
3. Stressors that do not have a clear association with climate change such as fish harvest and urban contaminants.

We address four levels of ecological response. At the organism level, we are concerned with how changes in a habitat affect the ability of individuals to survive and reproduce. At the population level, we are interested in whether changes to a particular habitat supports the increase or decrease (source or sink) of a species population. At the community level, we are interested in the groups of species that regularly interact with each other within our three ecosystems. At the ecosystem level, we are concerned with ecological processes and whether they will be disrupted by climate change. For example, if the environmental changes result in different species of zooplankton becoming dominant, will food web processes change, or will the new dominant species provide an equivalent food source to predators?

The general conceptual model (Figure 1) is intended to provide an overview of some of the likely effects of climate change on Delta ecosystems. We developed sub models for the three ecosystems of interest. All these models follow the same general framework; however, the models omit factors not applicable to that particular ecosystem (i.e., sea level rise for floodplains) and add detail on factors with direct impact.

Climate Change Effects

Introduction

We briefly review the evidence for the effects of climate change applicable to the upper SFE, east of the Carquinez Strait. We do not attempt to review the literature in detail at the global level, but we provide more detail at the regional and local level where possible.

We limited the conceptual model to four climate change effects (Figure 1) that have direct impacts on ecosystems of the upper SFE: sea-level rise, air temperature in the upper SFE, precipitation in the watershed, and the position and characteristics of the salinity gradient. We address each of these topics at the global scale and then focus down through one or more regional levels to the scale of California, the Central Valley watershed, and the SFE.

Wind is not addressed directly but interacts with other factors. First, alongshore winds drive the California Current, which creates upwelling conditions that support high ecosystem production in near-shore ocean waters. On-shore winds that move cool air from the ocean and San Francisco Bay into the Delta strongly affect water temperatures in the Delta. Wind is discussed as needed to understand its interactions with other effects. Other substantial global climate change impacts are not included because they have little effect within our geographic scope. Ocean temperature and ocean-water chemistry affect species that move through the upper SFE to rear in San Francisco Bay or the ocean, such as anadromous salmonids (*Oncorhynchus* spp.), sturgeon (*Acipenser* spp.), and Longfin Smelt (*Spirinchus thaleichthys*) and are discussed briefly in the Other Stressors section.

Species and ecosystem responses to climate change have been observed from every ocean subregion. Marine organisms are moving to higher latitudes, consistent with warming trends, with fish and zooplankton migrating at the fastest rates (Hoegh-Guldberg et al. 2014). This will affect estuaries as the poleward migrations may introduce new species in search of suitable habitat (Shelton et al. 2020, Champion et al. 2021). Because aquatic organisms in estuaries represent the intersection between marine and freshwater environments, they are especially vulnerable to climate change, experiencing the changes of both. Globally, climate change effects on estuaries show a wide variety of predicted changes, and some are already taking place. A 12-year monitoring study of 166 estuaries in Australia showed an increase in temperature and acidification rate over that time span, with the final values for both exceeding the Intergovernmental Panel on Climate Change (IPCC) projection by 2100 (IPCC 2021). The changes observed are significantly more extreme than the predictions from global models, which indicate a need for regional-scale estuarine models (Scanes et al. 2020, Collins et al. 2013). Analysis of expected and potential impacts to estuaries in Australia, the United Kingdom and Chesapeake Bay found diverse impacts to species from the locally predicted changes in precipitation, water temperature and chemistry, salinity, flow, primary productivity, turbidity

and geomorphology (Gillanders et al. 2011, Robins et al. 2016). In the SFE, research is showing regionally positive water temperature trends (Bashevkin et al. 2021), and the present report discusses ongoing and predicted regional changes to ecosystems and species (Chapters 2-4).

Sea level rise

Effects to date of sea level rise (SLR) on coastal systems can be attributed to a delayed response of ocean warming to atmospheric warming (Wong et al. 2014). Large spatial variations in projected sea level rise, together with local factors, mean regional sea level rise (RSLR) at the local scale varies considerably from projected global mean sea-level rise (GMSLR) (Wong et al. 2014). Using three different approaches, the reconstruction of the yearly average GMSLR using tide gauges shows a mean rate of increase of 1.5 mm per year (range, 1.3-1.7 mm per year depending on approach) between 1900 and 1990 and a mean rate of increase of 3.2 mm per year (2.8-3.6 mm per year depending on approach) from 1993 to 2010 (Wong et al. 2014). Ocean thermal expansion and water from melting glaciers drove most of the sea level rise from 1993 to 2010. The latter period was the first to include satellite data from the Greenland and Antarctic ice sheets (Church et al. 2013). Observed losses in Antarctic and Greenland ice sheets from 2007-2017 track the upper loss estimates from the IPCC 5th Assessment Report the closest (Slater et al. 2020). Rates of GMSLR during the 21st century are projected to exceed the rate of 2.0 mm per year observed over the recent 40 years (1971-2010, range, 1.7-2.3 mm per year) for all modeled scenarios. The low-end range of GMSLR using the low emission scenario (Representative Concentration Pathway (RCP) 2.6) estimate 280 mm of GMSLR by 2100, and the high end of the range, using the high emission scenario (RCP 8.5) estimate 980 mm of GMSLR by 2100, relative to 1985-2005 (Wong et al. 2014).

Considering regional variations and local factors, sea level rise can be higher or lower in places than that projected for the GMSLR (Wong et al. 2014). South of Crescent City, regional SLR is similar along the California coastline (up to 800 mm). From Crescent City north, SLR it is projected to be reduced by 250 mm compared to San Diego or San Francisco. Regional and local SLR depend not only on ocean dynamics, but also on change in tectonics such as the Cascadia subduction zone and isostatic rebound from the melting of ice sheets from the last ice age (~18,000 years ago; Wong et al. 2014). The Earth's crust does not respond uniformly to these events, creating localized differences in rate of uplift or subsidence (Cayan et al. 2016, Simms et al. 2016). Ocean dynamics like El Niño events accumulate water along the California coast due to wind and ocean circulation and have the largest impact on seasonal to interannual SLR rise. Storm surges, especially in northern California are another contributor to SLR fluctuation (Cayan et al. 2016).

The most recent estimates of sea-level rise in California were developed using a probabilistic approach based on the IPCC 5th Assessment (CNRA 2018); however, these estimates only considered the lowest and highest emissions scenarios (RCP 2.6 and RCP 8.5, respectively), plus

an extreme scenario (H++ with unknown probability). For San Francisco, the differences in sea-level rise projections under different emissions scenarios (RCP 2.6 to RCP 8.5) are minor before 2050. Since the differences are small between scenarios and the world is currently on an RCP 8.5 emission path, only RCP 8.5 estimates were included in the report. Past mid-century however, they diverge significantly and are therefore separated out (Table 1).

Table 1. Sea level rise predictions for San Francisco by year and Representative Concentration Pathway (RCP); CNRA 2018)

Year & Emission scenario	Likely Range 66% probability sea-level rise is between...	1-in-20 chance 5% probability sea-level rise meets or exceeds	Extreme (H++) scenario (Sweet et al. 2017)
2050 (RCP 8.5)	0.2-0.3 m (0.6-1.1 ft)	≥ 0.6 m (1.9 ft)	0.82 m (2.7 ft)
2100 (RCP 2.6)	0.3-0.7 m (1.0-2.4 ft)	≥ 1.0 m (3.2 ft)	
2100 (RCP 8.5)	0.5-1.0 m (1.6-3.4 ft)	≥ 1.3 m (4.4 ft)	3.1 m (10.2 ft)

Sea level rise will bring increased inundation area and higher salinity into San Francisco Bay and the Delta. The resulting increased area of saltier water will directly affect fish and aquatic invertebrates, plants, and wildlife of the marsh and wetland habitats in San Francisco Bay (Ghalambor et al. 2021, Goals Project 2015) and areas of Suisun Marsh and the Delta now supporting freshwater species will become increasingly brackish. The increased inundation will also lead to increased predator exposure for terrestrial wildlife such as salt marsh harvest mouse (*Reithrodontomys raviventris*), while aquatic species may have less exposure to avian predators (Goals Project 2015).

Sea level rise will require increases in Delta out flow to maintain the Hydraulic Salinity Barrier and in-Delta water quality, which would thereby decrease the amount of water available for Delta exports (Schwarz et al., 2019). Historically, maintenance of the Hydraulic Salinity Barrier has been the limiting factor on Delta exports for most months of most years (Reis et al. 2019). Multiple studies of the state and federal project operations indicate that sea-level rise will trigger decreasing exports or other tradeoffs to prevent salinity from penetrating into the Delta (Schwarz et al. 2019, Wang et al. 2018). MacWilliams and Gross (2010) explored the relationship between sea level rise and the salinity gradient in the estuary by modeling Delta conditions under historical operations with multiple levels of sea level rise—allowing water quality in the Delta to respond unconstrained by regulatory requirements. This study estimated SLR of up to 1.4 m could result in an eastward shift of the upstream edge of ocean salts of about 7 km, increasing salinity in Clifton Forebay by 0.2 PSU (practical salinity unit) (MacWilliams and Gross 2010). Considering the importance of the Delta to statewide water supply, considerable effort will likely be expended to prevent salinization.

Air temperature

Global Mean Surface Temperature has increased since the late 19th century. Each of the past four decades has been successively warmer than all the previous decades in the instrumental record, and the second decade of the 21st century has been the warmest (IPCC 2021). Over the period 1880–2012, the globally averaged combined land and ocean-surface temperature data, as calculated by linear trend, show a warming trend of 0.85°C [range, 0.65 to 1.06°C] (90% confidence interval), and about 0.72°C [range, 0.49 to 0.89°C] (90% confidence interval), over the period 1951–2012 (Hartmann et al. 2013). Global mean surface temperature exhibits substantial decadal and interannual variability, but it is very likely the numbers of extreme cold days and nights have decreased, and the numbers of extreme warm days and nights have increased globally since about 1950 (Hartmann et al. 2013). Across most continents, as the global mean temperature increases, we expect increases in the number of unusually warm days and nights and decreases in unusually cold days and nights. These changes are expected for extremes on both daily and seasonal time scales (Collins et al. 2013, Hartmann et al. 2013), and some regions have already experienced close to a doubling of the occurrence of warm and a halving of the occurrence of cold nights (Choi et al. 2009).

Global mean temperatures will likely continue to rise (Collins et al. 2013). Under the assumptions of the concentration-driven RCPs, global mean surface temperatures for 2081–2100 (relative to 1986–2005) will likely be in the range of 0.3°C to 1.7°C (RCP 2.6, some emission abatement) to 2.6°C to 4.8°C (RCP 8.5, business as usual). Globally averaged changes over land will likely exceed changes over the ocean by 2100 by a factor in the range 1.4 to 1.7 (Collins et al. 2013).

For California and the Delta, climate projections of increased temperatures are more certain than those for precipitation (Schwarz et al. 2019). Higher mean and extreme temperatures will play a large role in future droughts and water supply impacts because of the associated increase in evaporation and evapotranspiration. By 2100, temperatures in California are projected to increase by 2–4°C under the RCP 4.5 scenarios and up to 4–6°C for the RCP 8.5 scenarios (Pierce et al. 2018). Relative temperature impacts are projected to be greatest in areas of moderate to high elevation (Ullrich et al. 2018) and are therefore more likely to impact snowpack by less precipitation falling as snow, snowmelt during winter rain events and earlier seasonal snowmelt (Reich et al. 2018). By mid-century, temperatures at high elevations in the Sierra Nevada could increase by 2°C, versus 1.5°C at mid-elevations, and 0.8 to 1.4°C in the Central Valley (Ullrich et al. 2018). Nighttime heat wave events have clearly intensified in the California-Nevada region since the 1980s, especially since 2000, and the latest events also brought extreme daytime temperatures. More recent studies show that greater increases in nighttime temperatures result in a decreased daily temperature range (Gershunov et al. 2009, Zhao et al. 2020). An increased frequency and intensity of heat waves, in addition to general

warming is predicted to be less severe in the Sacramento Valley and Bay Area than in other regions of California, probably because of a projected increase in Delta breezes (Zhao et al. 2020).

Precipitation

Climate-precipitation projections for California consistently show a transition from snow to rain due to an increase in temperature. By mid-century, peak runoff may occur a month earlier than historical conditions (Wang et al. 2018). By end of century, under a business as usual warming scenario, projections show 85% snow loss for the Sierra Nevada during drought conditions otherwise similar to the period 2012-2016, and 66% loss during wet years similar to the precipitation in 2016-2017 (Reich et al. 2018). By mid-century (2045-2074), earlier snowmelt and a greater rainfall-to-snow ratio will shift approximately 2.1 Million Acre Feet (MAF) of runoff to earlier in the year, or nearly twice the total volume of Folsom Reservoir (Wang et al. 2018). The shift in peak runoff is projected to be especially pronounced in rain-dominated watersheds, with runoff peaking earlier and higher (He et al. 2019). In snow-dominated watersheds, relatively little change in seasonality or peak runoff is expected by mid-century (2045-2074), but large April-July decreases in peak runoff are expected by 2100 (He et al. 2019).

Several studies have assessed the potential for greater variability, frequency, and magnitude of seasonal precipitation (Dettinger et al. 2011, 2016, He et al. 2019, Huang et al. 2020, Medellín-Azuara et al. 2008, Swain et al. 2018, 2020). One significant simulated change is an intensification of storm events, with fewer days with precipitation but greater intensity of the large storms that do occur (Dettinger et al. 2016). Although California's climate has always been variable, intra-annual variability may increase substantially (Dettinger et al. 2016, Swain et al. 2018). The shift in seasonality, concentration of maximum precipitation and runoff during winter months, and increased variability and intensification of storms could strain existing water infrastructure (Swain et al. 2018). A large ensemble of climate model simulations projects a more than three-fold increase in intra-annual wet extremes by 2100, with a smaller but still significant increase in dry extremes. These simulations also indicate a compression of precipitation, with 35- 85% more (from north to south in California) falling in the core winter months of November to March and less falling in autumn and spring (Swain et al. 2018). A delay in the onset of the rainy season is already being observed and appears consistent with the predicted shorter rainy season in California (Lukovic et al. 2021).

Salinity ecocline

The river-sea interface of estuaries provides high habitat heterogeneity and supports high biodiversity across freshwater and subtidal zones (Basset et al. 2013). Estuarine ecosystems have been impacted both by SLR and human influences resulting in increased flooding, salinization, land degradation and erosion of coastal areas around estuaries (Wong et al. 2014,

Hoegh-Guldberg et al. 2018). Marine biotic communities in estuaries are redistributing farther inland because of increased seawater intrusion. Such distribution shifts are limited for some species, particularly benthic organisms, by physical barriers, such as unsuitable benthic substrates, thus reducing suitable habitats for estuarine communities.

The salinity gradient is the primary driver of species assemblage structure and distribution (Ghalambor et al. 2021, Baumsteiger et al. 2017, Cloern et al. 2017, Thompson et al. 2013, Feyrer et al. 2015, Watson and Byrne 2009). The position of the salinity gradient in the upper SFE is much more sensitive to variation in river inflow than to oceanic factors (Jassby et al. 1995, Feyrer et al. 2015). The high seasonal and interannual variability of river inflow, as described above, is expected to increase; this will often obscure effects of sea level rise. Previous studies of climate change in SFE have suggested that SLR will result in salinity intrusion into the upper SFE and degrade habitat conditions for some species, particularly Delta Smelt (Feyrer et al. 2011, Cloern et al. 2011, Brown et al. 2013). However, predicting the effects of climate change on the salinity gradient is not straightforward because water is highly managed in the upper SFE to protect water quality for human uses and the ecosystem. Thus, water management will be implemented to resist salinity intrusion. The exact management strategies that will be implemented, and how effective they will be, remain uncertain.

Increased nutrient inputs from intensive human development increases bacterial respiration, which is exacerbated by warming and leads to an expansion of suboxic and anoxic areas. These changes reduce the survival of estuarine animals and increase the occurrence of harmful algal blooms (HABs) and pathogenic microbes (Acuña et al. 2012, Ger et al. 2009, Lehman et al. 2017). Projected warming, SLR and tidal changes in the 21st century will continue to expand salinization and hypoxia in estuaries (Scanes et al. 2020). These impacts will be more pronounced under higher emission scenarios, and in temperate and high-latitude estuaries that are eutrophic, shallow and have naturally low sediment supply (Lehman et al. 2013, 2020b, Gillanders et al. 2011, Robins et al. 2016). In the Delta, hypoxia has been a rare or localized problem and is likely to remain so, largely because tidal energy is high and water flows and velocities are high throughout most channels. Changes to the Delta hydrodynamics, such as flooded islands would bring, could lead to changes in frequency of hypoxia. (Jassby and Van Nieuwenhuyse 2005, Cloern and Jassby 2012).

Environmental Conditions

Introduction

In the previous section, we addressed large-scale climate change effects that we expect to have important impacts in the upper SFE. In this section, we are concerned with the direct and interactive effects of those climate changes at the watershed level on environmental conditions

and ecological processes in the upper estuary. We also discuss water and landscape management that occurs upstream of tidal influence but influences hydrology.

Hydrology

California has a Mediterranean climate with distinct wet and dry seasons. Most precipitation falls from December to March with some portion of that precipitation occurring as snow at higher elevations in the Sierra Nevada. The water year (WY) starts Oct 1, putting the entire wet season at the start of the WY and the dry season at the end. The amount of rain and snow during the wet season is extremely variable from year to year. In most years, the snowpack serves as the state's largest surface reservoir of water. As air temperature increases, the snow gradually melts and fills reservoirs. Despite this seasonal pattern, annual precipitation in California is difficult to predict, and California experiences extended droughts and large floods (Ingram and Malamud-Roam 2013). This highly variable, but recurrent, pattern of flow has influenced the evolution of California fishes (Moyle and Herbold 1987, Moyle 2002). River and stream restoration aims to restore natural flow patterns globally (Poff et al. 1997, 2017, Yarnell et al. 2015, 2020) and in California (Kiernan et al. 2012).

Although it has been recognized for many years that warm storms originating in the tropics (known as the "pineapple express") are an important part of California's climate, only recently have these "atmospheric rivers" been studied in detail (e.g., Ralph and Dettinger 2011, 2012, Ralph et al. 2019). These substantial atmospheric rivers largely determine annual precipitation in the SFE watershed (Dettinger 2011, Dettinger and Cayan 2014, Dettinger et al. 2016, Ralph et al. 2019). These warm, intense storms that are concentrated in a fairly small geographic area of one or a few large watersheds are difficult to manage and can lead to flooding.

The effect of climate change on precipitation in the SFE watershed was variable among the individual CMIP models (Knowles et al. 2018). The average across all scenarios was an increase of 0.23 mm/d (9%) for the period of 1995-2099 starting from an initial value of 2.5 mm/d; however, individual models varied from a decline of 0.44 mm/d to an increase of 1.3 mm/d. These changes in precipitation and warming air temperature resulted in an 89% decline in April 1 snowpack liquid-water equivalents in the Sacramento River drainage. For all scenarios combined, total annual Sacramento River basin unimpaired runoff increases 9.7% but with high variability. Projected increases in precipitation during the wet season, defined here as October 1 to March 31, and reduced snowmelt runoff in the dry season (April 1 to September 30) lead to a shift in unimpaired flow timing, with an average 33% increase in the fraction of WY total unimpaired flow arriving before April 1, with all scenarios showing an increasing trend. When all scenarios are combined, extreme daily flows, (the number of days during each WY when flow exceeds the 99th percentile from the WY 1980–2009 historical baseline period) increased from 3.46 to 9.53 d/year, an increase of 175% (Knowles et al. 2018). Using a smaller set of GCM

scenarios, Das et al. (2011) found that extreme flows increased in Sacramento River basin headwaters.

It is unclear to what degree existing water infrastructure will be able to mitigate these anticipated changes in hydrology (Knowles et al. 2018). Across all scenarios, WY means, wet-season fractions, and extreme flow frequencies for managed Sacramento River basin outflow increased 13%, 15%, and 170%, respectively, compared to increases in the corresponding unimpaired quantities of 9.7%, 33%, and 175%, respectively. In terms of Delta inflow, these changes have multiple effects. For example, the frequency of severe drought is likely to increase (Figure 2). For RCP 4.5 scenarios, the changes only occur for extremely dry years (3rd and 10th percentiles of annual historical flow). For RCP 8.5 scenarios all ranges of dry years examined increased in frequency (Knowles et al. 2018).

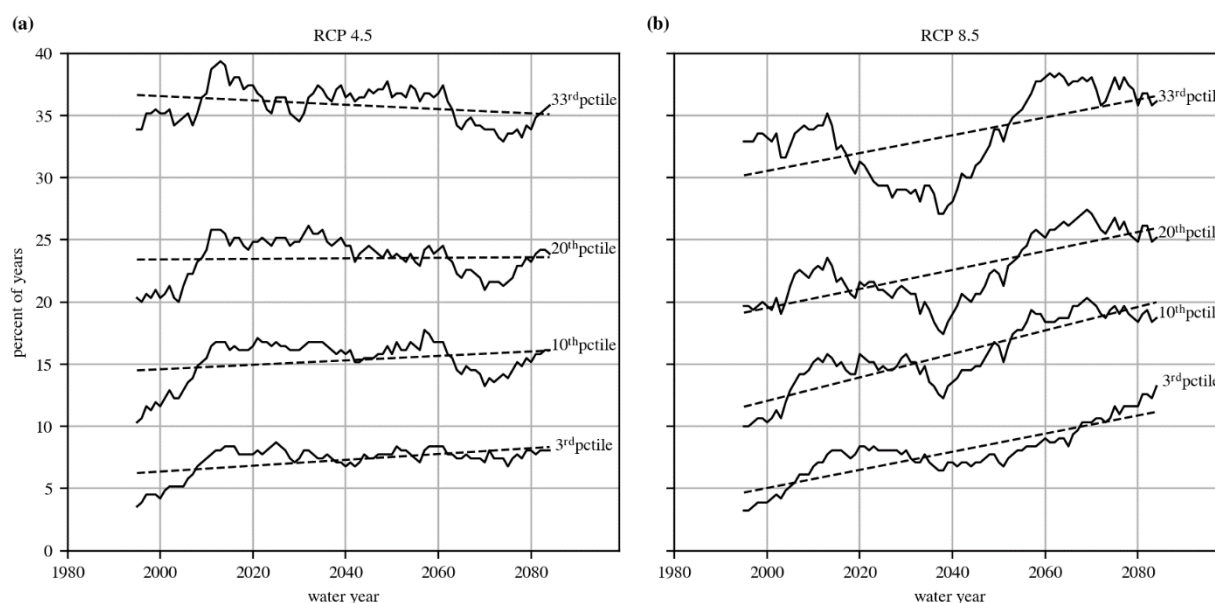


Figure 2. The 31-year moving-window percentages of years with projected impaired Sacramento River basin WY outflow below global climate model historical-period (WY 1980–2009) percentile values, averaged over (a) RCP 4.5 scenarios and (b) RCP 8.5 scenarios. Percentile thresholds are indicated. Dashed lines are linear fits. RCP = representative concentration pathway; WY = water year (from Knowles et al. 2018).

Upstream changes in hydrology produce substantial changes in the timing and magnitude of Delta inflows and extreme flows during the wettest months December–March and reduced inflows during the drier months of April–July (Figure 3). Delta inflows are projected to increase 45% (with respect to WY 1980–2009 inflows) during the months of December–March and to decline 20% in the remainder of the year, averaged over RCP 8.5 scenarios (Knowles et al. 2018). These values assume no management actions are taken to mitigate these changes.

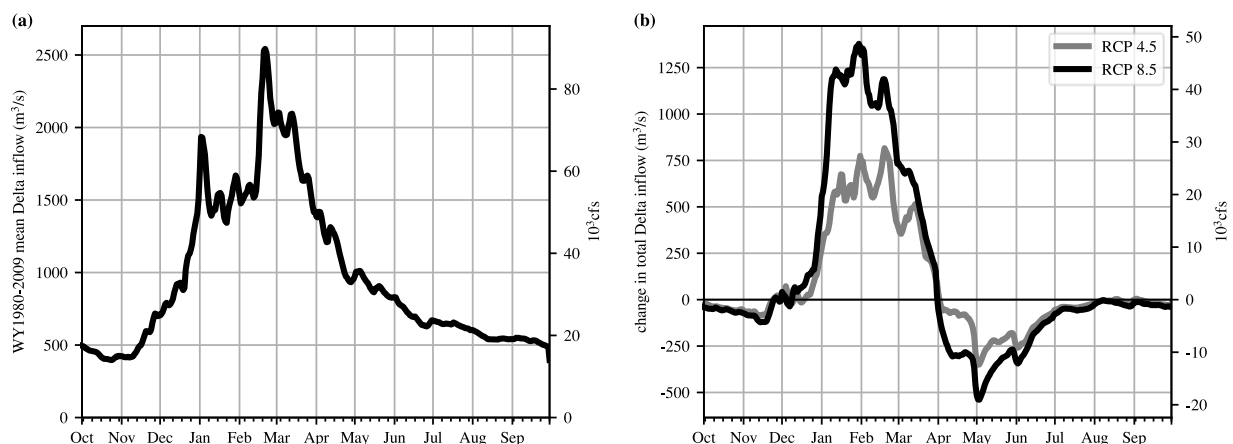


Figure 3. (a) WY 1980–2009 mean annual cycle of total Delta inflow. (b) Difference between WY 2070–2099 and 1980–2009 mean annual cycles of managed total Delta inflow averaged over scenarios of each RCP. WY = water year; RCP = representative concentration pathway (from Knowles et al. 2018).

These projected changes have important water supply and ecological implications. The historical spring runoff peak will be reduced as climate change proceeds. Species dependent on floodplains may be affected by this change in several ways. High flows will be restricted to fewer but more intense floods that do not result in prolonged inundation of floodplain habitat. Earlier winter flooding will likely not support successful spawning or rearing for species evolved to take advantage of the sustained spring snowmelt pulse, such as Sacramento Splittail (*Pogonichthys macrolepidotus*). The frequency of extended (30 days or greater) floodplain inundation of Yolo Bypass significantly declines in the latter half of the century for a warmer, drier scenario (Cloern 2011). We do not consider levee integrity directly in this report, but flooding of Delta islands is more likely with more frequent, more intense winter floods. More intense floods combined with a projected median sea level rise by 2100 (relative to 2000 average level) of 0.74 m for RCP 4.5 scenarios and 1.37 m for RCP 8.5 scenarios (Cayan et al. 2016), would imperil the already fragile Delta levee system. The island interiors behind the levees, and the levees themselves, continue to subside (Brooks et al. 2012), exacerbating the problem (Mount and Twiss 2005). These changes would likely result in flooding of multiple Delta islands due to levee breaches and dramatically alter the landscape of the Delta. Seawater intrusion would increase with the tidal prism, and the role of the Delta as a freshwater habitat and conduit could be seriously impaired.

Wind

For the SFE, winds can be important at several scales. Winds drive upwelling along the California coast, which is important for migratory species that use the coastal ocean during certain parts of their life cycle, such as Chinook Salmon (*Oncorhynchus tshawytscha*), Striped Bass (*Morone saxatilis*), lampreys, and Longfin Smelt (*Spirinchus thaleichthys*). For the upper

SFE, the most important winds are local and influence vertical and spatial gradients in air temperature and turbidity.

Climate change drives fluctuations in wind-driven upwelling along the California coast. Evidence suggests that a trend of increasing winds during the upwelling season due to climate change (Garcia-Reyes & Largier 2010, Bakun 1990, 2010), and the increased along-shore wind speeds will be sufficient to overcome factors promoting increased stratification, resulting in no major negative effects on upwelling (Auad et al. 2006). Upwelling events are becoming stronger and longer in duration, but less frequent (Iles et al. 2012) and with a delay of onset by about a month (Snyder et al. 2003).

For the upper SFE, local, summertime, onshore winds (i.e., Delta breezes) are generated by monsoonal onshore flow related to offshore high pressure and density differences between cool, moist coastal air and warm dry Central Valley air (Fosberg and Schroeder 1966, Mayor 2011). These winds enter the Central Valley through Carquinez Strait and move to the north (Sacramento Valley) and south (San Joaquin Valley) and can exert a strong impact on Delta air temperatures (Hayes et al. 1984). From May-September in 1991 at Davis in the northwestern delta, winds were from the south by evening at 72% of the days producing air temperatures up to 6°C cooler compared to days with northerly winds (Zaremba and Carroll 1999). Bever et al. (2018) found statistically significant declines in Delta breezes over recent decades (1995-2015). Declines occurred over the entire Delta for October-January period and the North Delta declines occurred throughout the year, while the Suisun Bay region showed no significant trends from late winter to early fall. The factors associated with these declines are unknown, so any tie to climate change processes is unknown. These declines in Delta breezes affect water temperatures and turbidity. At odds with the recent unexplained declines in Delta breezes, downscaled global climate models give predictions of Delta breeze events occurring with an increase in frequency and intensity (Zhao et al. 2020). This predicted increase in Delta breezes may help explain why the Bay Area and Sacramento Valley are anticipated to have a smaller future change in heat wave events and extreme heat in their model.

Water Temperature

Water temperature in the upper SFE is largely driven by temperature of inflowing water and air temperature (Wagner et al. 2011, Vroom et al. 2017, Bashevkin et al. 2021). The expected warmer atmospheric rivers, the shift in snowpack size, water content and timing, and earlier snowmelt will therefore impact the warmer temperature in the upper SFE (Dettinger et al. 2016, Swain et al. 2018, Ralph et al. 2019, He et al. 2019). The importance of inflow decreases farther downstream as the inflowing water equilibrates with air temperature and tidal mixing occurs. In the upper SFE, there appears to be little difference between surface and near-bottom water temperatures (Brown et al. 2016a, Figure 4) because the water column is relatively shallow and well mixed (Vroom et al. 2017). Differences of up to 2°C have been observed, but

these occurrences appear to be rare and ephemeral (Brown 2016). The substantial influence of air temperature is likely due to the relatively long distances from tributary sources of cold water, which allow released water to warm in response to high air temperatures before reaching tidal waters of the upper SFE. Within the upper estuary, tidal “sloshing” results in relatively long travel times through the upper SFE to San Francisco Bay, especially during the summer, providing additional time for air temperature to influence water temperature.

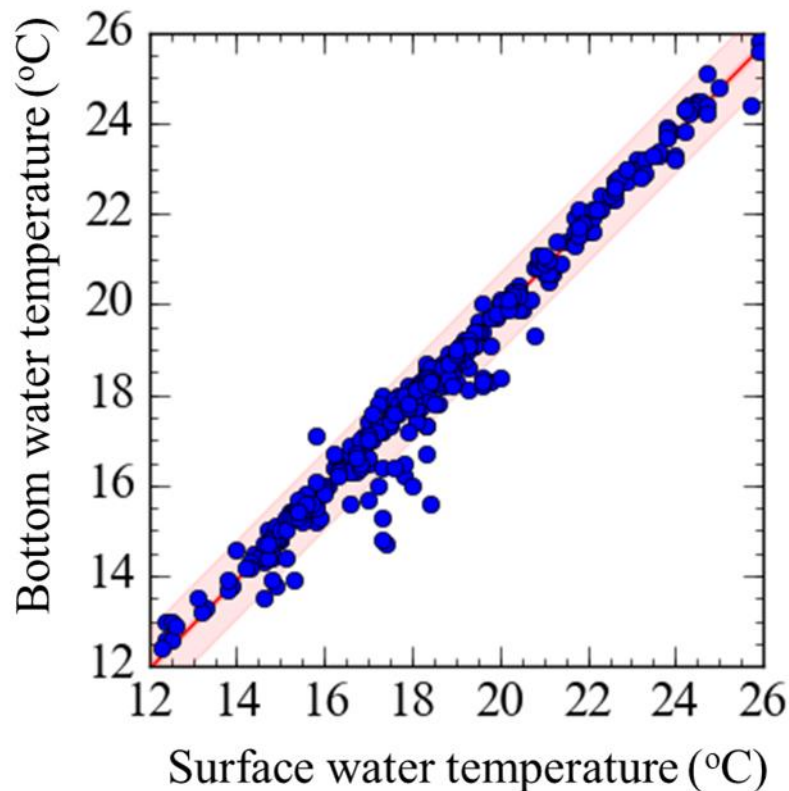


Figure 4. Linear regression between bottom water temperature (Y) and surface-water temperature (X) in the upper San Francisco Estuary during April-July 2017 (data from Enhanced Delta Smelt Monitoring 20-mm tows, EDI Data Portal). $Y = 0.12 + 0.98X$ ($R^2 = 0.98$, $P < 0.05$, 400 df) (Figure from FLOAT-MAST 2020).

As noted in the wind section, the intrusion of marine air from the Delta breezes creates a temperature gradient from Carquinez Strait into the Central Valley. This is reflected in summer water temperature as a consistent pattern of cool water temperatures in the brackish waters of Suisun Bay with warmer waters in the fresh waters of the Delta. This pattern is expected to remain the same as climate change continues (Figure 5).

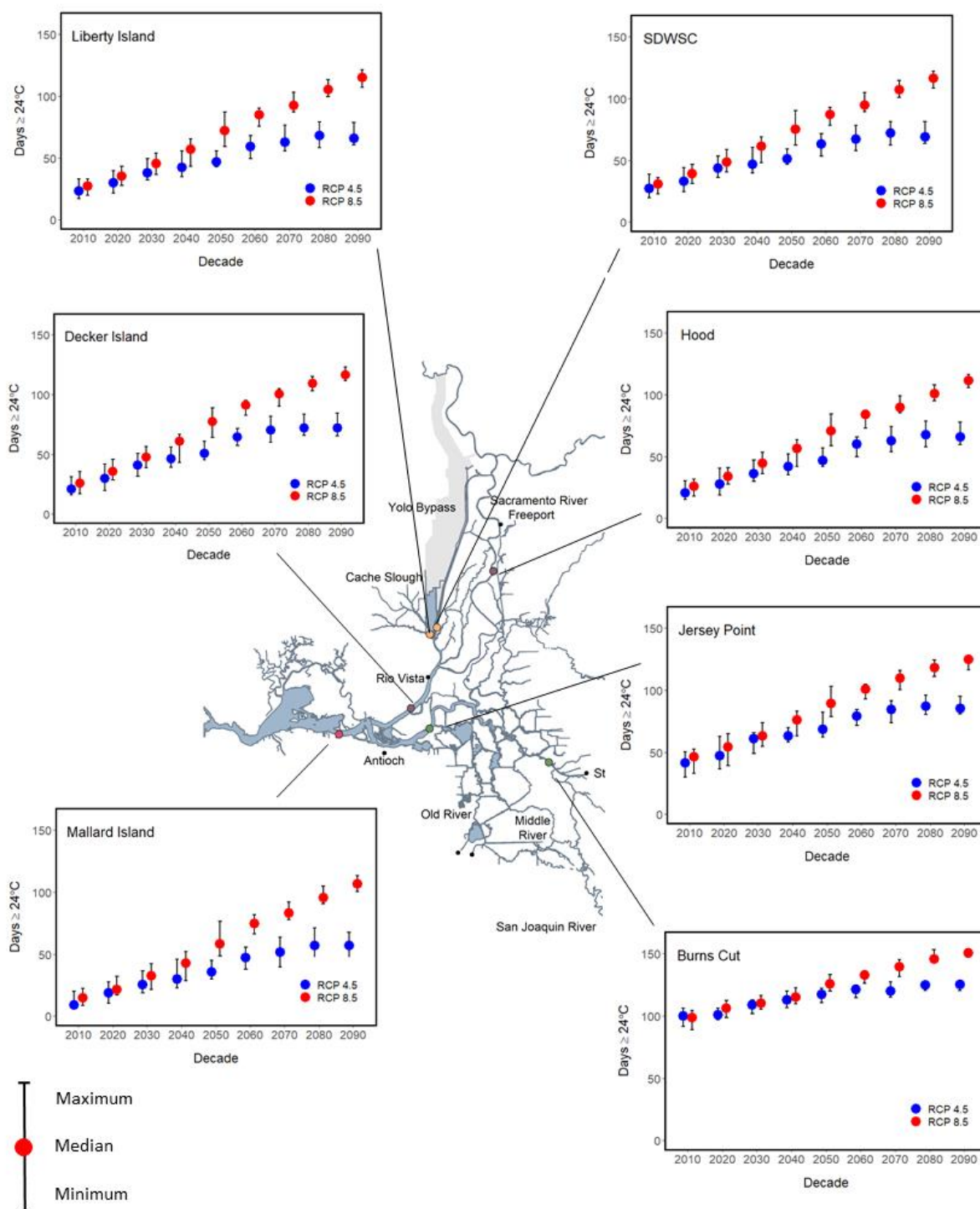


Figure 5. Plots of median, maximum, and minimum for number of days each year with calculated average daily water temperature greater than or equal to 24°C (above optimal for many native species) during the indicated decades during the 2000s. Results from CASCade 2 CMIP5 scenarios. (Graphs generated by B. Huntsman of the U.S. Geological Survey from data in Wulff et al. 2021, map provided by S. Bashevkin).

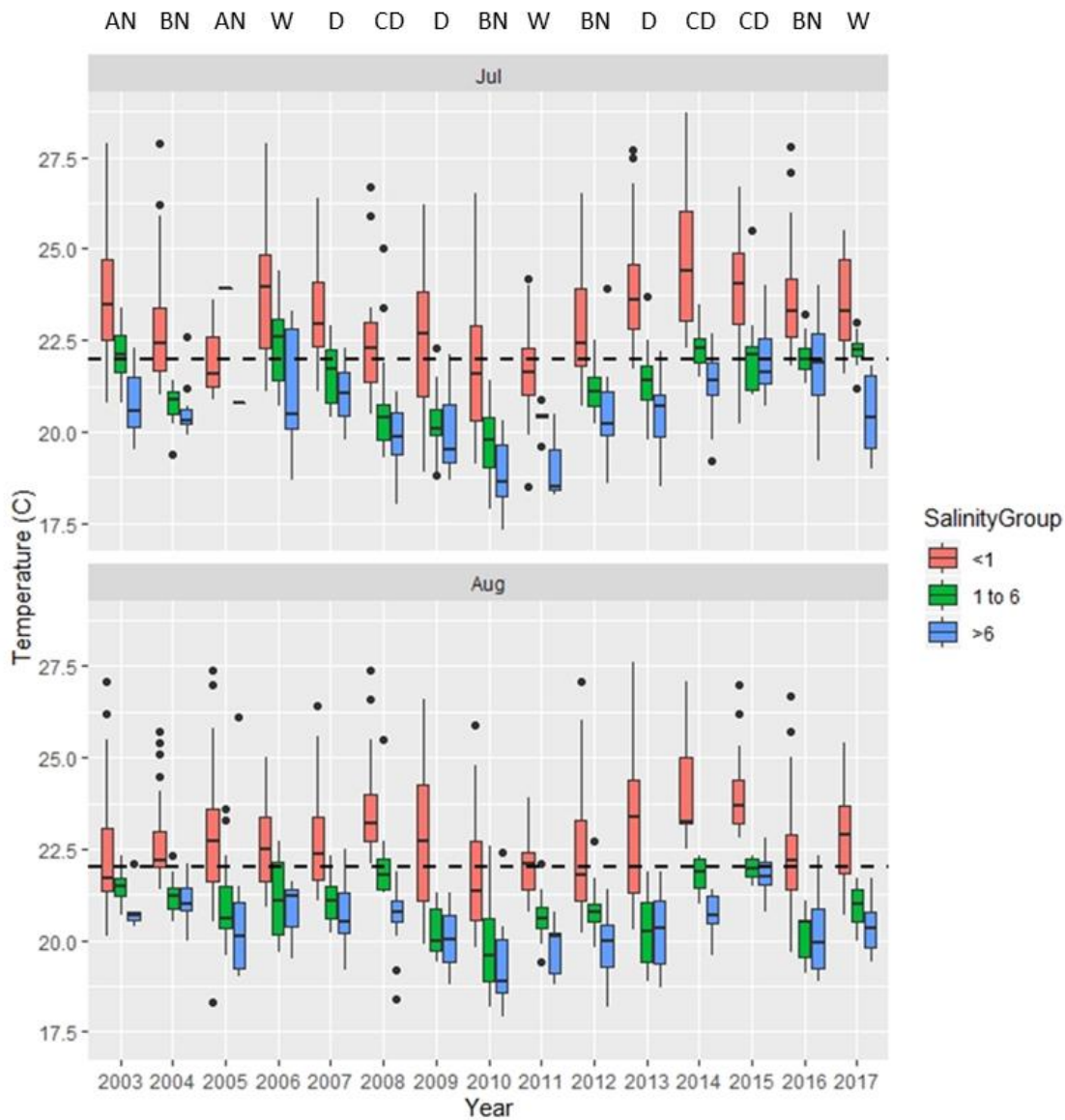


Figure 6. Water temperature at sites with salinity <1, 1-6, and ≤ 6 ppt, for July and August collected by CDFW [Summer Townet Survey](#) at index stations during 2003-2017. Water Year Type per Sacramento Valley Index across top of figure; Wet (W), Above Normal (AN), Below Normal (BN), Dry (D) and Critical (CD). For a description of the box plot see [geom boxplot documentation](#)

Available estimates of future air temperatures over the Delta have only been published for a few scenarios of climate change (Cloern et al. 2011). A relatively steady increase of about 0.14 to 0.42°C per decade is expected for annual mean air temperature, water temperature increases at a somewhat lower rate of 0.11 to 0.30°C per decade (Cloern et al. 2011). The extreme scenario considered by Cloern et al. (2011) is no longer considered extreme because indicators such as temperatures and sea levels are rising faster than predicted (i.e., CNRA 2018; NOAA 2021; Scanes et al. 2020).

In the upper SFE, the response of water temperatures to climate change has generally been explored with regard to metrics of water temperature associated with thresholds for fish, particularly Delta Smelt (Brown et al. 2013, 2016a). In general, greater warming is expected along the Sacramento River corridor and in the Cache Slough Complex (Figure 5). Warming occurs along the San Joaquin River corridor as well; however, these areas are already quite warm during the summer, so there is less of an increase expected. As SLR continues, both more saline and cooler waters will intrude farther into the Delta, aided by increases in tidal amplitude. Currently, thermal stratification occurs in Central and North Bay, enhanced by salinity stratification (Vroom et al. 2017). Modeling results indicate the thermal stratification in North Bay is not a significant contributor to temperature in the Delta, and it is unlikely that Delta water temperatures will be affected by intruding ocean water because the water will have time to equilibrate with the atmosphere before reaching the Delta (Vroom et al. 2017).

Sediment Supply

Transport of sediment from the upper watershed “sets the stage” for many important ecological processes. Accretion of transported sediment onto tidal wetlands helps those wetlands keep pace with SLR. Similarly, deposition of sediment on floodplains is necessary to preserve landforms subject to erosion by flood waters and to support succession of floodplain plant communities. Sediment deposition within aquatic habitats and floodplains is necessary to replace bed sediments that have eroded and moved downstream. Subsequent interactions of sediment supply, wind, and tidal currents determine turbidity.

Sediment supply and transport has been relatively well studied in the SFE because of a noticeable clearing trend in recent decades (Schoellhamer 2011). Historical trends in sediment supply and transport have changed over time. Hydraulic gold mining in the late 1800s and early 1900s resulted in a large increase in supply in the lower watersheds. This sediment supply has been moving out of the system for many years coincident with the construction of reservoirs, which reduced sediment inputs. The clearing of the Delta marked a transition from sediment transport limitation to upstream sediment supply limitation. Subsequent to this transition, sediment supply was relatively steady, with the caveat that wet years with high peak flows could cause step changes (Schoellhamer et al. 2013). Currently, upstream sediment supply consists of existing deposits within the active flood channels of rivers below large dams, small,

undammed drainages, and limited quantities of suspended sediments that can pass over or through dams during storms.

Based on the data available at the time, Cloern et al. (2011) concluded that climate change would have little effect on sediment supply. Their climate change projections (spanning 2010-2099) assumed either a steady state or a continuing 10% decline in suspended sediment concentration based on the studies available. Subsequent studies indicate that sediment loads to the SFE from the watershed have stabilized or may increase (Schoellhamer et al. 2013; Schoellhamer et al. 2018). A recent model developed by Stern et al. (2016) of hydrology and sediment supply for the watershed to address questions about effects of climate change suggests that the increased frequency of extreme flows expected with climate change (see earlier section on Hydrology, Stern et al. 2020) would likely result in increased sediment supply to SFE. Stern et al. (2020) found that ensemble averages for RCP 4.5 and RCP 8.5 scenarios showed average increases of +5% and +7% for suspended sediment concentration, and +39% and +69% for sediment loads, respectively, by end-of-century compared to the historical baseline. Uncertainty remains regarding future sediment supply. As mentioned, earlier studies predicted a minimal effect, or possible decrease of sediment supply with climate change (Cloern et al. 2011, Schoellhamer 2011, Schoellhamer et al. 2012). More recent research points to an increased sediment mobilization from expanded wildfire burns (Sankey et al. 2017) and more extreme events leading to higher streamflow, suspended sediment, and sediment discharge (Stern et al. 2016). The predicted increased frequencies of intense storms and flooding add concerns about infrastructure such as levees already in need of repair and reinforcement, and water quality since sediment can transport contaminants in agricultural runoff and mercury (Stern et al. 2020).

Stressors

Introduction

Considering trends in environmental drivers with climate change is useful; however, individual species and ecosystems are often affected by relatively short-term phenomena, such as heat waves, floods, and droughts. Here we consider how climate change might affect the occurrence of some of these stressors.

Temperature extremes

Water temperature substantially affects the physiology of fishes and other poikilothermic (i.e., “cold-blooded”) organisms. Species survive within a range of temperatures, with a smaller range of ideal temperatures where growth, survival, and other measures of individual and population performance are near optimal. In this context, whether a temperature extreme actually represents a stressor depends on the individual species being assessed. There is

substantial evidence that the current temperature regime can have negative effects on Delta Smelt growth and life cycle (Hobbs et al. 2019, FLOAT-MAST 2020) and that climate change will exacerbate these detrimental conditions (see Figure 5; Brown et al. 2013, 2016a, Moyle et al. 2016). Similarly, present and future water temperatures are likely to be detrimental for anadromous salmonids in upstream areas of the watershed (Johnson et al. 2016, Martin et al. 2020, Dusek Jennings and Hendrix 2020) and during migration through the Delta (Baker et al. 1995, Cloern et al. 2011).

Although episodic periods of high water temperatures have not been assessed for future scenarios, there is some information on air temperature heat waves. Hayhoe et al. (2004) examined heat wave days (3 or more consecutive days with temperature above 32°C) for 2 climate change models and 2 emissions pathways. Heat wave - days for Sacramento increased from a baseline of 58 to a range of 109-138 heat wave - days by the end of the century. Heat waves can be parameterized as increases in the maximum daily temperatures or as increases in the minimum daily temperatures (daily T_{\max} and T_{\min} exceeding their respective 95th percentile (p95) thresholds computed from the local daily historical data during May through September for the years 1950–1999). Both types of heat waves are expected to increase for the Central Valley and North Coast (Gershunov and Guirguis 2012). As the mean temperature increases with climate change, the baseline, or basis for defining extreme values changes. From an ecological perspective, assessments in terms of fixed baseline thresholds are more conservative since they do not assume an organism could adapt in response to rapid climate change.

Precipitation extremes

Floods and droughts are a dominant feature of California's climate. There is evidence in the paleoclimate record of both large floods and extended droughts in the SFE watershed exceeding those recorded by Europeans (Malamud-Roam et al. 2006, Brown et al. 2007). California's native fishes are well adapted for persisting through both large floods and persistent droughts (Moyle 2002, Herbold et al. 2018). California's aquatic species are also highly adapted to the seasonal patterns in precipitation and streamflow that create the natural hydrograph. Indeed, changes in the natural hydrograph resulting from human activities (e.g., (Brown and Bauer 2009, Zimmerman et al. 2018) are often cited as an important factor in the decline of native fishes (Moyle et al. 2011, Herbold et al. 2014). Restoration of more natural flows to restore natural ecological processes has been identified as one method to recover California's aquatic communities (Yarnell 2015, 2020). The changes in hydrology resulting from projected climate change are unlikely to have positive ecological outcomes.

Droughts have increased in frequency in California over the period 1995-2014 (Diffenbaugh et al. 2015). The increase was related more to increases in air temperature than changes in precipitation. For a given low precipitation year, the characterization of the year as a drought year or not, depended on whether air temperatures were above or below average. Given that a

trend of increasing air temperature has already been documented in California and that this trend is projected to continue (see above), the frequency of drought is expected to increase (Diffenbaugh et al. 2015). A large suite of climate change scenarios showed an increasing trend for extremely dry years but not for consecutive dry years (Swain et al. 2018). Low flows resulting from drought have long been recognized as a stress on fishes in the SFE and watershed. In droughts over the last 50 years, pelagic fishes have consistently declined during droughts, suggesting these fishes had low resistance to droughts (Mahardja et al. 2020). Although the pelagic fishes exhibited a considerable amount of resiliency and often rebounded in subsequent wet years, full recovery did not occur in all wet years following droughts, leading to permanently lower baseline numbers for some pelagic fishes. In contrast, littoral fishes seemed to be more resistant to drought and sometimes increased in occurrence during dry years (Mahardja et al. 2020).

Extremely wet years are also expected to increase in frequency and magnitude, and peak outflows are expected to occur earlier in the water year (see Hydrology section). The increasing frequency of extremely wet and extremely dry years leads to an increased frequency of rapid transitions from extremely dry to extremely wet conditions, what has been termed a ‘whiplash’ effect (Swain et al. 2018). Wet years are generally beneficial for native fishes; however, the beneficial aspects are largely associated with high flows recreating aspects of the natural flow regime. Frequent, large, episodic floods early in the season could disrupt species phenology (i.e., timing of life-cycle events) and could have other consequences, such as disturbance of riverine spawning grounds and sporadic rather than continuous inundation of floodplain habitats used for spawning and rearing. The eroding baseline for abundance of pelagic species (Mahardja et al. 2020) is likely to be exacerbated by more frequent transitions. Interactive effects of flow and water temperature are also to be expected, as not only flow, but also temperature determine the success and life-history strategies for many native fish species (Bush 2017). The last “good year” for Delta Smelt reproduction was 2011, which has been characterized as a cool, wet year. As climate change proceeds and water temperatures increase, the frequency of such events is likely to decline, similar to the decline in cool droughts described by Diffenbaugh et al. (2015).

Landscape Change

Introduction

Landscape change will occur from diverse, interacting drivers:

1. Climate change impacts including increased intensity and frequency of storms and droughts and shifts in sea level, wind intensity, and fog distributions.

2. Human reactions to climate change impacts including flood control efforts, migration to less affected areas, changes in land and water use as salinity changes, and other adaptations as we have seen in response to fire and drought.
3. Ongoing human efforts that alter land use that are partially independent of climate change, such as increased population density, increased reliance on local water supplies, and increased efforts to protect environmental values by habitat restoration and altered water management.
4. Ongoing changes to the California landscape that are at least somewhat independent of climate change such as, ever-changing contaminant composition, and increased numbers of introduced species.

This report focuses on only the first category, but future abundance and health of all the native and listed species we are concerned with are affected by all of the drivers.

Patch Number, Location, Size, Shape and Connectivity

The pre-Gold Rush Delta was a vast expanse of wetlands, including tidal marsh and floodplains penetrated by two main rivers and several smaller rivers and creeks (Whipple et al. 2012). Post-Gold-Rush development of the Delta transformed most of the flatlands into agricultural fields or human infrastructure. In particular, river channels were deepened and widened and connected to one another to produce an abundance of open water habitats edged by levees that isolated island interiors from the open water, even during most floods.

Tidal marshes are now a very small and fragmented part of the landscape. Smaller patches have much more edge relative to interior areas and are isolated from other such habitats, usually by considerable distances. Most areas that were allowed to remain as wetlands were in undesirable areas, usually because they were too prone to flooding, or were too small to support agriculture. Smaller habitat patches support smaller populations of the organisms that rely on them (Simberloff 1998). They often do not support the geomorphic processes of larger patches that result in channels, pannes, tussocks, and other aspects of habitat diversity that support a variety of organisms. Much effort is being invested in restoring marsh habitats, with the goal of 12,140 hectares (30,000 acres) being completed in the relatively near future. Most restored wetlands will be around the perimeter of the Delta, and few will be larger than 400 hectares (1,000 acres; EcoRestore 2021).

Floodplains were included in agricultural development during the Gold Rush, but the inability to keep them from flooding limited what could be grown on them and kept them more frequently connected to the rivers. After many failures to control flooding by building levees, the floodplains were incorporated into flood management (Kelley 1989). Three remnant floodplains are located in the northern Delta and retain much value to riverine species (Sommer et al.

2003). About 7,100 hectares (17,544 acres) of floodplains expansion or improvements are planned for the near future.

Channels and embayments are now the largest wildlife habitat in the Delta. Connections of formerly dendritic and blind channels have produced extreme connectivity among these formerly isolated habitats. The levees that protect the island interiors provide a substrate for edge species, which grow as narrow bands of aquatic plants at levee bases, and occasionally provide substrate for riparian or terrestrial species that grow in a narrow band above the water line. Most levees are topped with a road that allows for rapid dispersal of terrestrial predators (Frey and Conover 2006). Failed levees have produced shallow embayments within the Delta, particularly at Franks Tract, Big Break, and Mildred Island. Climate change is expected to produce more frequent and intense flood flows that may overtop and destroy some of these levees. Such destruction will produce additional shallow embayments, the location and size of which cannot be predicted. To some extent, these flooded islands will be less connected to each other than the other open water habitats because of remnant levees.

Site-level environmental change

Introduction

The location of a particular patch of habitat largely controls how climate change affects it. Most obviously, floodplains are adjacent to riverways and have some form of intermittent interconnection with the river. The flood-based nature of floodplains minimizes the impacts of sea level rise and salinity change but increases susceptibility to floods and droughts. Marsh habitat that is closer to the ocean is more susceptible to salinity change and impacts of greater tidal inundation than upstream sites. Similarly, open water and edge habitats are affected differently by climate change largely due to their location along the salinity gradient.

The physical formation of a site (e.g., elevation and materials that comprise it) controls the habitats and species that will be found within a site and how they will be affected by climate change.

Topography and elevation

The elevation of a site and its location along the salinity gradient determines the frequency and duration of tidal inundation. That frequency and duration of inundation is the primary determinant of wetland type and the plants and animals that will live there. Topography and elevation interact to determine spatial variation so that a site with topographic variety will support many more types of plants and animals than one with more invariable conditions over the tidal cycle (Morzaria-Luna et al. 2004, Larkin et al. 2008).

Most wetland plants are sensitive to the degree and duration of inundation. Floating and submerged forms require constant water presence to survive, while emergent forms are limited by the depths (and turbidities) that will allow them to grow out of the water and into the

sunlight (Schile et al. 2014). Woody riparian forms often tolerate occasional inundation, and some even require it for successful reproduction (Nichols and Viers 2017). A variety of herbaceous forms can be found only on high ground, above the usual floodplain or marshplain. Thus, sites with diverse topography are likely to support more diverse plant communities.

Topographical diversity also allows more diverse aquatic habitats. Brackish marshes that possess elevation gradients typically feature more salt-tolerant plant species (e.g., *Salicornia* spp.) at low elevations (Grewell et al. 2014). Many patches of wetland habitat that have maintained themselves in the Delta are small and have little topographic diversity. These patches are often simply swaths of one vegetation type that is best suited for that location; they generally support low abundances and diversities of fish. More topographic diversity leads to channels and pools, where some water may be retained throughout the tidal cycle. Such refugia are used by smaller fish to escape predation during low tides when they would otherwise be swept into the large channels where there are larger fish. Small channels also offer foraging opportunities for fish that are small enough to use them, thus reducing potential competition with larger fish (Colombano et al. 2021).

Substrate

As discussed above, sediment supply is not expected to decline with climate change and may even increase somewhat depending on the frequency and magnitude of storms (see Sediment Supply section and Stern et al. 2020). There may be site-level changes associated with topography and elevation or the presence of aquatic vegetation that might affect site-level distribution of different grain-sizes. For the purposes of the conceptual model, we assume no change in substrate quantity or quality in the upper SFE with the recognition that site-level changes in hydrodynamics related to landscape change (e.g., levee breaches or barrier installation) or aquatic vegetation would likely affect local distributions of different substrate particle sizes.

Salinity

As discussed earlier, projections of the effects of climate change on the salinity field are highly uncertain. Preventing salinity intrusion will be a primary goal of water managers responsible for exporting fresh water from the Delta for human uses. Therefore, it is likely that changes in operations and infrastructure will occur in the future that we cannot anticipate or include in current models.

MacWilliams and Gross (2010) explored the relationship between sea level rise and “X2,” which is the distance in kilometers from the Golden Gate Bridge to where the tidally averages salinity at the bottom is roughly 2 parts per thousand, making up the Low Salinity Zone. It is often used in ecosystem and species management context. They modeled Delta conditions during historical operations in 2002 with multiple levels of sea-level rise—allowing water quality in the

Delta to respond without new water operations intended to meet regulatory requirements. This study estimated that SLR of up to 140 cm could result in a median increase (eastward shift) of X2 of 7 km, or 7.3 km with a 5% increase in tidal amplitude (Figure 7; MacWilliams and Gross 2010). These changes in X2 could translate to minimal or substantial changes in the salinity field, depending on the level of SLR from the lowest (15 cm) modeled to the highest 140 cm (Figures 8a & b).

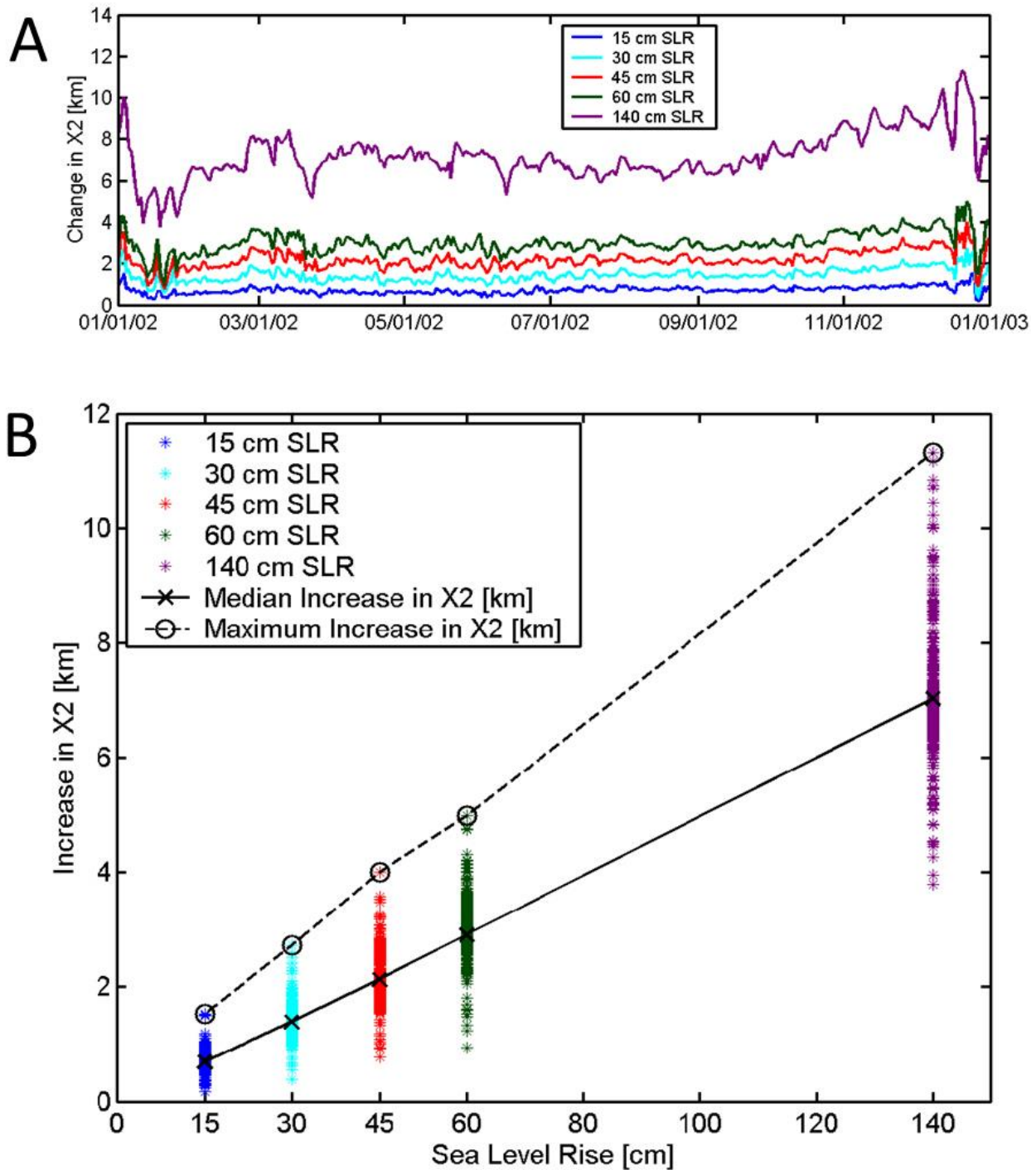


Figure 7. (A) Predicted change in X2 relative to the baseline scenario for the 15-cm, 30-cm, 45-cm, 60-cm, and 140-cm SLR scenarios; (B) Scatter plot of the predicted increase in X2 for each day during 2002 for each of the sea level rise scenarios; solid black line shows the median increase in X2 for each SLR scenario, and the dashed black line shows the maximum increase in X2 for each SLR scenario. From MacWilliams et al. (2016).

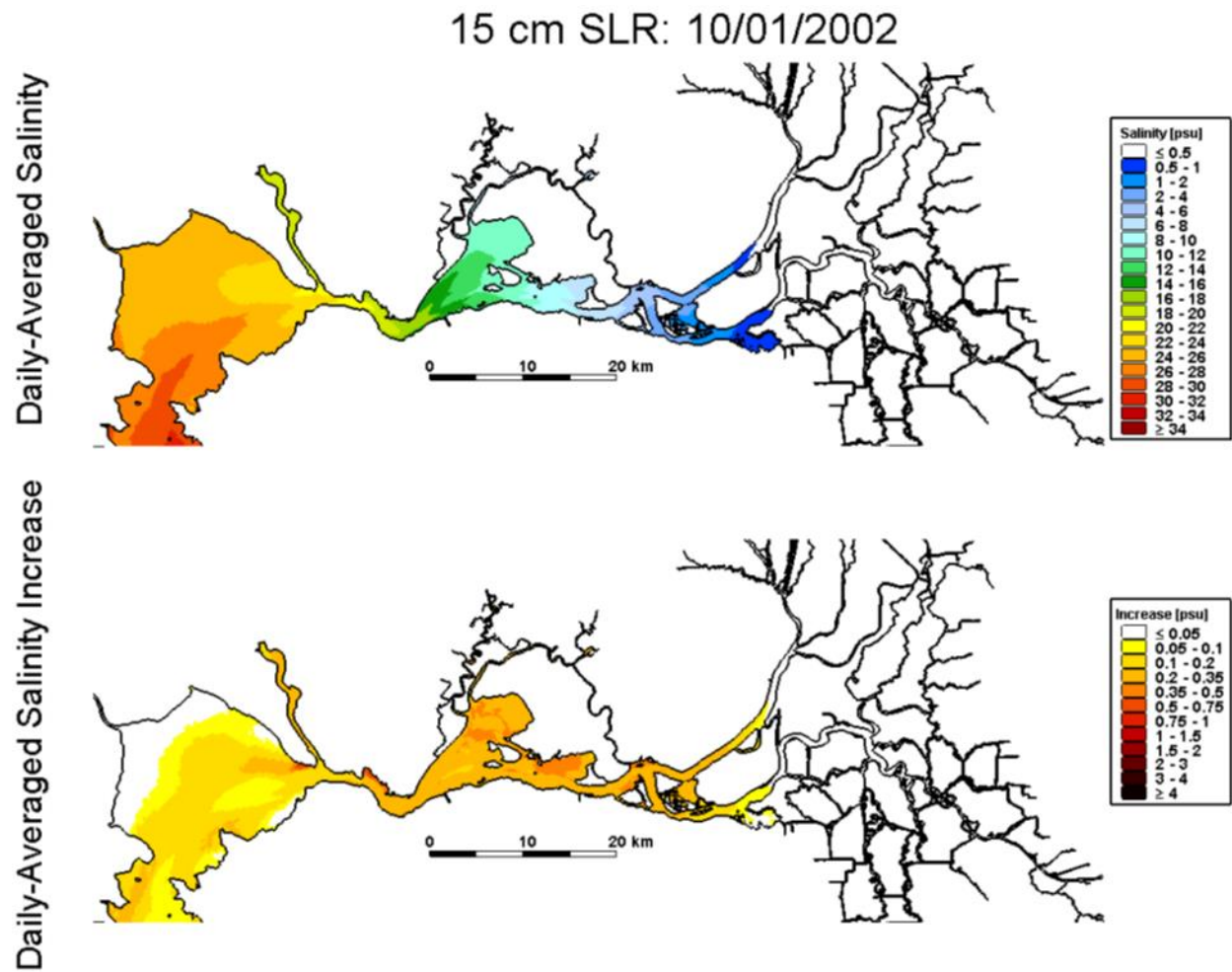


Figure 8a. Predicted daily averaged depth-average salinity on October 1, 2002, for the 15 cm SLR scenario (top); predicted increase in daily averaged depth-average salinity on October 1, 2002, relative to the Baseline (0 cm SLR) scenario for the 15 cm SLR scenario (bottom) (from MacWilliams and Gross 2010).

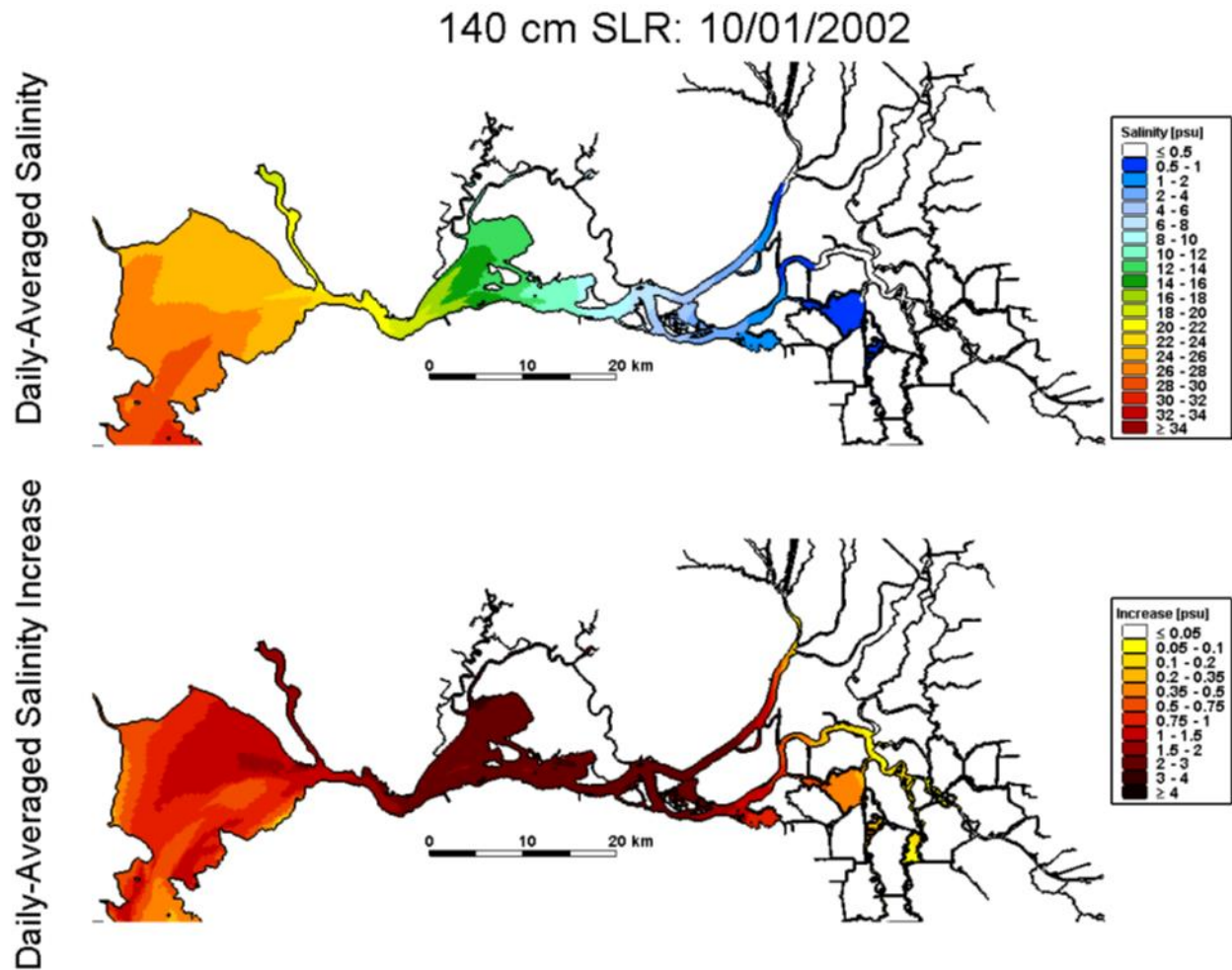


Figure 8b. Predicted daily averaged depth-average salinity on October 1, 2002, for the 140 cm SLR scenario (top); predicted increase in daily-averaged depth-average salinity on October 1, 2002, relative to the Baseline (0 cm SLR) scenario for the 140 cm SLR scenario (from MacWilliams and Gross 2010).

Turbidity

In addition to salinity gradients, estuaries often have turbidity gradients. An optical property of water, turbidity describes the loss of transparency due to scattering of light by suspended particles. In the upper SFE, turbidity is largely determined by the amount of suspended inorganic sediment in the water, although organic components can also play a role. Sediment particles are constantly deposited, eroded, and resuspended, and are transported into, within, and out of the SFE. The amount of sediment suspended in the water column depends on the available hydrodynamic energy, which determines transport capacity, and on the supply of erodible sediment in the SFE and suspended sediments from the watershed. In the upper SFE, the two main physical processes controlling turbidity are sediment transport and sediment resuspension. Winter turbidity may change in response to changes in timing of large storms that deliver suspended sediment from the watershed to the upper SFE. Turbidity may also

change in response to physical drivers of sediment resuspension within the upper SFE, such as changes in wind, especially in the summer and fall.

Suspended sediment is transported from the watershed into the upper SFE during high flows associated with winter and spring storm runoff (Schoellhamer et al. 2012). The first large storm of the rainy season often carries the highest concentrations of suspended sediment (locally known as “first flush”). Some portion of the transported sediment moves through the system to San Pablo and San Francisco Bay, and the remainder is stored within the system as bottom sediment. The first flush is a management concern because adult Delta Smelt preparing for spawning appear to avoid clear water, and the water in the southern Delta near the Central Valley Project (CVP) and State Water Project (SWP) pumps tend to be clear. Thus, first flush occurring earlier in the year or more sustained winter turbidity might result in fish closer to the export facilities (USFWS 2019). Current climate change scenarios show an average increase in suspended sediment concentrations (Stern et al. 2020), but the precise changes in timing of storms is uncertain; therefore, projecting changes in first flush conditions is problematic.

During the remainder of the year, turbidity is primarily dependent on interactions of stored bottom sediment with other environmental drivers (Schoellhamer et al. 2012). Water moving with the tides can resuspend fine sediments because of turbulence resulting from interactions between the bottom topography and water moving at high velocities. At a larger scale, irregularities in the bottom topography may define geographic regions of greater turbulence and greater turbidity. In the upper estuary, such regions occur at a large bathymetric sill between Carquinez Strait and Suisun Bay and at another location within Suisun Bay (Schoellhamer 2011). Sediments may also be resuspended by turbulence due to wind. Wind induced resuspension is mainly limited to areas with fine sediments on relatively shallow shoals as in the shallows of Suisun, Grizzly, and Honker Bays and Liberty Island (Ruhl and Schoellhamer 2004, Warner et al. 2004, Morgan-King and Schoellhamer 2013). Suspended sediment can also move upstream and concentrate in upstream areas by tidal pumping (producing a turbidity maximum where fresh water meets saltier bay waters). This is one mechanism that increases turbidity in the northern Delta (Morgan-King and Schoellhamer 2013). Turbidity can be reduced by aquatic vegetation, with submerged aquatic vegetation (SAV) responsible for up to a 70% decline in turbidity in the Delta from 2004-2008 (Hestir et al. 2013, 2016, Cloern & Jassby 2012, Jassby et al. 2002).

The several environmental drivers of turbidity make it difficult to predict site-level environmental change. SLR will increase water depths and may reduce wind-wave energy reaching the bottom of water column to resuspend fine sediments. The effect of climate change on turbidity will also depend on the effects of climate change on the abundance and distribution of aquatic vegetation. Submerged aquatic vegetation is an effective sediment trap contributing to reduced turbidity and reductions in sediment accretion on tidal wetlands in the

Delta (Drexler et al. 2021, Work et al. 2021). Areas that are currently turbid are likely to remain turbid due to the potential increase in sediment supply and Delta breezes in the absence of increased abundance of submerged aquatic vegetation.

Other Stressors

Secondary climate change effects

Ocean temperature

The ocean is expected to continue to warm and acidify, although the rates will vary regionally (Hoegh-Guldberg et al. 2014). Mean sea-surface temperature in 2090 is expected to be as much as 2.7°C warmer than in 1990, depending on future greenhouse gas emissions (Bopp et al. 2013). Sea surface temperatures are expected to be 1°C to 3°C higher by 2100 under RCP 8.5 than RCP 2.6 across most ocean sub-regions (Hoegh-Guldberg et al. 2014).

The California Current regions exhibited a significant rate of change in the average sea-surface temperature (SST; 0.12°C per decade) and the average temperature of the California Current warmed by 0.73°C from 1950 to 2009 and by 0.14-0.80°C from 1985 to 2007 (Demarcq 2009). The California Current is characterized by large-scale interannual and inter-decadal climate-ecosystem variability (Peterson and Schwing 2003, McGowan et al. 1998, Hare and Mantua 2000, Chavez et al. 2003, Checkley and Barth 2009) that make it difficult to isolate the effects of global change. During an El Niño, coastal upwelling is severely reduced, and ocean temperatures increase from California to Washington (Peterson and Schwing 2003, King et al. 2011). Inter-decadal variability in the California Current stems from variability in the Pacific-North America pattern (Overland et al. 2010), which is influenced by the Pacific Decadal Oscillation (PDO) (Mantua et al. 1997, Peterson and Schwing 2003) and the North Pacific Gyre Oscillation (NPGO) (Di Lorenzo et al. 2008). There is robust evidence that the California Current has experienced a decrease in the number of upwelling events but an increase in duration of individual events, resulting in an increase of the overall magnitude of upwelling events from 1967 to 2010 (Demarcq, 2009, Iles et al. 2012). This is consistent with expected climate-related changes yet remains complicated by the influence of decadal-scale variability (Iles et al. 2012). The high level of productivity in the California Current is a result of large-scale atmospheric pressure gradients and wind systems that blow surface waters offshore, leading to the upwelling of cold, nutrient-rich waters (Chavez and Messie 2009, Chavez et al. 2011). Upwelling stimulates primary production that is transferred to mid and upper trophic levels, resulting in substantial fish, seabird, and marine mammal populations off the California coast (Block et al. 2011). Species that use both the upper estuary and the near coast region seasonally benefit from the increase in productivity.

Upwelling waters are low in pH and high in CO₂ and are likely to continue to enhance changes in pH and CO₂ resulting from rising atmospheric CO₂ (Feely et al. 2008, Gruber, 2011). Upwelling

strength and temperature of coastal water is likely to increase (Bakun et al. 2015, Garcia-Reyes et al. 2015, Wang et al. 2015). Understanding how climate change will influence ocean upwelling is central to understanding ecosystems and resolving fishery responses (Hoegh-Guldberg et al. 2014).

Nearshore ocean conditions driven by large-scale oceanographic changes propagate into San Francisco Bay with subsequent effects on ecosystems, such as movement of planktonic species, and shift in species with salinity shifts from climatic variability (Cloern et al. 2007, Cloern et al. 2010, Feyrer et al. 2015). Therefore, it seems likely that changes in ocean conditions in response to climate change will affect San Francisco Bay. However, those conditions generally do not propagate into the upper estuary, which is dominated by conditions in the watershed that affect outflow through the estuary (Feyrer et al. 2015). Therefore, we do not consider ocean temperature and associated oceanographic factors to be an important driver of conditions in the upper SFE.

Water chemistry

Several aspects of ocean water quality are expected to change globally. Here we review information on dissolved CO₂ concentrations (i.e., ocean acidification), dissolved oxygen, and nutrients. Rising CO₂ concentrations in the atmosphere have caused increased concentrations of dissolved CO₂ in the upper waters of oceans (Watson et al. 2009). The increase in dissolved CO₂ results in ocean acidification (measured as declining pH), which drives a decline in both carbonate ion concentrations and calcium carbonate mineral saturation states for various carbonates (calcite, magnesium-calcite and aragonite; Zeebe and Westbroek 2003, Jiang et al. 2019). This makes it more difficult for marine taxa to generate and maintain calcified structures like shells and bony skeletons. Mean surface ocean pH has declined by more than 0.1 below the preindustrial average of 8.17. By 2100, pH is expected to decline by an additional 0.13-0.42 (Pörtner et al. 2014). Since the pH scale is logarithmic, each unit on the pH scale represents a tenfold change in acidity and represents a 30 percent increase in the relative acidity of ocean water. Increased acidity will be higher in coastal areas where eutrophication and coastal upwellings are an issue, with negative effects on many calcifying organisms (Davis et al. 2018, Wong et al. 2014) such as calcifying plankton, corals, mollusks, and crustaceans. Direct impacts on these ecosystem engineers will have large indirect impacts on food webs (Wootton et al. 2008).

Dissolved oxygen (DO) concentrations in the ocean are highly variable, and upwelled waters are less oxygenated than surface waters. Oxygen concentrations have undergone large and consistent decreases from 1984 to 2006 throughout the California Current, with the largest relative decreases occurring below the thermocline (21% at 300 m). The hypoxic boundary layer, or Oxygen Minimum Layer (<1.92 mg/L) has also shoaled by up to 90 m in some regions, reaching closer to the surface (Bograd et al., 2008). These changes are consistent with the

increased input of organic carbon into deeper layers from enhanced upwelling and productivity, which stimulates microbial activity and results in the drawdown of O₂ (Bakun et al. 2010, but see also McClatchie et al. 2010, Koslow et al. 2011). Although non-climate anthropogenic factors are responsible for virtually all hypoxia in estuaries and inner continental shelves, climate drivers such as ocean warming, altered hydrological cycles, coastal current shifts, and increases in upwellings may interact with eutrophication in coming decades (Rabalais et al. 2010, Meire et al. 2013).

There is little evidence that climate-driven changes in water chemistry have propagated into the SFE and had any effect on ecosystems. Long term observations from the estuary show little evidence of eutrophication or anoxia (Cloern and Jassby 2012, Cloern 2018) in recent decades, despite an increase in the concentrations of some nutrients (Cloern and Jassby 2012, Cloern 2018). This is not to say that climate change has had no effect on water quality, but estuaries are highly responsive to a wide range of climatic and anthropogenic forcings (Cloern et al. 2016). This makes it difficult to isolate a climate change signal; however, as climate change proceeds, such effects might emerge more clearly.

Resilience and Risk

The ability of a species to adapt to change is affected by many factors, but maybe most important to the native species of California is the severely reduced geographical ranges and therefore reduced abundances due to human impacts since the 1849 gold rush (Moyle 2002). Climate change is likely to interact with the traditional stressors on aquatic species and intensify them (Moyle et al. 2013).

Resilience of any species is a function of its life-history strategy, especially the interaction and nature of its mortality and fecundity patterns (Holling 1973). Ecologists have long used conceptual models for plants (Grime 1988, 1997) and fish (Winemiller and Rose 1992, Winemiller 2005) to predict species response to change by separating those who favor stable versus chaotic environments based on their life histories. Tolerant plant species thrive in stressful conditions, while competitive species flourish in a species-rich, stable environment, and ruderal species are weedy species that thrive in an environment with frequent disruptions (Grime 1988, 1997). For fish species, stable environments favor species with intense biotic interactions (predation, competition, parental care). Chaotic environments favor short lived, hardy species that reproduce early. Environments that are highly variable, but with conditions that recur reliably either seasonally or interannually, support long-lived hardy species (Winemiller and Rose 1992, Winemiller 2005). These categories are not mutually exclusive nor completely independent, but they help to identify which species are controlled by various environmental factors and how the species occupying a habitat can be expected to change as it is exposed to changing conditions, such as changes in climate.

California's Mediterranean climate yields a highly seasonal and highly variable hydrograph for the Sacramento and San Joaquin Rivers. Prior to the gold rush, the Delta was a vast wetland with diverse habitats (Whipple et al. 2012). High interannual variability in precipitation imposed large-scale variability in flows and inundation patterns. These environmental conditions favored species with high fecundity and/or high adult survivorship, like California's large minnows (Moyle 2002). Eight large rivers fed by springs and snowmelt provided high spawning-habitat stability supporting more of an equilibrium strategy of California's salmonids. During the last 170 years, levees, dams, and diversions provided environmental disruptions suited for opportunistic species with short generation times and tolerance for environmental disturbance. The impacts of climate change are expected to generally favor such opportunistic species as has been observed in the Colorado River (Olden et al. 2006).

The sensitivities of California freshwater fish and particularly the fishes of the San Francisco Bay Area to climate change were evaluated using a suite of life history parameters (Moyle et al. 2013, Quinones and Moyle 2014). All California fishes were evaluated as critically, highly, less, least vulnerable to risk, or likely to benefit. These sensitivities were evaluated against the expected impacts of climate change as well as the ongoing impacts of water and land management since the Gold Rush.

Stressful environments lead to high juvenile mortality, and the characteristic life-history strategy for survival includes high physiological tolerances, long life of survivors, and high fecundity. Most of the low-elevation freshwater environments in California are inherently stressful – streams dry out, temperatures are extreme within and across years, and salinity regimes vary across seasons and years. Most native cyprinids, as well as sturgeon, show remarkable longevity with periodic bouts of high reproduction.

Stable and productive environments foster life-histories that focus on competition. These life history strategies usually involve high specialization and lower fecundity, but with higher care for the young. Before dam construction, salmon enjoyed spawning grounds with the consistent cold-water flows off the Sierra Nevada and Mount Shasta and the high productivity of the nearshore ocean for maturation. At the other extreme, Delta Smelt and Tidewater Gobies (*Eucyclogobius newberryi*) are restricted to the interface of ocean and fresh water – an environment that may move but always exists in the estuary. Threespine Stickleback (*Gasterosteus aculeatus*) and Desert Pupfish (*Cyprinodon macularis*) are other examples of this specialist strategy. Interestingly, the wide array of Centrarchid and Ictalurid species in California reflect the evolution of these species in stable, productive environments east of the Rocky Mountains. Their limited dispersal abilities were overcome by railroads and shipping; their need for stable, lowland aquatic environments was provided by the dams that simultaneously blocked access to the high elevation cold, reliable flows for native salmonids.

Disturbed environments promote a weedy life history. Such species are usually short-lived, with good dispersal characteristics, and with little specialization to a particular food or environment. Inland Silversides (*Menidia beryllina*), Threadfin Shad (*Dorosoma petenense*), Shokihaze Gobies (*Tridentiger barbatus*), Mosquitofish (*Gambusia affinis*), and a host of other invasive plants and animals are examples of this strategy. Common Carp (*Cyprinus carpio*) and Goldfish (*Carassius auratus*) are longer-lived variants.

By assessing representative species of each of the three targeted ecosystems with this framework, we begin to predict how populations, communities and ecosystems in the Delta respond to climate change.

Species Characteristics

Life-history strategies

Aquatic species of the Delta cover a wide range of life-history strategies that tie them to the habitats they require. Many are very long-lived and wide ranging, like sturgeon, salmon, a number of cyprinids, and lampreys (*Entosphenus spp.*). Some are shorter-lived and more restricted in distribution, notably Delta Smelt. Species with longer lifespans can have extreme differences in life stages and in the timing and duration of those life stages such as lampreys and salmon; others change little after hatching, such as the cyprinids and sturgeon. However, even shorter-lived species can show strong developmental changes – notably Prickly Sculpin (*Cottus asper*) with their pelagic larvae and benthic adults. Some species show very little change in life history with growth, notably live-bearing Tule Perch (*Hysterocarpus traskii*) and nest-guarding Centrarchids. Species with more complex strategies are likely to be less resilient to climate change because they are exposed to more of its impacts through their life stages. Having varying life history strategies such as found in salmonids and Delta Smelt are considered to have a stabilizing effect on the population as a whole (Hilborn et al. 2003, Schindler et al. 2010, Hobbs et al. 2019) as different strategies will be more successful depending on the environmental conditions at the time.

For many invertebrates, rising temperatures favor smaller species with shorter generation times (Garzke et al. 2015, Rice et al. 2015) and can lead to declines in zooplankton biomass (Richardson et al. 2020). In the SFE, the small cyclopoid copepod, *Limnoithona tetraspina*, has dominated over the larger calanoid copepods in recent years (Bouley and Kimmerer 2006) and the smaller mysid *Hyperacanthomysis longirostris* is now more abundant than the larger *Neomysis mercedis* (Avila and Hartman 2020).

Phytoplankton

Phytoplankton are single-celled photosynthetic organisms. In the SFE, they primarily consist of bacteria, diatoms, dinoflagellates, chrysophytes, cryptophytes, and green algae. Phytoplankton biomass, commonly measured as chlorophyll *a* concentration, is closely linked to streamflow and residence time. Increased chlorophyll *a* concentrations can occur at low streamflows that allow phytoplankton to accumulate (Conomos et al. 1979, Cloern et al. 1985, Peterson et al. 1989, Lehman 1992, 1996, Jassby 2008). Smaller phytoplankton taxa typically form high concentrations in backwaters with long residence time, while large diatoms dominate fast-flowing areas (Lehman 2007, Stumpner et al. 2020). Toxic blooms of the cyanobacterium *Microcystis* began in 1999, and low streamflow and elevated water temperature are associated with cyanobacteria blooms and reduced diatoms within the Delta (Lehman et al. 2017, 2020b). Moderate streamflows flush phytoplankton from the Delta into Suisun Bay (Lehman 1996; Jassby 2008). However, phytoplankton biomass in Suisun Bay has been reduced since the mid-1980s by grazing of the invasive clam, *Potamocorbula amurensis*, which is effective at removing large diatoms in shallow water (Nichols et al. 1990, Alpine and Cloern 1992, Kimmerer 2004, Dugdale et al. 2016, Lucas et al. 2016).

Cyanobacteria HABs have increasingly become a concern as they are more frequent and negatively affect fish health (Acuña et al. 2012) and change species composition in the lower trophic levels of the food web (Lehman et al. 2010).

Vascular plants

Vascular plants in Delta waterways consist of floating aquatic vegetation (FAV) like invasive water hyacinth (*Eichhornia crassipes*), SAV like invasive Brazilian waterweed (*Egeria densa*), and emergent vegetation (EV) like native tules (*Schoenoplectus* spp. and *Schoenoplectus californicus*). Most invasive FAV and SAV are tropical species with high temperature tolerances and low salinity tolerances (Santos et al. 2011, Boyer and Sutula 2015); they thrive in the Delta's tidal lakes where water is shallow and sheltered by the surrounding remnant levees (Khanna et al. 2015, Kimmerer et al. 2019). Invasive aquatic vegetation species play a sizable role in the Delta by altering the physical and biotic environment of the ecosystem. They modify channel velocities, sediment flow, and water quality, and facilitate the spread of invasive fish species (Nehring and Kolthoff 2011, Conrad et al. 2016, Hestir et al. 2016, Tobias et al. 2019, Drexler et al. 2021). Extensive efforts to control the spread and reduce the persistence of *Egeria densa* and water hyacinth were mandated by the State of California in the late 1990s (Santos et al. 2009), but the weeds have generally continued to expand their ranges and abundance (Khanna et al. 2018). Higher winter flows can wash FAV out of the Delta and its abundance briefly declined after the high flows of 2017. SAV may be uprooted and washed out by high-velocity flows, but regenerates rapidly from segments and so can spread to new areas after fragments are transported by floodwaters (Ustin et al. 2014). Emergent vegetation such as tule

(*Schoenoplectus acutus* var. *occidentalis*), broadleaf cattail (*Typha latifolia*), California bulrush (*Schoenoplectus californicus*) and pickleweed (*Salicornia pacifica*; formerly *Salicornia virginica*) are the dominant vascular plant types in marshes, including saline marshes, but also make up fringing marshes along levees in the Delta.

Phenology

Shifts in phenology can cause a mismatch in hatching and feeding opportunities and play a role in trophic interactions both for aquatic and terrestrial species. Species may respond at different rates or to other factors that cause rising temperatures and decouple trophic links (Winder and Schindler 2004). Changes to sea temperature over recent decades have altered the phenology, or timing, of key life-history events such as plankton blooms, migratory patterns and spawning in fish and invertebrates (Hoegh-Guldberg et al. 2014). These phenological changes are due to a direct physiological response to temperature increases occurring earlier in the year. The peak abundance of zooplankton taxa in the upper SFE and Delta has shifted earlier by approximately 5 weeks in the past 40 years. This shift may have exacerbated food limitations for larval and juvenile delta smelt and contributed to their decline (Merz et al. 2016). Increased temperatures earlier in the year will likely cause this shift to continue. These shifts in coastal phytoplankton blooms may affect outmigrating fish species which have relied on such food sources during their outmigration (Winder and Schindler 2004). Terrestrial species such as birds nesting in the Arctic, some of which use the Delta as their winter habitat, migrate on a circadian rhythm. The arrival of spring has already shifted significantly in the Arctic, risking hatchlings to emerge after the peak insect period. This results in a diminished food supply for new hatchlings and less opportunity for adults and young to acquire energy reserves before the fall migration begins (Saalfeld & Lanctot 2017).

Physiology

Physiological differences across species expose different levels of sensitivity to climate change impacts. The ability of a species to acclimate or adapt to changing environmental conditions may play a large role in determining persistence during climate change. Many of the longer-lived fish species with greater differences in life-history stages show substantial changes in tolerance to different salinities and temperature between different life history stages (Sturrock 2019). Species with smaller differences in life-history stages, like Striped Bass, often show greater tolerance for rapid changes in temperature and/or salinity than longer lived species with more complex life histories (Moyle et al. 2013). In addition, short-lived, annually spawning species may be more vulnerable to demographic failures than long-lived species with more than one life-history strategy (Moyle 2002). Physiological impacts of increased temperature can be difficult to unravel; high temperatures are often also temperatures of fastest growth if food production is also high (Poletto et al. 2018). In the open waters of the Delta, food is often

limiting, and food limitation often alters physiological processes and reduces temperature and salinity tolerances (Komoroske et al. 2016, Poletto et al. 2018, Bennett 2005, Bennett et al. 2008). Different species have different phenological plasticity, but even within a species, variations exist. In a study of fall-run and winter-run Chinook Salmon from several hatcheries (north to south in the Central Valley), Zillig et al. (2020) found the ability to increase thermal tolerance varied significantly between native river systems. The variations necessary to adapt to climate change are decreasing because the overall genetic diversity in Central Valley Chinook Salmon has been greatly reduced (Meek et al. 2014, 2016)

Behavior

The behavior of species can greatly affect the risk posed by environmental changes. Striped Bass undergo seasonal migrations for spawning and wide-ranging travel in search of food. The seasonal migration and feeding movements make the Striped Bass flexible in the face of changing environmental conditions. Largemouth Bass in contrast, generally have small home ranges and so are more likely to be affected by localized changes in temperature or salinity. Salmonids make long migrations from freshwater natal areas, through the estuary to the ocean and back; they consequentially require a broader range of habitats. Because they experience climate change in each of their required habitats, they are at particular risk because changes in any of their required habitats may negatively impact the species. Shelton et al. (2020) modeled fall-run Chinook Salmon individuals using tagged fish from California to British Columbia during a 40-year period and found different stocks would seek out different sea surface temperatures. The fish are now responding to changes already taking place by seeking out areas where they were previously not found but now have optimal temperatures. This shift is not uniform in direction or magnitude. Alternatively, climate change impacts may alter the behavior of fish resulting in higher metabolism, more activity, and more exposure to predators (Davis et al. 2019). Increased activity and feeding by predators can pose increased risk to prey, altering the food web connections and survival of lower-trophic species such as smaller fishes and zooplankton.

Survival and Fecundity

Many fish show a positive relationship between survival and fecundity; fish that live longer generally produce more offspring, and the larger members of a population generally are the most fecund. Higher fecundity is often associated with a “periodic” strategy that is considered advantageous in predictable environmental patterns, and fish with higher fecundity might do better in longer lasting droughts. Lower fecundity is often associated with an “opportunistic” strategy that is considered advantageous in a less predictable environment; fish with lower fecundity may be less successful during an extended drought (Chessman 2013) but more successful during a period of “weather whiplash” (Swain et al. 2018). Higher fecundity is often associated with lower parental investment in offspring. This may result in offspring ill-prepared

for conditions in which the species did not evolve, especially if food supplies are limited. Climate change creates an increasingly environmentally stressful environment and may have a greater impact on species with this reproductive strategy. Short-lived, temperature-dependent spawners such as Delta Smelt may find themselves unable to grow large before maturity due to the combination of temperature stress during juvenile growth and an earlier spawning window due to increasing temperatures, especially if food supplies are limited. Because egg quality and quantity in Delta Smelt is size dependent, nutrition and growth of juveniles is important for fecundity (Brown et al. 2016a). Water quality combined with the invasion of *Potamocorbula amurensis* has led to food limitation in Delta Smelt, particularly in Suisun Bay where juvenile Delta Smelt sometimes rear (Hammock et al. 2015, 2016, Brown et al. 2016b).

Populations

Size, Distribution, and Isolation

Small populations are at greater risk of any disturbance than larger populations, but just as important is the scale of inter-generational population fluctuations. Large fluctuations introduce a greater risk of reaching zero abundance. For example, the abundance indices for Longfin Smelt show extreme year to year variance through the decades leading up to 2000 but have been on a low and downward trajectory since then (Moyle 2002, Sommer et al. 2007).

Population size and the total number of populations are important variables. For example, initial studies of steelhead (*Oncorhynchus mykiss*) estimated there were around 22 populations spawning in most streams flowing into the Central Valley and Suisun Bay with great variability in abundance. Now there are likely four populations, all at low abundance (NMFS 2014).

Greater geographic distribution of the populations comprising a species reduces the risk of extinction. Disturbances, catastrophes, or stressful conditions generally have a geographic boundary, so populations outside that area can help the species recover. The many populations of Fall-run Chinook Salmon spawn in most major streams of the Central Valley and suffered from the warm temperatures of the 2012-2016 drought, some faring better than others, further highlighting the importance of the portfolio effects for species (Satterthwaite & Carlson 2014; Shindler et al. 2010). Winter-run spawning occurs in only one location below Shasta Dam, which was one of the hardest hit areas and therefore much more impacted by the drought (Herbold et al. 2018, Phillis et al. 2018).

Population connectivity can also have important consequences for climate change effects. Isolated populations with low connectivity can limit the impacts of some stressors and help buffer the species overall. Introduction of new diseases or predators can be limited if populations are isolated from one another. The isolated populations of Desert Pupfish and Sacramento Perch (*Archoplites interruptus*) have kept those species from extinction, but they rely on human intervention to recolonize extirpated habitat (Black et al. 2016, Crain and Moyle

2011). Conversely, limited population connectivity can constrain the exchange of genotypes, limiting genetic diversity within populations, which may then reduce the potential for evolutionary adaptation to a changing climate. Over-connectivity can also hinder evolutionary adaptation when gene flow overpowers natural selection at the local scale (Simberloff & Cox 1987, Kawecki & Ebert 2004).

Density Dependence

Density dependence is seen in many species and can impact growth, behavior, and survival. If experiencing resource limitations, larger populations produce fewer recruits per adult than smaller populations. This can be because of adult competition for spawning substrates, juvenile competition for food or shelter, increased predator attraction, or inter-generational cannibalism. The overall effect of density dependence on population size is to reduce variability. Density dependence is often typified in California by reference to salmon, where later spawners destroy the redds of earlier spawners and limit the amount of spawning that a given stream will support (Fukushima et al. 1998, McNeil and Ahnell 1964). With a shorter spawning season for some runs due to a lack of runoff, this competition for spawning ground may intensify. However, some life-history strategies do not show increased recruitment at lower populations. Livebearers like Tule Perch have no spawning substrate limitation and little opportunity for competition between the juveniles that feed on benthic invertebrates that are seldom in limiting abundance (Baltz and Moyle 1982, Moyle and Baltz 1985). A contrary example is Sacramento Splittail, a highly fecund fish whose reproduction is tightly tied to floodplain inundation (Moyle et al. 2004). In years when the floodplain is inundated, recruitment is strong almost independent of how many adults are available, while in drier years spawning is limited regardless of how many adults may exist (Sommer et al. 2003). This species may benefit because more precipitation falling as rain will increase the likelihood of flooding in the bypasses, but the predicted long droughts will be severely detrimental because floodplains will not be available.

The impacts of climate change on density-dependent processes are diverse and difficult to anticipate. Reductions in suitable spawning sites will increase density-dependent effects, whereas reduced population sizes will tend to reduce density dependent effects. Climate change-induced reductions in suitable spawning habitat is likely the effect most specific to a particular species, site, and spawning period of Delta species.

Density dependence can involve negative feedback at very low abundances; this process is known as the Allee Effect (Stephens et al. 1999), which indicates reduced recruitment at low abundance levels because of the difficulty of spawning adults to find suitable mates at the right time and place. There have been concerns that Delta Smelt may be in this downward spiral (Bork et al. 2020).

Communities

Species richness and resilience

In general, more complex communities with many components and redundant trophic pathways are more resilient because if one species is affected by a change in one stressor, other species fill their trophic niche (Downing and Leibold 2010). This is less true for communities with changing composition where invasions of new species or extinctions of members keep trophic and other species interactions in flux. In such cases, species that may be better suited to a new climate can be disrupted by stresses associated with new predators or competitors, or the loss of a dominant food item. These unstable communities may lead to new associations with different sensitivities to subsequent climate change. Species such as freshwater mussels can be thought of as ecosystem engineers, providing habitat, organic matter, and nutrients to primary producers and grazing consumers. The optimal temperature varies according to mussel species, and species composition therefore has a significant influence on primary production in different temperature regimes. The biodiversity effect can therefore extend across trophic levels when shifts occur (Spooner et al. 2012).

Disease and parasites

Warmer temperatures can stress species, make species more susceptible to disease, and increase the virulence of the pathogens (Dietrich et al. 2014, Richter et al. 2005). The Central Valley currently lacks a disease monitoring program, but recognizing the impacts that higher temperatures and lower flows have on disease prevalence and recommendations for how to initiate such an effort for salmonids in particular came out of a 2018 Delta Science Program workshop (Lehman et al. 2020a). Similarly, reduction of the area of habitat as salinity or temperatures change can crowd individuals into the remaining suitable habitat and thereby promote the transmission of disease and parasites.

Ecosystems

Complexity, Connectivity, and Redundancy

In general, more complex ecosystems with many component habitats are more resilient because if conditions in one habitat become unsuitable, other habitats may offer refugia (Strum et al. 2017, Colombano et al. 2021). The value of alternative and multiple habitats requires connectivity so species can access refugia or other habitats they require. Redundancy in habitat types greatly increases value and accessibility of the habitat to species that require them. The interconnectedness of estuaries also allows for smaller changes to have a cascading impact on communities in the estuary, moving through several trophic levels. One such example is the invasion of *Potamocorbula amurensis*, which was first found in the estuary in 1986 and had expanded its range into Suisun Marsh by 1988 (Carlton et al. 1990). In part due to year-round reproduction, the population of overbite clams grew quickly (Parchaso and Thompson 2002, Thompson and Parchaso 2012, Baumsteiger et al. 2017), and their efficient filtering capability

was responsible for a sharp decline in phytoplankton biomass, altering the food webs and reducing the abundance of pelagic fish (Greene et al. 2011, Sommer et al. 2007, Kimmerer 2006).

Conclusions

Estuaries are highly variable places and will continue to be so as climate change continues. This variability is also seen in the changes expected in each habitat and the responses by the species living there. For example, increased salinity, both measured as water quality and increased inland reach, is a concern for tidal marshes and decreased habitat area for freshwater species but will not be a concern for floodplains. The continued existence of current tidal marsh will depend largely on the amount of sediment delivered from the atmospheric rivers and the salinity tolerance of the vegetation. The open water habitat will continue to provide a salinity gradient, though shifting inland. This will affect some, but not all species, expanding habitat for some, while shrinking it for others. The littoral areas (or edge of the open water) will continue to undergo large fluxes in salinity with the daily tides, extending the salt water farther inland as sea level rises.

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Chapter 2: Open Water and Climate Change

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Introduction

Estuaries are generally exposed to multiple anthropogenic impacts, including hydrological and morphological modifications, habitat loss, introduced species, and contaminants (Lotze et al. 2006). Given the worldwide uptrends in climate change, species extinctions, human population, water use, and development pressures (Vörösmarty et al. 2010; Walters et al. 2013; Liu et al. 2018), maintaining and improving ecosystem health of estuaries and preserving native species that inhabit them have become increasingly challenging. The San Francisco Estuary (the estuary), which includes the San Francisco Bay, Suisun Marsh, and the Sacramento-San Joaquin Delta (Delta), has also been altered considerably since the mid-19th century and faces similar conservation challenges. What was once a habitat mosaic largely dominated by tidal wetlands and floodplains has undergone large-scale conversion into levee-protected agricultural tracts, surrounded mostly by open water. These landscape-level changes, along with alteration to the natural hydrograph, flow, and the introduction of non-native species, have resulted in an open water ecosystem that is vastly different from pre-gold rush era.

To understand the potential impacts of climate change, it is important to consider the variety of ecosystems that are encompassed within this open-water category. Aquatic areas in the upper estuary now primarily consist of subtidal, open water that has been, and will be in the foreseeable future, managed as a freshwater system (Whipple et al. 2012) (Figure 1). Open water ecosystem in the Delta consists mostly of diked channels with shallow water edge habitat at levee margins. Large areas of shallow water habitat (i.e., tidal lakes such as Franks Tract) are also present within the Delta due to unrepaired levee failures. Open waters in the lower parts of estuary (Suisun Bay, Suisun Marsh, and San Pablo Bay) are often influenced by ocean conditions and experience a wider range of salinity from freshwater to brackish. Aquatic communities array themselves along the salinity gradient of the estuary (Bollens et al. 2014; Feyrer et al. 2015; Castillo 2019), so, the communities that occupy the lower estuary are also more variable than those in the upper estuary. Although subtidal channel networks can be found in Suisun Marsh, the majority of open water ecosystem downstream of the Delta consists of deep channels surrounded by vast expanses of shallow bays.

The upper estuary marks the transition from brackish water to freshwater and is strongly influenced by water management operations (Moyle et al. 2010). Multiple fish species of interest depend on the open waters of the upper estuary for migration routes, nursery areas, or permanent habitat (Hobbs et al. 2017). Steep declines in the abundance of native and introduced pelagic species of the upper estuary have been reported since the mid-20th century (e.g., Thomson et al. 2010; Castillo et al. 2018; Polansky et al. 2019), which led to the listing of some species as threatened or endangered and to increased research into the environmental drivers responsible for these declines. The combined effects of climate change and direct anthropogenic impacts pose conservation challenges in aquatic systems globally (Vörösmarty et

al. 2010; Komoroske et al. 2014; Robins et al. 2016; Scanes et al. 2020), and they could increase the potential for additional non-native species invasions and ecological shifts (Winder and Jassby 2011).

The vulnerability of estuaries and estuarine-dependent species to climate change has been inferred from literature reviews (e.g., Kimmerer and Weaver 2013) and by downscaling modeled climate scenarios (e.g., Cloern and Jassby 2012). In the upper estuary, climate change, through its influence on multiple environmental aspects, is expected to produce a very different ecosystem by mid 21st-century. Although climate change is considered among the most predictable influences on the future trajectory for the open waters of the upper estuary (Kimmerer 2004), determining the extent of ecological impacts due to climate change is difficult due to the complexity of interactions among multiple abiotic and biotic processes.

Nevertheless, climate change is expected to greatly alter the structure and function of estuarine communities through its influence on multiple ecosystem drivers, including:

- Increased frequency of high inflow in wet or above average water years. Runoff from the Sierra Nevada is shifting from spring to winter, increasing the likely frequency of winter floods if reservoir capacity is reached earlier (NRC 2010).
- Higher drought severity. Extreme droughts are more likely in California (Pathak et al. 2018) under climate change projections in the estuary (Knowles and Cronkite-Ratcliff 2018).
- Trends of increasing water temperature across most months in the upper estuary over the past 50 years (Bashevkin et al. 2021), and projected increase in air temperature (Knowles and Cronkite-Ratcliff 2018) which could result in an even warmer estuary given the strong positive relationship between air and water temperatures (Wagner et al. 2011).
- Significantly increased rate of sea level rise due to melting of ice fields and thermal expansion of oceans resulting from warming is projected for the estuary, which would lead to encroachment of salinity field into the upper portion of the estuary and potentially increase subtidal open water. The baseline for the period 1900-2008 in San Francisco Bay is 1.92 mm yr⁻¹ (National Research Council 2012).

Regional and local ecological studies evaluating climate change effects in the estuary have largely focused on fishes (but see Delta Stewardship Council 2021). Climate change vulnerability assessments have been done on freshwater fishes in California (Moyle et al. 2013); fishes of the San Francisco Bay area (Quiñones and Moyle 2014); and estuarine-dependent fishes in the upper estuary (Feyrer et al. 2011; Brown et al. 2013; Jeffries et al. 2016). While these studies have revealed high risk for many species, no ecosystem level conceptual models in the upper estuary exist to inform researchers and managers on the likely complex responses to climate change at individual, population, community, and ecosystem levels. Hence, there is a critical

need to develop a conceptual model to evaluate the emergent climate change responses at multiple levels of biological organization within the upper estuary's open water. Here we describe a conceptual model of the climate change drivers we expect to affect the open water ecosystem. We highlight the likely impacts on the taxa that occupy this ecosystem based on the latest research findings. We selected several representative ecological functional groups to evaluate how a broad range of organisms at the different trophic levels, including native and introduced taxa, are likely to respond to climate change.

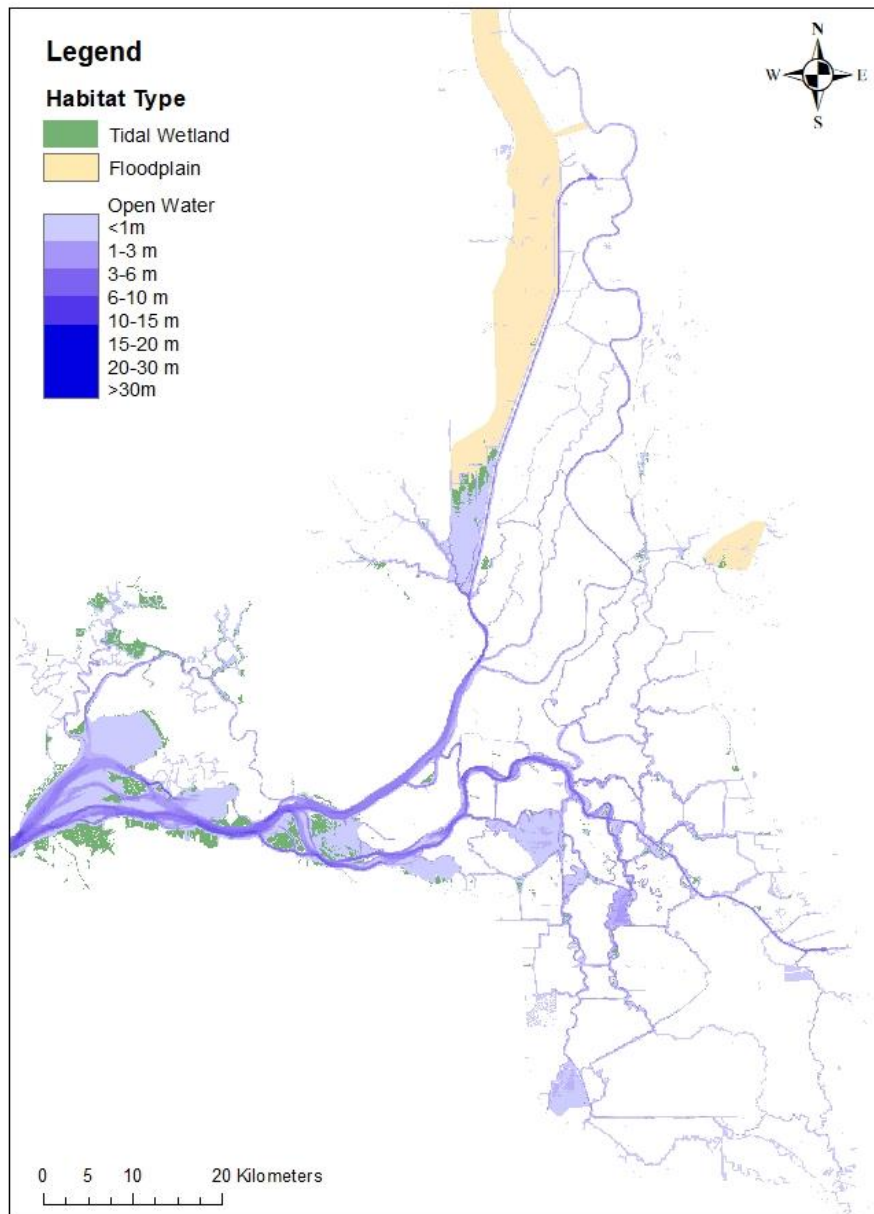


Figure 1. Map of ecosystem types in the Upper San Francisco Estuary. Open water areas are in blue. Delta floodplain and tidal wetlands come from SFEI’s Delta Landscape Scenario Planning tool (SFEI 2020). Suisun habitat types come from the California Aquatic Resource Inventory (SFEI 2017). Bathymetry comes from Fregoso et al. (2017).

Definition of Open Water

In this article, we define the open water ecosystem as any subtidal aquatic environment in the estuary (Figure 2). The geographical extent of this open water ecosystem for the purpose of this article range from western portion of Suisun Bay near Carquinez Strait to the lower Sacramento and San Joaquin Rivers (Figure 1). Whereas much of the tidal wetlands and floodplains in the estuary have been lost since the mid-19th century, the area of open water has essentially doubled over this timespan (Robinson et al. 2014; Cloern et al. 2021). Today, it encompasses a wide variety of sub-ecosystem types and taxa, which we discuss briefly below.

The deep, pelagic open water areas of the estuary have received the most research over the past sixty years. Here, freshwater flow interacts with tidal currents and wind, producing a dynamic ecosystem that varies within a day, as well as across months and years.

Hydrodynamics of the estuary's open water are also highly influenced by anthropogenic controls, because the amount and timing of freshwater inflow into the estuary is controlled by the existing water conveyance infrastructure and environmental policies (e.g., reservoir releases, amount of water export out of the Delta, etc.). Most studies on this ecosystem have largely revolved around the Delta Smelt (*Hypomesus transpacificus*), a California-endemic pelagic fish species listed under the federal and state Endangered Species Act with a sizeable role in the estuary's management.

Historically, the estuary's open waters have been largely unvegetated and therefore dependent on phytoplankton for primary productivity. The system has undergone extensive changes since the gold rush of 1849. A couple of notable events occurred in more recent times. One was the introduction of the overbite clam *Potamocorbula amurensis* in 1987 that led to consistently lower abundance of many phytoplankton and zooplankton species (Kimmerer et al. 1994; Lehman 2000a). Another large shift in the pelagic community occurred around 2002, when Delta Smelt, along with a few other pelagic fish species and invertebrates, suffered a collapse in numbers (dubbed the Pelagic Organism Decline (POD) (Cloern 2007; Sommer et al. 2007; Mac Nally et al. 2010; Thomson et al. 2010).

The open water ecosystem of the estuary consists of two fairly distinct regions: the channels of the Delta and the bays downstream. The vast, tidally-influenced, interconnected channels network of the Delta are managed to be fresh year-round, regardless of water year types (i.e., wet or dry). Therefore, it is occupied by more freshwater-oriented zooplankton and resident fish species, most of which are not native to the estuary. The central and southern portions of the Delta are heavily influenced by the large water export facilities in the southwestern corner of the Delta; these facilities and the greatly reduced inflows from San Joaquin River often cause reverse (i.e. upstream) net flow within the channels. In contrast, the bays downstream of the confluence between Sacramento and San Joaquin Rivers (including parts of the Suisun Marsh) tend to have variable salinities and a complex bathymetry. They are inhabited by more mobile

species that either move with the salinity field (e.g. Delta Smelt), are salinity tolerant (e.g. Pacific Staghorn Sculpin *Leptocottus armatus*), or use the estuary as a migratory pathway (e.g., salmon and sturgeon) (Feyrer et al. 2015). The salinity field of the estuary is indexed by “X2”, the distance in kilometers from the Golden Gate Bridge to where the tidally-averaged salinity at the bottom is roughly 2 parts per thousand (the low salinity zone, LSZ). For most seasons and years, the LSZ is between Carquinez Strait (X2 = 55) and the Delta confluence (X2=85).

While pelagic productivity has declined in the bays and channels over the years (Kimmerer et al. 1994; Mac Nally et al. 2010; Thomson et al. 2010), productivity in the shallow, open water within the Delta appears to have increased and now plays a larger role in the food web of the upper estuary. Submerged and floating aquatic vegetation (SAV and FAV, respectively) have become more widely distributed over the past few decades and the abundances of non-native fishes associated with these vegetations have increased (Brown and Michniuk 2007; Conrad et al. 2016; Mahardja et al. 2017; Ta et al. 2017). The shallow open water ecosystem of the Delta differs in several ways from the historical tidal marshes and floodplains. We refer to this novel environment as “littoral habitat”, which we specifically define as open waters less than 3 meters in depth at mean water level (Figures 1, 2). Therefore, “littoral habitat” includes the tidal lakes of the Delta (e.g., Franks Tract, Liberty Island), as well as the edge habitats that surround the Delta’s network of open water channels and the bays downstream. We do not categorize the extended shallows of Suisun and Grizzly Bays as “littoral” because they are not edge habitat and remain largely unvegetated. Our definition of littoral habitat encompasses a variety of edge microhabitats such as rip-rap banks, sandy beaches, fringing emergent vegetation, and woody debris; however, detailed discussion of these microhabitats is beyond the scope of our document.

Littoral habitat has aided the establishment of many invasive species that played prominent roles in changing the conditions of the upper estuary (Conrad et al. 2016; Hestir et al. 2016). In contrast to the historical tidal marshes, this novel environment lacks dendritic channels and is less dominated by emergent vegetation (though some emergent vegetation may form fringes on the edges of channels). Non-native SAV species dominate the littoral habitat of the Delta and serve as a food source for the non-native fishes often associated with this habitat (Young et al. 2020). The POD in the early 2000s seems to have resulted in a corresponding increase in non-native littoral fish species (Mahardja et al. 2017). However, the young of native species of high management importance such as Chinook Salmon (*Oncorhynchus tshawytscha*) also utilize this habitat as they migrate through the Delta (Brandes and McLain 2001).

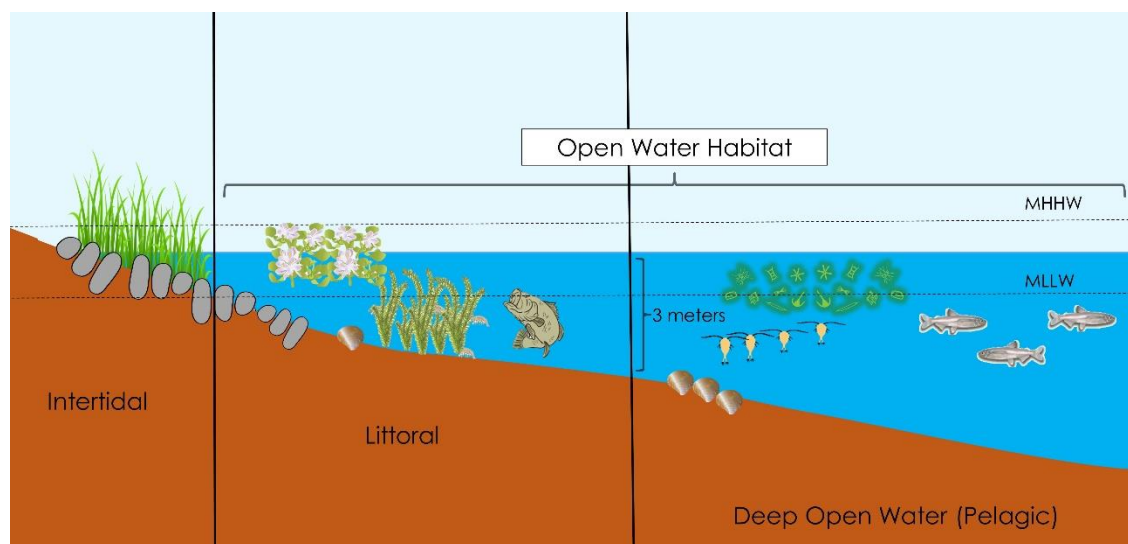


Figure 2. Diagram of the open water ecosystem as defined in this document. MHHW: Mean higher high water level, MLLW: Mean lower low water level.

Conceptual Model Framework

We followed the conceptual model framework in Chapter 1, where the scope progressively narrows down from large-scale climate change impacts to the impacts on functional groups or taxa that occur in the open water (Figure 3). We put broad climate change processes expected to impact the estuary into context of open water ecosystem and how management actions affect these changes, demonstrated by the arrows in Figure 3. We focus on environmental factors we deem more important to the estuary's open waters. Aspects or traits of species within the functional groups that may impact their resilience to climate change impacts are summarized in the bottom-most box of the conceptual model. Because open water ecosystem makes up the majority of the estuary and covers a wide geographical extent, we noted two major dynamic components of the ecosystem that determine the species composition and distribution of functional groups using double-pointed arrows: salinity and depth. We also highlight the potential future trajectories for several key species of high management interest.

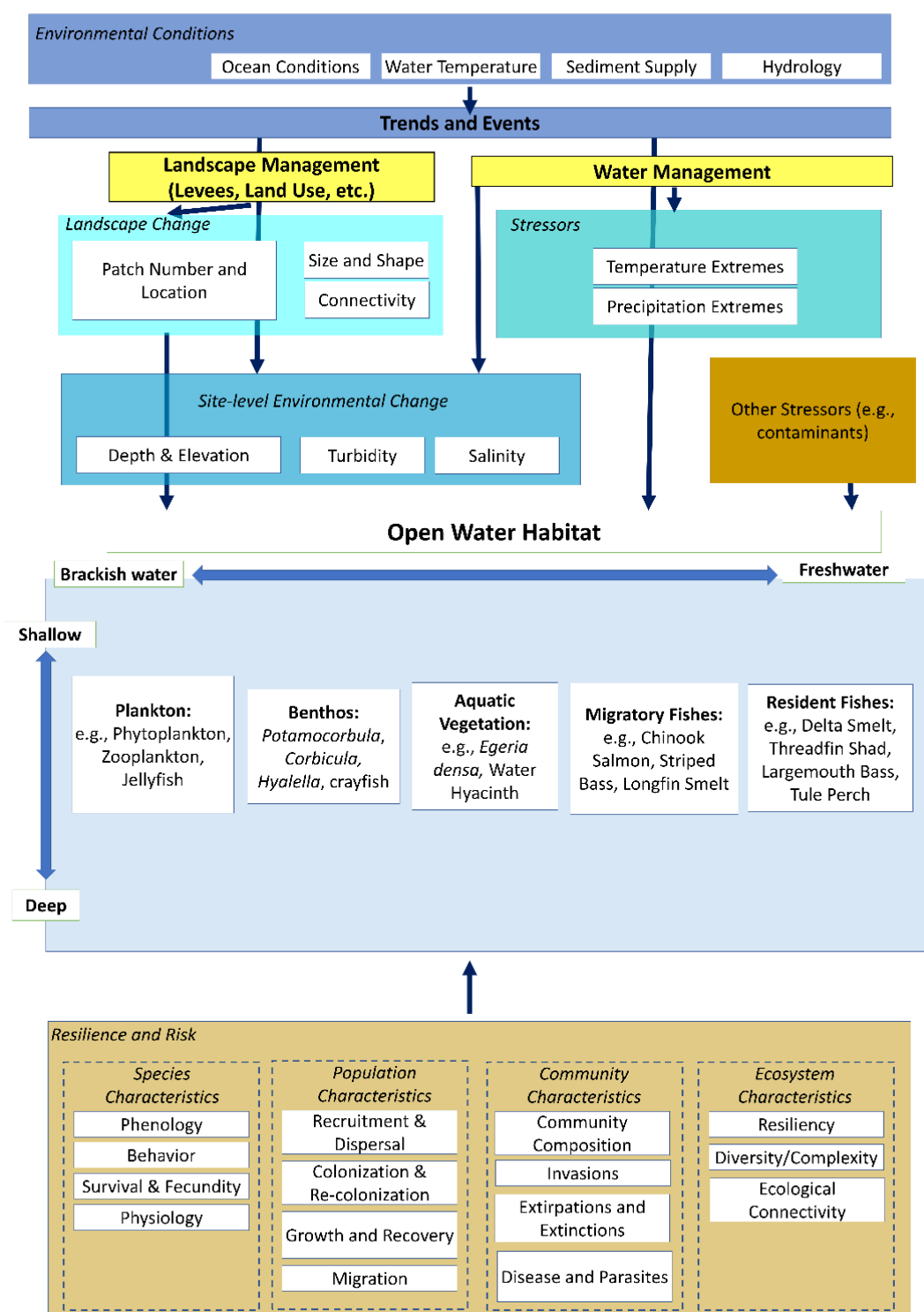


Figure 3. Model diagram for climate change impacts on the open water ecosystem of the upper San Francisco Estuary

Environmental Conditions

Water Temperature

Atmospheric warming leads to increased water temperature, because water and air temperature are closely linked in the estuary (Cloern et al. 2011; Wagner et al. 2011). However, towards the seaward portion of the estuary ocean conditions will influence water temperature relative to local atmospheric conditions (Dettinger et al. 2016). Expansive shallow water areas such as Grizzly Bay, Honker Bay, and the various tidal lakes within the Delta, are likely to be more responsive to air temperature than the network of deep channels and main rivers in the upper estuary (Shellenbarger and Schoellhamer 2011). The southern portion of the Delta tends to be warmer on average than the north Delta or the bays downstream, which may inhibit cold-water species from thriving in this area. Although thermal stratification, where the water is cooler towards the bottom of the water column, can occur in the estuary, it occurs more often towards the bays and is largely absent from the Delta (Vroom et al. 2017).

Sediment Supply

Sediment affects turbidity in open-water areas and may decrease the depth of the littoral area as sediment accumulates. Over the past few decades, there has been a trend of declining turbidity in the estuary as the erodible sediment pool has become depleted (Kimmerer 2004; Wright and Schoellhamer 2004; Schoellhamer 2011). However, uncertainty remains on how climate change will affect sediment supply in the estuary. While some studies predict that sediment supply will stabilize or decrease (Cloern et al. 2011; Hestir et al. 2013; Schoellhamer et al. 2013, 2018), a recent study indicates that increased frequency of extreme flow events may lead to increased sediment transport and supply into the estuary (Stern et al. 2020).

Hydrology

Climate models predict that there will be an increased frequency of both extremely dry and wet years in California (Swain et al. 2018). In addition, snowmelt peak will arrive earlier, and the rainy season will be truncated, resulting in shorter, flashier wet seasons and a more prolonged dry season (Dettinger et al. 2016). Already, over the last six decades the autumn precipitation is delayed by 27 days on average (Luković et al. 2021). The shift in precipitation patterns may adversely affect the phenology of species as well. For example, predation on juvenile Chinook Salmon may occur more frequently due to increased overlap in timing with spawning migration of Striped Bass (Goertler et al. 2021). Sea level rise and higher frequency of droughts are expected to bring higher salinity waters more often into the shoals in Suisun, Honker, and Grizzly Bays. Open-water ecosystem within the Delta would remain mostly fresh due to California water management. Unplanned levee breaches may occur more often, as continued subsidence, sea level rise, and increased flow variability add pressure to the existing network of levees in the Delta (Bates and Lund 2013). Littoral and open water areas will expand if

additional Delta islands are flooded and left unrepaired, though this depends on the water level and island elevation. Certain islands, if left flooded, may become tidal lakes that are too deep for SAV and not ideal for FAV.

Trends and Events

Landscape Change

Open water ecosystem can be divided into four subcategories: the brackish habitats that exist downstream of the Delta (e.g., Honker Bay, Grizzly Bay, Montezuma Slough), the freshwater tidal lakes that exist due to permanent flooding of subsided islands, the edge habitats that are found within the network of channels of the Delta, and the deep shipping and water management channels of Suisun Bay and the Sacramento and San-Joaquin Rivers.

It is uncertain how future shoal accretion rates will change while sea level rises, making it difficult to predict how the subtidal shallow-water habitats around Honker and Grizzly Bays will change in depth and salinity. Sea level rise will also affect the freshwater littoral habitats of the Delta as the overall depth of tidal lakes may increase and edge shallow-water habitat may become more constricted. The tidal lakes of the Delta can be thought of as “patches” of littoral habitat and they may increase in number and connectivity if additional Delta islands become permanently flooded. Most islands in the Delta are below sea level (Lund et al. 2008) and their levees are under increasing pressure from land subsidence, sea level rise, and more frequent high flow events. Therefore, levee breaches may be more likely as climate change progresses. The unpredictability of levee failures, how they will interact with sea level rise, and uncertainties surrounding management response preclude us from anticipating the size, shape, and connectivity of these littoral habitat “patches.” Some of the deeper islands within the Delta, if flooded, will produce deep open-water habitat rather than shallow, vegetation-filled lakes, while the flooding of shallower tracts may produce marsh habitat (addressed in the Tidal Marsh model).

Stressors

Temperature and Precipitation Extremes

Although mean precipitation under climate change is not expected to change significantly (Swain et al. 2018), the frequency of very wet and very dry years will increase, while the frequency of average years will decrease. The result will be more frequent extreme wet-dry swings, sometimes referred to as “precipitation whiplash” (Swain et al. 2016, 2018; Persad et al. 2020). Species will have a shorter recovery period due to these quickly shifting extremes, which may cause long term decline in population abundances. This precipitation whiplash, combined with the increase of precipitation as rain instead of snow, will make attempts at

managing upstream flows and water temperatures for listed native species increasingly challenging (Zarri et al. 2019).

The annual mean temperature in California has already increased by 2° C and temperatures will continue to increase. The number of days of extreme heat are also expected to increase (Bedsworth et al. 2018). Shallow, littoral habitats may see an increase in temperature due to the higher overnight lows reducing opportunities for cooling. Deeper water may provide thermal refugia in some locations, however the estuary is generally well-mixed, with little difference between surface and bottom temperature (Vroom et al. 2017). As climate change progresses it will be important for littoral species to be able to move among littoral habitat patches, making it important they are spaced to allow for inter-patch movement. This may allow escape from stressful conditions caused by high temperature or unfavorable salinity or turbidity conditions. Ecological connectivity also allows the recolonization of suitable habitats where a subpopulation has become extirpated by a weather event.

Site-level Environmental Change

The Delta of today contains an 1,800 km long levee system which means that most of the littoral zone consists of rip-rapped levee banks. Between these rip-rapped banks, the deep open-water habitat consists of channels that are often dredged for ship passage. On the other side of these levees is deeply subsided land with a surface elevation 3-7.6 m (10-25 ft) below mean sea level (Mount and Twiss 2005). Deeper subsidence increases the risk of levee failure, and failure of highly subsided islands would create deeper open water habitat.

Turbidity is affected by the amount of sediment flowing into the Delta from the watershed (see Sediment Supply, above), and the amount of hydrodynamic energy (flow) present to suspend the available material (Schoellhamer et al. 2012). With climate change fewer, but more powerful storms are predicted to occur, changing the frequency and amount of sediment transport and thereby the turbidity in the Delta (Swain et al. 2018; Stern et al. 2020). During most of the year, turbidity is caused by resuspension of bottom sediments by tidal action in deeper areas or wind waves in the shallower areas. Sea level rise will increase the water depth and may therefore decrease resuspension of bottom sediment. A decline in wind speed has been observed from 1995-2015, which caused a reduction in turbidity (Bever et al. 2018), but sediment loading may increase with an increase in storms (Stern et al. 2020). The interaction of these two factors makes the future of turbidity in the estuary difficult to predict.

As the sea level rises, salt water will more frequently intrude into the shoals of Suisun Bay, Suisun Marsh, and the Delta. To protect water quality for in-Delta use, exports, and the Delta ecosystem, more freshwater will be needed from the watershed to “push” saltwater into the bay and keep the Delta fresh. This is mandated under the current X2 standard (set by D1641, see above) which requires X2 from February to June to be maintained 64 – 81 km from the

Golden Gate Bridge. Greater use of freshwater to comply with the X2 standard will reduce the ability to meet temperature goals below dams and carryover storage for future needs.

Water and Landscape Management

The Delta is a complex socio-ecological system. Therefore, forecasting the state of the system under various climate change scenarios involves not only predicting the impact of increased temperature, changes in precipitation, and extreme events, on the ecosystems, but also predicting society's response to these changes. While in this report we assume management of the system to remain the same, we list the most relevant issues for water and land management that could occur in response to climate change.

Much of the littoral zone in the current Delta is dominated by armored levee banks. Some levee setback/restoration projects have been completed or are underway, increasing the amount of shallow-water habitat at the edge of the major channels. These projects are designed to create habitat for fish and wildlife, as well as increase flood resiliency (Smith et al. 2017). If successful, more of these projects may occur in the future.

Levees in the Delta are not uniform in their maintenance status or value. Some are federally-maintained flood control project levees, and will almost certainly be invested in for many years (Suddeth et al. 2010). Other levees are less well-maintained and may be allowed to fail if the cost of maintenance outweighs the benefits (Suddeth et al. 2010; Deverel et al. 2016). Because many of these levees surround highly subsidized islands, new levee failures will result in more shallow tidal lakes similar to Franks Tract, Mildred Island, or Liberty Island (Mount and Twiss 2005). Increases to flooded area could also increase salinity intrusion and decrease tidal range.

Sea level rise and changes to runoff patterns may increase salinity intrusion (MacWilliams et al. 2016). Water management will most likely attempt to offset this salinity intrusion by increasing outflow during the summer, operating the Suisun Marsh Salinity Control Gates (Sommer et al. 2020), and emplacing new temporary or permanent barriers (as seen during 2016; Kimmerer et al. 2019). Changes in the structure of the Delta can also affect the degree of salinity intrusion; the proposed redesign of Franks Tract includes elements to reduce salinity intrusion.

The other major management action in response to impacts of climate change will be vegetation management. Submerged and floating vegetation communities may change in distribution and community composition as climate change progresses, but vegetation management by the California State Parks Division of Boating and Waterways will also work to adapt control techniques to keep waterways free of invasive plants as much as possible. Current control practices mainly consist of spraying of herbicides. Floating vegetation is treated with glyphosate and 2,4-D; submerged vegetation is controlled with Fluridone (DBW 2018). However, recent analyses have shown Fluridone to be ineffective in the tidal waters of the

Delta (Rasmussen et al. 2020), so exploration of new control techniques, such as physical methods and biological controls (DBW 2018; Conrad et al. 2020), may be needed.

Functional Groups

We are focusing on five functional groups of organisms that inhabit the estuary's open water: aquatic vegetation, plankton, benthos, resident fishes, and migratory fishes. Plankton, including both phytoplankton and zooplankton, form the foundation of the pelagic open water food web. Phytoplankton are the primary organic matter source in the open water (Jassby and Cloern 2000; Cloern et al. 2016). Meanwhile, towards the littoral habitat, today's trophic pathway relies more on submerged and floating aquatic vegetation which has become much more prevalent in the Delta in the past two decades (Howe and Simenstad 2011; Khanna et al. 2015; Schroeter et al. 2015). The benthos includes mostly invertebrates and algae that are found more towards the bottom, as well as epiphytic algae. Fishes generally feed at higher trophic levels and are more mobile than the invertebrates of the estuary. Fishes move between habitats (e.g., tidal marsh, pelagic vs. littoral zone, etc.) more readily and therefore utilize different organic matter sources (Young et al. 2020). We divide fishes into two functional groups: resident and migratory, because anadromous species, travel long distances and are affected by climate change in the estuary, ocean, and upstream riverine systems.

We provide an overview of each functional group's status in the estuary and qualitative predictions of how they are likely to respond to the various effects of climate change. A summary of these expected responses is shown in Table 1. This evaluation helps identify knowledge gaps that prevent qualitative assessment and key uncertainties regarding the open water ecosystem. In the case of functional groups that utilize habitats other than open waters in the upper estuary, inferences are based on reviews for those habitats whenever possible. Because of the conceptual and qualitative nature of these predictions, no attempt will be made to downscale responses for particular end points based on the Intergovernmental Panel on Climate Change Assessment Report (e.g., by mid- or end of the century).

Table 1. Predicted qualitative responses of functional groups and taxa to climate change forcing on abiotic factors (water temperature, salinity, droughts, and floods). This summary table is not meant to capture every scenario and assumes the absence of management intervention.

Functional Group	Taxon or Species	Increased temperature	Greater saltwater intrusion	Increased frequency of droughts	Increased frequency of floods
Aquatic Vegetation	Overall	May increase prevalence of aquatic vegetation	SAV may shift towards <i>Stuckenia</i> spp. if Delta becomes more saline	May increase prevalence of aquatic vegetation	Unclear. Additional studies needed.
Aquatic Vegetation	Brazilian Waterweed (<i>Egeria densa</i>)	Likely to remain stable but may be detrimental to the species	Little impact if Delta remains mostly fresh, may have more truncated distribution otherwise	Increased prevalence	May be relatively unaffected or decline due to high flows. Additional studies needed.
Aquatic Vegetation	Water Hyacinth and Water Primrose	May benefit	Little impact if Delta remains mostly fresh, may have more truncated distribution otherwise	Increased prevalence	Increased distribution due to dispersal or displacement to unsuitable habitat (depending on flow levels). Impacts on growth and abundance unclear.
Aquatic Vegetation	<i>Stuckenia</i> spp.	Likely to remain stable but may be detrimental to the species	Little impact if Delta remains mostly fresh, may increase prevalence otherwise	Unclear. More information needed.	Unclear. More information needed.
Plankton	Phytoplankton	May increase or decrease biomass depending on	Communities will move with the salinity field	May cause local increase in biomass	Increase in some diatoms and green algae

		severity and temperature patterns, phenological shift			
Plankton	Zooplankton	Smaller body size may be favored, phenology may shift	Communities will move with the salinity field	Invasive species may become even more prevalent, or new invasions may occur	Unclear. More information needed.
Plankton	Harmful algal bloom (HAB)	Increased prevalence	Likely decreased prevalence, though may depend on species	Increased prevalence	Likely decreased prevalence
Benthos	Benthic and epiphytic algae	May increase productivity, but more studies needed	Unclear. More information needed.	Unclear. More information needed.	Unclear. More information needed.
Benthos	Epibenthic and epiphytic invertebrates	Dominant taxa may be relatively unaffected, but more studies needed.	Unclear. More information needed.	Unclear. More information needed.	Unclear. More information needed.
Benthos	Crayfish	Likely to be relatively unaffected, may benefit certain species	Unclear. More information needed.	Unclear. More information needed.	Unclear. More information needed.
Benthos	Benthic invertebrates (other)	Likely would change species composition and increase grazing rate	More truncated distribution for the tidal freshwater species, increased prevalence of brackish-water species	Unclear. More information needed.	Unclear. More information needed.

Benthos	Overbite clam (<i>Potamocorbula amurensis</i>)	Likely to be relatively unaffected or remain stable	Shift upstream	Likely to shift distribution but remain stable	Likely to shift distribution but remain stable
Benthos	Asian clam (<i>Corbicula fluminea</i>)	Likely to be relatively unaffected or remain stable	Shift upstream	Detrimental to the species	Likely to benefit the species
Resident Fishes	Overall	Largely detrimental for native fishes, beneficial for most non-natives	Truncated habitat for some native & non-native, otherwise little to no impact	Detrimental or unclear for native fishes, unclear or beneficial for non-natives	Largely beneficial for native fishes, detrimental for most non-natives
Resident Fishes	Largemouth Bass	Likely to be relatively unaffected or remain stable	Little impact if Delta remains fresh	Little impact, more studies needed	Little impact, more studies needed
Resident Fishes	Mississippi Silverside	Likely to be relatively unaffected or remain stable	Likely to be relatively unaffected or remain stable	Likely to benefit the species	Likely to be detrimental to the species
Resident Fishes	Tule Perch	Likely to be relatively unaffected or remain stable	Little impact if Delta remains fresh	Unclear. More information needed.	Unclear. More information needed.
Resident Fishes	Delta Smelt	Lower survival, truncated spawning event	Higher osmoregulatory cost, reduction of freshwater spawning and rearing areas	Detrimental to the species	Likely to benefit the species

Resident Fishes	Wakasagi	Unclear. More information needed.	Reduction of freshwater spawning areas	Unclear. More information needed.	Could increase immigration from reservoirs. More information needed.
Resident Fishes	Threadfin Shad	Little to no impact	Truncated habitat due to preference for freshwater	Likely to be detrimental to the species	Likely to benefit the species
Migratory Fishes	Overall	Likely to be detrimental to most species	Reduction in rearing habitat for some species and/or mismatch in phenologies	Species-dependent	Species-dependent
Migratory Fishes	Chinook	Likely to be detrimental to the species	Unclear. More information needed.	Detrimental to the species	Generally beneficial to the species, but may be harmful under certain conditions
Migratory Fishes	Striped Bass	Likely to be relatively unaffected, may increase consumption	Shifts in available nursery habitat	Unclear. More information needed.	May delay spawning migration upriver.
Migratory Fishes	Longfin Smelt	Lower survival	Reduction of spawning areas in freshwater	Detrimental to the species	Likely to benefit the species

Aquatic Vegetation

Aquatic vegetation plays a key role in the food web of the estuary and alters the physical habitat in open waters (Yarrow et al. 2009; Brown et al. 2016a; Hestir et al. 2016; Tobias et al. 2019). Unlike planktonic primary producers, aquatic vegetation provides structural complexity and substrate for epiphytic algae and invertebrates (Schultz and Dibble 2012; Young et al. 2020). Aquatic vegetation also provides spawning habitat and foraging opportunity for the estuary's fishes (Grimaldo et al. 2009b; Ferrari et al. 2014; Conrad et al. 2016).

Status

Aquatic vegetation (floating [FAV], submersed [SAV], and emergent [EAV]) grows mostly in the littoral zone of the estuary. FAV has unlimited access to water, light, and atmospheric carbon dioxide, but is generally limited to slower-moving water (Ta et al. 2017). In contrast, SAV is often limited by lower levels of light and carbon dioxide and tends to be found in areas with higher water velocity relative to FAV. EAV occurs along the nearshore edge; common species include the native tules (*Schoenoplectus* spp.), cattails (*Typha* spp.), and the invasive common reed (*Phragmites australis*). FAV in the Delta is largely composed of water hyacinth (*Eichhornia crassipes*) and water primrose (*Ludwigia* spp.), both invasive species. The SAV community is dominated by the Brazilian waterweed (*Egeria densa*), although the introduced water milfoil (*Myriophyllum spicatum*) has recently increased in coverage (Table 2, Khanna et al. 2015, 2018). The estuary's bays are mostly devoid of vegetation, but more salinity-tolerant species such as the native SAV *Stuckenia pectinata* are present in the shallow margins (Boyer and Sutula 2015).

Table 2. Summary of status and relative cover of SAV species in the Delta from 2019 (unpublished data from Shruti Khanna).

Common name (Scientific name)	Status (year of invasion in the Delta)	Relative cover of species in 2019
SAV species		
Brazilian waterweed (<i>Egeria densa</i>)	Non-native (1946)	51.9%
Watermilfoil (<i>Myriophyllum spicatum</i>)	Non-native (1979)	12.6%
Fanwort (<i>Cabomba caroliniana</i>)	Non-native (1980)	6.7%
Curly leaf pondweed (<i>Potamogeton crispus</i>)	Non-native (1946)	3.0%
Waterthyme (<i>Hydrilla verticillata</i>)	Non-native (1976 upstream of Delta)	0%*
Coontail (<i>Ceratophyllum demersum</i>)	Native	13.4%
Sago pondweed (<i>Stuckenia pectinata</i>)	Native	4.0%
American pondweed (<i>Potamogeton nodosus</i>)	Native	< 1%
Richardson's Pondweed (<i>Potamogeton richardsonii</i>)	Native	4.0%
Waterweed (<i>Elodea canadensis</i>)	Native	3.2%

Historical data on the composition and extent of aquatic vegetation is limited, but recent evidence suggests that invasive floating and submerged aquatic vegetation have become dominant over the years despite control efforts (Ta et al. 2017; Kimmerer et al. 2019). Coverage of both FAV and SAV in the Delta increased substantially between 2004 and 2014, with water hyacinth, water primrose, and Brazilian waterweed being the dominant species (Khanna et al. 2015; Ta et al. 2017). Both of these vegetation types appear to thrive in the Delta's tidal lakes where water is generally shallow and sheltered by the surrounding remnant levees (Khanna et al. 2015; Kimmerer et al. 2019). Invasive aquatic vegetation species play a sizable role in the Delta by altering the physical and biotic environment of the ecosystem. They modify channel velocities and water quality, and facilitate the spread of invasive fish species (Nehring and Kolthoff 2011; Conrad et al. 2016; Hestir et al. 2016; Tobias et al. 2019; Drexler et al. 2021). Extensive efforts to control the spread and reduce the persistence of *Egeria densa* and water hyacinth were mandated by the State of California in the late 1990s (Santos et al. 2009).

Response to Climate Change

Climate change impacts will likely further increase the prevalence of invasive aquatic vegetation in the estuary. Warmer temperatures, reduced frequency of frost, and increased frequency of drought events may benefit invasive species such as water primrose, water hyacinth, and Brazilian waterweed (Santos et al. 2011; Boyer and Sutula 2015). In contrast, increased frequency of flood events and higher winter flows could have a negative effect on the FAV by washing the plants out of the Delta. SAV may be uprooted and washed out by high-velocity flows (Ustin et al. 2014). Drought-related increase in salinity seemed to have little impact on most invasive aquatic vegetation species in the Delta (Kimmerer et al. 2019). However, salinity intrusion due to sea level rise may potentially lead to a shift towards more salinity-tolerant native species such as *Stuckenia* spp (Borgnis and Boyer 2016). The overall trajectories of FAV and SAV communities are highly uncertain because new species can be introduced into the estuary and significantly alter the aquatic plant species dynamics. Alligatorweed (*Alternanthera philoxeroides*), a species native to South America, was found in the Delta in 2017 (CDFW 2018), and there are indications that another new SAV species has been introduced into the Delta in the past few years (Shruti Khanna, personal communications). Below we offer more detailed information on potential climate change impacts for three problematic invasive species that have become dominant forces within the Delta: water hyacinth, water primrose, and Brazilian waterweed, as well as one native genus that is somewhat common in the more saline waters downstream of the Delta, *Stuckenia* spp.

Water Hyacinth and Water Primrose

Status

Water hyacinth, *Eichhornia crassipes*, is an exotic floating macrophyte native to the Amazon River basin. Its introduction to the Delta dates back to 1904 (Bock 1968); it has spread throughout the Delta and has become an influential component of the littoral plant community. Water hyacinth surface coverage in the Delta peaks in the late fall following the summer growing season and dips in the winter and early spring when plants lose leaf density due to cold stress (Spencer and Ksander 2005; Kriticos and Brunel 2016). Water hyacinth has numerous ecological impacts, including lowering dissolved oxygen concentration and turbidity (Tobias et al. 2019). Water hyacinth alters the invertebrate prey assemblage for littoral fish species (Toft et al. 2003).

Water primrose in the Delta consists of two species: *Ludwigia peploides* and *Ludwigia grandiflora* (Okada et al. 2009). Both species originate from South America, but while their distribution is rather limited in their native range, they often rapidly spread in new environments and thus are considered to be some of the most invasive plants in the world (Lambert et al. 2010; Nehring and Kolthoff 2011). Unlike water hyacinth, water primrose are generally rooted to the soil and form floating, dense canopies that extend several meters into channels from the shore (Khanna et al. 2018). Water primrose can increase sedimentation (reduce turbidity), their decaying mats can deoxygenate water, and provide habitat for West Nile virus-carrying mosquitoes (Meisler 2009; Nehring and Kolthoff 2011; Khanna et al. 2018). Between 2004 and 2016, water primrose cover in the Delta has increased fourfold (Khanna et al. 2018). Today, water primrose has the highest cover in the Delta out of all the FAV species, though they seem to be more common in tidal marsh than open water. Given the high growth rate and extent of water primrose and water hyacinth in the Delta, eradication is not currently feasible, and managers focus primarily on mitigating its impacts to navigation and critical infrastructure through biological and chemical control (DBW 2018).

Response to Climate Change

Water hyacinth and water primrose are likely to increase in coverage in freshwater areas of the Delta in response to climate change impacts. The population expansion of water hyacinth and water primrose concurrent with temperature increases in Delta since the late 20th century suggest that these species may already be responding to climate change in the estuary. If adequate nutrient levels are available, higher air and water temperatures are likely to increase water hyacinth growth rates during the summer and reduce cold stress and freezing, thus extending the growing period during wintertime (Spencer and Ksander 2005; Ustin et al. 2014; Kriticos and Brunel 2016). Similarly, water primrose are not likely to experience negative impacts from increasingly warm temperatures (Ta et al. 2017). Flooding during the winter and

spring would likely break apart FAV patches and increase the dispersal rate of water primrose (Gillard et al. 2017). If water primrose and water hyacinth patches increase in size and abundance during the summer and fall, they could be increasingly problematic for navigation and critical infrastructure during these wet years. However, if flows are very high, they could transport water hyacinth downstream where habitat is less suitable. A possible counter-acting force to the increased growth of water hyacinth are biological control agents (e.g., the weevil *Neochetina eichhorniae*) that are currently believed to be limited by cool winter temperatures (Reddy et al. 2019). As air and water temperatures increase, the effectiveness of these water hyacinth control agents could increase and be a valuable tool for resource managers. In addition, water hyacinth does not grow in brackish water (Muramoto et al. 1991), so areas of the lower Delta that increase in salinity will likely see a reduction in water hyacinth. However, encroaching salinity may not impact water primrose to the same extent as water hyacinth. Water primrose can better tolerate high flow, tidal and wave action, and higher salinity relative to water hyacinth (Ta et al. 2017).

Brazilian Waterweed

Status

Brazilian Waterweed, *Egeria densa*, is a submerged aquatic plant from South America. Due to its popularity in the aquarium trade and its invasiveness, this species has proliferated in many temperate littoral habitats throughout the world (Yarrow et al. 2009). Brazilian waterweed was introduced into the Delta by 1946 (Light et al. 2005) and has spread throughout much of the freshwater littoral habitat (Jassby and Cloern 2000). Outside of its native range, Brazilian waterweed has a number of documented detrimental effects on aquatic ecosystems including the reduction of water turbidity and sediment supply (Drexler et al. 2021), decreased nutrient availability for phytoplankton (Vanderstukken et al. 2011), and increased abundance of nonnative fish species (Conrad et al. 2016). Distribution of Brazilian waterweed is limited by turbidities above 5 NTU (Durand et al. 2016) and salinity of roughly 5 ppt (Borgnis and Boyer 2016). Water velocity has also been observed to limit distribution (Gantes and Caro 2001), however this relationship in tidal systems such as the Delta is not clear (Durand et al. 2016). High outflow has been predicted to have a negative influence on this species (Castillo 2019). Brazilian waterweed is tolerant of cold water (Yarrow et al. 2009) and winter temperatures in the Delta likely decrease its growth rate, but are insufficient to limit its distribution (Santos et al. 2011).

Response to Climate Change

Decreases in upstream sediment supply and turbidity would further promote the proliferation of Brazilian waterweed (Durand et al. 2016). Increased coverage of Brazilian waterweed could

further decrease turbidity, which would promote more growth, thus forming a positive feedback loop. Although high velocities may limit the growth of Brazilian waterweed (Gantes and Caro 2001), flooding events as predicted by climate change models are not likely to have the same effects in the tidal Delta. Such events are predicted to occur intermittently and over relatively short time periods (Dettinger et al. 2016), which may actually help spread Brazilian waterweed through dispersed fragments (Gillard et al. 2017). Evidence from a recent drought also indicate that higher frequency of drought will subsequently increase the coverage of Brazilian waterweed (Kimmerer et al. 2019). In contrast, Brazilian waterweed growth and distribution will be greatly reduced in areas of the Delta that experience salt water intrusion if salinities exceed 5 ppt for prolonged periods (Borgnis and Boyer 2016). Increasing water temperatures in the Delta are expected to increase the growth rate of Brazilian waterweed by increasing the number of days that fall within its optimal water temperature range (16 to 32 °C, Yarrow et al. 2009). However, Borgnis and Boyer's (2016) study indicates that sustained high temperature of 26° C or above can be detrimental to the growth of Brazilian waterweed. The negative effects of higher salinity on growth and survival are compounded when temperatures are high, so summer and late fall salinity intrusions will likely play an important role on this species' distribution.

Stuckenia pectinata

Status

The California native *Stuckenia pectinata* is fairly common at the shallow edges of the open waters of the estuary, especially in Suisun Bay and the westernmost portion of the Delta. *S. pectinata* is the most widespread native SAV species in the upper estuary today and can help reduce erosion because they dampen wave actions, though less so than invasive SAV species (Kantrud 1990, Santos et al. 2016). *S. pectinata* beds occur in the migratory path and rearing habitat of native fish species, and host invertebrates that these fish species consume (Borgnis and Boyer 2016). *S. pectinata* appears to have increased in acreage over the past several decades (Boyer et al. 2015), possibly due to increased water clarity that led to greater light availability (Boyer and Sutula 2015). In contrast to Brazilian waterweed, the canopies of *S. pectinata* are more sparse, allowing more stable dissolved oxygen levels, providing more accessible invertebrate food resources, and offering less cover for ambush predators.

Response to Climate Change

S. pectinata can grow well at low salinities under a controlled setting, which suggests that its current limited distribution in the Delta is at least partly inhibited by Brazilian waterweed (Borgnis and Boyer 2016). As salinities increase with climate change this may shift as *S. pectinata* is more salinity tolerant than *E. densa*, growing in salinities as high as 12 ppt while Brazilian

waterweed shows a significant decrease in salinity of 5 ppt (Borgnis and Boyer 2016). *S. pectinata* can withstand and even thrive in temperatures of 25°C and 30°C in mesocosm experiments, and salinity would only have a negative interacting effect with temperatures at the low end (Wittingham et al. 2019).

Resident Fishes

Resident fish species are those that typically spend their entire life cycle in one region or habitat. Here, we consider a fish species as resident if they are capable of spending the majority, if not all, of their lifespan in the upper San Francisco Estuary (area shown in Figure 1). In the upper estuary, the resident fish assemblage is a mix of native and non-native species (Brown and May 2006), a number of which have received considerable attention in the estuary due to either their listing under environmental regulations (e.g. Delta Smelt) or sizeable role in the ecosystem (e.g. Largemouth Bass).

Status

The abundance of resident fishes that occupy the pelagic open water habitat today is a fraction of the number observed decades earlier (Moyle et al. 2016; Hobbs et al. 2017). While Delta Smelt was likely the primary forage fish species in the freshwater pelagic habitat prior to European settlement of California (Moyle 2002), the introduced Threadfin Shad (*Dorosoma petenense*) has been the most commonly found resident fish species since the inception of various pelagic fish surveys (Feyrer et al. 2009; Castillo et al. 2018; USFWS et al. 2019; Stompe et al. 2020a). Delta Smelt has played a central role in water management of the estuary for many years due to its listing; however, their numbers have continued to decline precipitously since the POD event in 2002 (aside from the cool and wet year of 2011). As of 2021, some of the longest-running monitoring programs that provided the initial information leading to the listing of Delta Smelt have failed to catch a single Delta Smelt for multiple years, and even Delta Smelt-focused fish surveys developed in more recent years have had difficulties catching this increasingly rare species. Towards the more brackish and saltwater portion of the bays, Northern Anchovy (*Engraulis mordax*) and Pacific Herring (*Clupea pallasii*) make up a significant portion of the fish catch in the pelagic habitat. The pelagic habitat of the bays and channels may also host a number of larger-sized fish year-round such as the native Splittail (*Pogonichthys macrolepidotus*) and the resident form of adult Striped Bass (Nobriga et al. 2005). Additionally, the introduced demersal White Catfish (*Ameiurus catus*) likely form a substantial portion of the fish biomass, especially towards the bottom of the water column (Moyle 2002; Nobriga et al. 2005; Grimaldo et al. 2009a). However, larger-sized fish and demersal species are unfortunately not monitored well in the upper estuary.

The littoral, resident fish assemblage of the Delta has also undergone massive shifts since the 1800s, with the extinction of Thicktail Chub (*Gila crassicauda*) and extirpation of Sacramento Perch (*Archoplites interruptus*), two native species that were previously dominant in the system (Moyle 2002), and the introductions of numerous invasive fish species that have quickly established themselves within the system. Over the past two decades, the resident fish assemblage in the littoral habitat appear to have increased substantially in numbers, especially within the Delta (Mahardja et al. 2017). This is in contrast to what has occurred in the open water habitat with the Pelagic Organism Decline (Sommer et al. 2007; Thomson et al. 2010). Today, the resident fish assemblage continues to be dominated by introduced species such as Mississippi Silverside (*Menidia audens*), Largemouth Bass (*Micropterus salmoides*), and other non-native centrarchids, but native species remain present, although in relatively low numbers (Brown and Michniuk 2007; Mahardja et al. 2017).

Response to Climate Change

Only a few resident fish species that occupy the pelagic and demersal zones of the estuary have been well-monitored and well-studied. Delta Smelt is likely headed towards extinction in the wild within the next few years, though management intervention such as hatchery supplementation is set to occur soon (Moyle et al. 2016, 2018). The prospect of Delta Smelt persisting over the next several decades looks fairly grim however, given that climate change is expected to impose a variety of negative impacts from truncated spawning period to increased frequency of high temperature events associated with mortality (Brown et al. 2013, 2016b). While many native species are expected to decline due to climate change, some less specialized species with high physiological tolerance (e.g., Sacramento Sucker *Catostomus occidentalis*, Splittail) may be more resilient (Moyle et al. 2013; Mahardja et al. 2021). The majority of introduced fish species that occur in the pelagic and demersal zone of the bays and channels such as Threadfin Shad and White Catfish, are expected to have low vulnerability to climate change impacts (Moyle et al. 2013).

Most resident fishes that occupy the littoral habitat of the upper San Francisco Estuary seem to be more tolerant of high temperature than some of the well-studied threatened and endangered fish species in the system (Moyle et al. 2013; Jeffries et al. 2016; Davis et al. 2019a). Nevertheless, it is worth noting that in the Mediterranean Sea (with climate similar to California), shallow-water fish species with affinity to warm climates have increased in relative abundance while cold-water associated species declined as surface temperature has been rising (Givan et al. 2018). Sea level rise and more frequent extreme water events (i.e., floods and droughts) appear more likely to cause shifts than rising temperatures, because the species that make up the majority of the biomass of the resident fishes are largely non-native freshwater-oriented species that are well-adapted to the stable conditions of the existing Delta (Mahardja et al. 2017; Young et al. 2018). It is possible that increased variability in flow and salinity within

the Delta may favor native fishes, given that native fishes evolved in a Delta that was more dynamic than its contemporary version (Moyle 2014).

It is important to note that these are broad generalizations and simplistic predictions of what may occur to this functional group with climate change. The resident fish assemblage that occupies the open waters of the estuary is made up of a diverse suite of species and their response to climate change is unlikely to be unidirectional. Effects of temperature can vary substantially, even between species within the same genus; as seen with Largemouth Bass and Smallmouth Bass (*Micropterus dolomieu*) (Whitledge et al. 2002). As such, we provide more detailed overviews for select representative species of high management interest below.

Largemouth Bass

Status

Largemouth Bass (*Micropterus salmoides*) is a fairly long-lived apex predator native to the eastern United States and was introduced to the Delta for recreational fishery purposes (Moyle 2002). Today, Largemouth Bass is one of, if not the most commonly found fish species in the littoral habitat of the Delta and likely represents a significant portion of the fish biomass (Brown and Michniuk 2007; Conrad et al. 2016; Mahardja et al. 2017).

Response to Climate Change

As a warmwater species, Largemouth Bass will likely continue to persist in high numbers as the climate warms (Hansen et al. 2017), especially if the amount of SAV-dominated tidal lake habitat expands due to sea level rise. The proliferation of SAV (i.e., *Egeria densa*) has been linked to the recruitment of Largemouth Bass (Conrad et al. 2016; Huntsman et al. 2020), and tidal lakes with warmer temperatures seem to support more introduced centrarchids such as Largemouth Bass (Young et al. 2018). To date, the evidence suggests that the salinity variability in the Delta is well within the physiological limitations of Largemouth Bass (Huntsman et al. 2020) and that floods and droughts do not appreciably change juvenile Largemouth Bass abundance (Mahardja et al. 2021). However, this may be largely due to the current salinity management practices of the Delta, where the Delta is kept fresh year-round. It remains a question whether high salinity water encroachment into the interior Delta would have a negative impact on the Largemouth Bass population.

Mississippi Silverside

Status

First introduced to California in the 1960s, Mississippi Silverside (*Menidia audens*) is an annual forage fish species commonly found in shallow water habitat of the San Francisco Estuary (Moyle 2002). Mississippi Silverside is of interest to management due to the species' status as

the most numerically dominant species in multiple fish surveys in the system (Mahardja et al. 2017; Stompe et al. 2020a) and their ability to prey on larval Delta Smelt (Schreier et al. 2016). Although Mississippi Silversides are more commonly found in low-salinity to freshwater areas (Mahardja et al. 2016), they occur anywhere from the South Bay to the lower Sacramento and San Joaquin Rivers. One reason for this is that Mississippi Silverside can tolerate a wide range of environmental conditions; they can survive in temperatures as high as ~35° C (Moyle 2002; Davis et al. 2019a) and salinities over 30 parts per thousand (Moyle 2002; IEP et al. 2020).

Response to Climate Change

Elevated salinity and warming in the upper San Francisco Estuary may lead to conditions that are closer to the physiological optima of Mississippi Silverside (Davis et al. 2019a). Data from long-term monitoring programs indicate that droughts lead to an increase of Mississippi Silverside catch in nearshore habitat of the Delta while floods result in a decrease of catch (Mahardja et al. 2016). However, it is somewhat unclear whether a decrease in Mississippi Silverside catch in the Delta during flood year is due to an overall decrease in the species' abundance or simply a transport of Silversides to downstream habitat (e.g. Suisun Bay). Increased variability of precipitation due to climate change seems unlikely to impact the species significantly, given that the species' occurrence in the upper San Francisco Estuary rebounds during dry years (Mahardja et al. 2021). Overall, we can expect Mississippi Silverside to continue to proliferate as climate change progresses.

Tule Perch

Status

Tule Perch (*Hysterocarpus traski*) is a California native fish species in the surfperch family (Embiotocidae) with three extant subspecies (subspecies *lagunae* in Clear Lake, subspecies *pomo* in the Russian River, and subspecies *traski* in the San Francisco Estuary) (Moyle 2002). Unlike many native fish species in the San Francisco Estuary, Tule Perch has remained somewhat abundant and continues to be fairly widely distributed in the San Francisco Estuary, ranging from the Petaluma River in the west up to the tributaries of the California Central Valley. Tule Perch has been one of the most frequently caught species by the long-term fish survey at Suisun Marsh (Colombano et al. 2020). While Tule Perch in the Delta may have seen an overall reduction in numbers since the 1980s (Brown and Michniuk 2007), their abundance may have increased since the early 2000s in certain regions within the Delta (Young 2016; Mahardja et al. 2017).

Response to Climate Change

There is limited information available on Tule Perch's temperature tolerance, but the species appears to prefer water temperature below 25° C (Cech et al. 1990). Effects of warming on Tule

Perch is rather unclear and Tule Perch overall has been less studied than other fish reviewed in this chapter; however, Tule Perch can persist in high salinity waters (Moyle 2002) and may be one of the few native species that have benefitted from the expansion of SAV in the Delta (Young et al. 2018). Due to the Tule Perch's reproductive strategy of giving birth to precocial live young, they may be buffered from adverse effects experienced by other fishes with pelagic early life stages. Saltwater intrusion into the Delta and increases in tidal lake habitat due to sea level rise and levee failures, may result in a positive overall benefit for Tule Perch.

Delta Smelt

Status

Delta Smelt is a small, euryhaline osmerid species endemic to the tidal freshwater and brackish portions of the estuary, occurring mostly in a narrow salinity range (1-6 ppt) known as the low-salinity zone (LSZ) (IEP 2015). Their limited distribution, short life span and low reproductive capacity, as well as relatively strict physical and feeding requirements, mean that Delta Smelt is at risk in a fluctuating environment, climate change, direct and indirect effects of water diversions, introduced species, contaminants and other stressors (Bennett 2005; Mac Nally et al. 2010; Castillo et al. 2018). Although Delta Smelt were historically abundant, they began to decline in the 1980s. Low abundance in the 1990s, coinciding with increased diversion of inflowing waters during a period of extended drought, led to state and federal listings as a threatened species (Moyle et al. 1992). Further declines since the early 2000s led to its up-listing to endangered status under the California Endangered Species Act in 2009. While federal up-listing was also warranted, it was precluded due to other listing priorities (Federal Register 2010). Population trends for Delta Smelt show that the estuary is no longer provides suitable habitat for this critically endangered endemic fish. Supplementation of the wild population using a captive Delta Smelt population is being evaluated as part of a supplementation strategy.

Response to Climate Change

Delta Smelt are vulnerable to both temperature and salinity increases projected under climate change given their physiological response to temperature and salinity (Swanson et al. 2000; Komoroske et al. 2014, 2016; Jeffries et al. 2016; Davis et al. 2019a). Although temperature tolerance decreases with life stage, juveniles are at higher thermal risk due to the narrow difference between critical thermal maximum (CT_{max}) and peak summer temperatures. Moreover, acclimation at the higher temperatures had little effect in increasing CT_{max} (Komoroske et al. 2014). Salinities outside the LSZ could impose energetic costs that limit Delta Smelt ability to effectively acclimate to exploit higher salinity habitats (Komoroske et al. 2016). In drought years, juvenile Delta Smelt may face increasing physiological challenges due to the lack of overlap between optimum ranges of temperature and salinity. Hence, maintaining

thermal homeostasis at cooler temperatures can only be achieved at a higher osmoregulatory costs in saltier habitats downstream of the LSZ. Comparative physiological studies (Swanson et al. 2000; Davis et al. 2019b) suggest Delta Smelt may also have disadvantages to cope with introduced species interactions under climate change (see Delta Smelt appendix). While intermediate levels of turbidity are important to Delta Smelt (Baskerville-Bridges et al. 2004; Feyrer et al. 2007; Nobriga et al. 2008; Hasenbein et al. 2013) it is unclear how climate change will influence this key habitat factor under increased suspended sediment projections (Stern et al. 2020, see Delta Smelt appendix). Feyrer et al. (2011) suggested further declines in Delta Smelt habitat across all water year types and Brown et al. (2013) suggested water temperature increases would render waters historically inhabited by Delta Smelt near the confluence largely uninhabitable. Unless Delta Smelt are able to adapt to higher temperatures to minimize sublethal and lethal effects (e.g., Klerks et al. 2019), increases in water temperatures and more extreme droughts projected under climate change may further endanger Delta Smelt throughout the estuary.

Wakasagi

Status

The Wakasagi (*Hypomesus nipponensis*) is a congener to Delta Smelt that is native to Japan (Moyle 2002). Wakasagi are primarily a brackish water species (Saruwatari and Okiyama 1992) and in California can tolerate a wide range of salinities 0-29 ppt (Moyle 2002). Wakasagi spawn between April and May and optimal temperatures for growth and reproduction are 14-21°C (Moyle 2002). However, during January-May Wakasagi were caught in open waters at $10.5 \pm 0.49^\circ\text{C}$ (mean \pm sd) (Castillo et al. 2018). Despite the reported migration flexibility between freshwater and marine habitats (Arai et al. 2006), they predominated at low salinities (0.68 ± 0.62 ; mean \pm sd) and at intermediate turbidities (31.9 ± 16.5 NTU; mean \pm sd) in open waters of the estuary during winter-spring (Castillo et al. 2018). Because the predominant water temperature, salinity, and turbidity are comparable to those reported for Delta Smelt (see Delta Smelt section), these two species spatially overlap in the estuary. However, unlike Delta Smelt which lacks wild populations outside the estuary, Wakasagi inhabit several reservoirs supplying freshwater to estuary. Individuals from these populations are likely regularly being transported downstream into the estuary (Moyle 2002; Wang 2007). Wakasagi and Delta Smelt respond similarly to water quality variables in terms of diet, growth and hatching, and have similar distributions in the Delta, but Wakasagi predominate upstream of the estuary (Davis et al. in prep.). Both species spawn at similar times, have parallel diets, and similar growth in early life stages; however, Wakasagi appear to grow faster than Delta Smelt after the mid-larval stage. Trends of declining growth and earlier hatching were observed during the last drought in both species, although the trend seems to be stronger for Wakasagi. The increasing catches of

Wakasagi and declining Delta Smelt catches across several surveys in recent years suggest the estuary only remains favorable to Wakasagi (Davis et al. in prep.).

Response to Climate Change

Besides the comparative physiological advantage of Wakasagi over Delta Smelt to cope with climate change (Swanson et al. 2000, see Delta Smelt appendix), the metapopulation structure of Wakasagi in the watershed could provide enhanced resilience to Wakasagi to cope with climate change impacts in the estuary, particularly since lotic estuarine environments such as the estuary may not be the best habitat for Wakasagi compared to lentic habitats such as reservoirs (Wang 2007). Because Wakasagi tended to occur in cooler areas across their distribution (Davis et al. in prep.), their potential advantage to thermal stress over Delta Smelt (Swanson et al. 2000) may not be apparent and masked by other environmental factors. While the extent to which different water year types influence spawning and reproductive success of Wakasagi in the estuary has remained unclear, Wakasagi seem to use Suisun Marsh more often in wet years than in dry years and spawning may not occur in Suisun Marsh tributaries regardless of water year type (Wang 2007). Whether Wakasagi are able to maintain a sustainable population in the estuary without recruitment from reservoirs and whether Wakasagi populations residing in reservoirs are able to withstand increasing climate change impacts may also be consequential to its native congener Delta Smelt, both in terms of species interactions and population recovery efforts (see Wakasagi appendix).

Threadfin Shad

Status

Threadfin Shad (*Dorosoma petenense*) is a non-native species, introduced to ponds and reservoirs by the California Department of Fish and Game (now California Department of Fish and Wildlife) in the 1950s as a forage fish. They subsequently spread downstream and became established in the estuary. Today, Threadfin Shad is one of, if not the most, commonly observed pelagic fish species in the estuary and appears to remain abundant relative to other species associated with the POD (Feyrer et al. 2009; Stompe et al. 2020a). Threadfin Shad and Delta Smelt have substantial overlap in their diet (Feyrer et al. 2003). As such, understanding Threadfin Shad's status, trends, and potential trajectory may provide important insight into the estuary's conditions, especially as Delta Smelt are becoming too difficult to monitor in recent years. Threadfin Shad is intolerant of cold temperatures; heavy die offs occur in the Delta when temperatures reach 6-8°C (Moyle 2002). The best growth and survival occur in waters which exceed 22-24°C in the summer (Griffith 1978). Threadfin shad is mainly a freshwater fish but can grow and survive in high salinities (Miller and Lea 1972). Salt water does inhibit reproduction, however. The Salton Sea population has failed to reproduce despite continuous

recruitment from fish arriving through the freshwater canals flowing into the basin (Hendricks 1961).

Response to Climate Change

Water temperature increases as projected are not likely to negatively impact growth or survival of Threadfin Shad, since the best growth and survival occur at 22-24°C (Griffith 1978). Therefore the species is considered less vulnerable to the effects of climate change than native and some non-native fish species (Moyle et al. 2013). Increased salinities due to intrusion from sea level rise or drought is also not likely to adversely affect the Threadfin Shad, because the estuary is not likely to become saline enough to inhibit reproduction. However, sampling of tidal lakes in the estuary revealed a clear preference by Threadfin Shad for the warm freshwater of Mildred Island, which reinforced earlier findings showing highest abundance and suitable habitat in relatively deep, clear water with low flow (Feyrer et al. 2009; Young et al. 2018). With increasing water temperatures, one concern for the Threadfin Shad are the *Microcystis* algal blooms and following low dissolved oxygen levels especially common in the San Joaquin River (see harmful algal bloom section below). The toxic effects of *Microcystis* impair the health and reproductive potential of Threadfin shad by causing ovarian necrosis and liver lesions (Acuña et al. 2012). The harmful algal blooms occur during the late summer and fall which is a critical time for newly spawned fish recruiting to the population. The blooms have been geographically centered where Threadfin Shad are most abundant and have been known to cause die-offs. The co-occurrence of juvenile Threadfin Shad and *Microcystis* blooms will become more common as blooms are expected to increase in frequency under climate change (Lehman 2007; Feyrer et al. 2009).

Migratory Fishes

Status

Outmigrating juveniles and/or returning adults of most migratory fishes rely on cooler water temperatures in the open waters of the upper estuary while rearing and migrating (Moyle 2002). Here we consider a species as migratory fish if they are capable of spending only part of their life cycle within the estuary. Native species such as Chinook Salmon (*Oncorhynchus tshawytscha*), Longfin Smelt (*Spirinchus thaleichthys*), Rainbow Trout/Steelhead (*Oncorhynchus mykiss*), White Sturgeon (*Acipenser transmontanus*), Green Sturgeon (*Acipenser medirostris*), and multiple lamprey species make up the majority of this migratory fish functional group. This functional group also includes two notable introduced fish species that are prevalent and relatively well-monitored in the estuary: Striped Bass (*Morone saxatilis*) and American Shad (*Alosa sapidissima*).

The Central Valley's anadromous salmonid and sturgeon numbers today are likely a small fraction of their numbers prior to California's gold rush. Construction of dams and water diversion facilities throughout the system have precluded these migratory species from their historical spawning and holding habitat. Other anthropogenic stressors include loss of floodplain and tidal wetland rearing habitats, fisheries pressure, and hatchery influences (Yoshiyama et al. 2000; Blackburn et al. 2019; Sturrock et al. 2019). Little attention has been paid to lampreys, but their runs are also likely to be smaller than they used to be given that they are also unable access much of their historical spawning and rearing grounds (Moyle 2002). The Longfin Smelt population has collapsed over the years, but they are highly correlated with freshwater outflow and their abundance can rebound in wet years (Nobriga and Rosenfield 2016). Striped Bass and American Shad juvenile numbers are magnitudes lower today than decades ago (Thomson et al. 2010), but their adult numbers may have remained stable (Nobriga and Smith 2020).

Due to the loss of wetland habitats and extensive modifications that have occurred in the upper estuary, it was thought that the open waters of the Delta and the bays were solely migration corridors for anadromous fish species (Williams 2006). However, this view of the Delta is not entirely accurate. For juvenile Chinook Salmon, most estuarine rearing occurs in the freshwater Delta and brackish bays, especially during high water years (Kjelson et al. 1982; Munsch et al. 2020). Additionally, recent work on otolith microchemistry indicates the Delta is important juvenile rearing habitat for Chinook Salmon (Sturrock et al. 2020), especially for fry that tend to occupy shallow littoral habitats (Munsch et al. 2016). White Sturgeon occur mainly in open water (Patton et al. 2020) and can overwinter in the Delta (Miller et al. 2020). Although not well-studied, it is also possible that resident Striped Bass and *O. mykiss* populations are present in the Delta year-round.

Response to Climate Change

For native species in this functional group, the estuary generally represents the southern limit of their natural range. As such, these species may often encounter conditions at or above their thermal limits in the estuary. Rising temperatures in the open waters of the estuary due to climate change are expected to have negative consequences for native migratory fishes, including Chinook Salmon and Longfin Smelt (Jeffries et al. 2016; Munsch et al. 2019). Salinity intrusion into the estuary from sea level rise seems to pose less of a risk for anadromous species due to their ability to osmoregulate at a wide range of salinity levels. However, it may lead to a reduction in suitable rearing habitat for some species (Feyrer et al. 2007) and/or mismatch in phenologies of these fish species and their prey items (Merz et al. 2016). Most migratory fish species in the estuary display multiple alternative life history strategies (e.g. anadromous vs. resident, variability in migration timing and holding pattern, etc.), which should buffer them to some extent against the increased frequency of extreme events associated with

climate change. Nonetheless, other anthropogenic impacts such as the use of hatcheries have reduced the life history diversity of anadromous species (Sturrock et al. 2019) and higher frequency of floods and droughts are not likely to be beneficial for this functional group.

Chinook Salmon

Status

Chinook Salmon is an anadromous fish species with high sociocultural and economic value in the estuary. This species exhibits a diverse set of life history strategies but has declined substantially over the past two hundred years largely due to habitat loss. In California's Central Valley, winter, spring, and fall-late fall runs of Chinook Salmon are federally listed as endangered, threatened, and "species of concern", respectively. Chinook Salmon travel through the open waters of the upper estuary twice throughout their life cycle: their outmigration to the ocean as juveniles and as adults returning to spawn upriver. Although adult salmon primarily use the open water as a migration corridor, juvenile salmon may rear in the Delta and bays from weeks to months prior to moving downstream (Kjelson et al. 1982; del Rosario et al. 2013). The residence time of juvenile Chinook Salmon in the upper estuary's open waters depends on the fish's run, size, origin (hatchery vs. natural), life history strategy, as well as the flow conditions and temperature in the system (Munsch et al. 2019).

Response to Climate Change

The estuary represents the southern end of Chinook Salmon's natural range so rising temperatures and increased frequency of extreme flow events pose additional conservation challenges (Yoshiyama et al. 2000; Williams 2006). The timing of flood pulses is an important driver for juvenile Chinook Salmon in California's Central Valley and the timing of these pulses can have huge effects on rearing numbers, migration rates, and survival (Michel et al. 2015; Friedman et al. 2019; Munsch et al. 2019, 2020). Munsch et al. (2020) found higher recruitment of fry migrants and a larger spatial distribution within the Estuary during high water years. Flood pulses are also associated with longer juvenile outmigration windows and higher flows are generally associated with higher overall survival (Michel et al. 2015; Friedman et al. 2019; Munsch et al. 2020, but see Buchanan and Skalski 2020). Therefore, depending on timing, duration, and severity of flood pulses as a result of climate change, we could see a wide range of effects on juvenile Chinook Salmon habitat use and survival ranging from beneficial to harmful.

Increased water temperatures increase metabolic demand of juvenile Chinook Salmon. As a result, individuals will need to forage more to maintain their basal metabolism and subsequently consume more to maintain high growth rates. To achieve adequate growth rates to smolt, they will need increased access to adequate foraging opportunities in areas of higher

prey densities or increased time spent foraging, both of which entail increased predation risk (Walters and Martell 2004). Alternatively, if their foraging behavior remains the same (i.e., if they maintain similar foraging rates regardless of water temperature), increased water temperatures will cause a decrease in growth rates as a result of increased basal metabolic demands. This could lead to prolonged rearing in littoral habitats of the Delta or smolting at smaller sizes, both of which correspond with an increase in predation risk. In addition to seeing changes in foraging behavior and/or growth rates, we also expect to see higher predator consumption rates associated with increased water temperatures (regardless of juvenile salmon growth patterns or changes in Delta residency time).

Collectively, we do not expect to see much of a change in juvenile habitat use as a result of climate change because the Delta is highly channelized with leveed and rip-rap banks. However, it is likely that we could see changes in juvenile growth rates and, more likely, increases in predation rates of juveniles utilizing these habitats for rearing and during outmigration periods. Increases in predation rates could also be influenced by the proliferation of SAV and non-native Centrarchids in the littoral habitats (Zeug et al. 2020).

Striped Bass

Status

Striped Bass were introduced in 1879 and the species rapidly became the dominant pelagic predator in the system. Due to concerns about the impacts of water exports on the Striped Bass population, several long-term monitoring programs (i.e., the Summer Townet Survey and Fall Midwater Trawl) were established to monitor the annual production of Striped Bass in the estuary. Since the inception of the long-term monitoring studies, Striped Bass have been consistently caught in the estuary making them a valuable indicator species for monitoring the impacts of climate change. Adult and juvenile Striped Bass can be found foraging in and near both littoral and open water areas of the estuary. However, Striped Bass use of shallow shoals has increased in recent years (Sommer et al. 2011), possibly in response to changes in pelagic food availability.

Striped Bass are versatile predators and may be able to offset increased metabolic demands through increased consumption, feeding on the dominant prey present in the system (Bryant and Arnold 2007). Historically this may have included native osmerids such as Delta Smelt and Longfin Smelt, but more recently Striped Bass have likely targeted more abundant invasive prey species (Nobriga and Smith 2020). Furthermore, Striped Bass larval growth was directly related to zooplankton food density (Eldridge, Whipple, & Bowers, 1982), although Foss and Miller (2004) observed greater larval striped bass growth in brackish water despite greater zooplankton densities in freshwater.

Response to Climate Change

We expect impacts on Striped Bass to be similar to those observed in juvenile Chinook Salmon (i.e., a range of responses as a result of increased variability in precipitation and higher predation mortality rates). Increased water temperature in the estuary could lead to higher metabolic rates and higher consumption rates for Striped Bass, though Kimmerer et al. (2001) found no impacts of temperature on the relative abundance of young-of-year fish and Foss and Miller (2004) observed no relationship between larval growth and temperature. Juvenile Striped Bass can rear for 2-4 years in the Estuary before migrating to the San Francisco Bay and/or Pacific Ocean, and as such, prolonged exposure to higher water temperatures in the estuary could have greater effects on growth and survival if adequate prey resources are not available (Loboschewsky et al. 2012). Similarly, larval Striped Bass may be sensitive to higher temperatures, increased metabolic rate, and higher salinity relative to ideal habitat such as Suisun Bay. Exposure of larval bass to these conditions will be impacted in part by the migration of adults upstream, which has been shown to be occurring earlier in the year with rising sea temperature and reduced freshwater outflow (Goertler et al. 2021).

Longfin Smelt

Status

Longfin Smelt (*Spirinchus thaleichthys*) is a short-lived, small, pelagic forage fish native to the Pacific coast of North America. The species is facultatively-anadromous (both anadromous and resident forms exist), but the estuary's population is largely anadromous (Rosenfield and Baxter 2007). The estuary is the southernmost extent of the Longfin Smelt range and the population found here is genetically distinct from other populations although with some amount of gene flow to nearby populations (Amanda Finger, UC Davis, unpublished data). Similar to other pelagic fishes in the upper estuary, Longfin Smelt is of high management interest because the species has experienced a steep decline in the past several decades and has been listed as threatened under the California Endangered Species Act (CDFG 2009). Longfin Smelt have also declined precipitously across North America's west coast estuaries since the late 20th century (Emmett et al. 2000). Mertz et al. (2013) suggested that Longfin Smelt spawning habitat could extend further downstream than its rearing habitat in the estuary, which was supported by evidence of spawning and larval recruitment in wetlands in SF Bay (Grimaldo et al. 2020; Lewis et al. 2020). The population is strongly associated with freshwater flows, and often rebounds after droughts when wet years occur. Yet, fall abundance indices in high outflow years over the past three decades shows the population has not been able to rebound to previous levels, with each abundance peak being lower than the previous one.

Response to Climate Change

The sensitivity of Longfin Smelt to high temperatures along with the increasing severity of droughts (Jeffries et al. 2016), and temperature uptrends in the estuary (Bashevkin et al. 2021) suggest this species is very vulnerable to climate change. Because Longfin Smelt in the estuary are at the southern limit of the species, they may be particularly vulnerable to climate change impacts which may be compounded by the low average freshwater flows prevailing in the estuary compared to those in other large estuaries (e.g., Emmett et al. 2000). Jeffries et al. (2016) tested whether temperature is a key stressor by exposing fish to 20°C; Longfin Smelt larvae had a pronounced cellular stress response, with an upregulation of heat shock proteins. Based on responses across multiple levels of biological organization, and linking such responses to habitat distributions in the wild, the authors concluded that Longfin Smelt larvae may be more susceptible than Delta Smelt to increases in temperatures, given their limited scope to tolerate projected temperature increases.

The projected increased frequency of droughts under climate change (Knowles and Cronkite-Ratcliff 2018) may further limit the Longfin Smelt population in the estuary given their strong response to outflow (see Longfin Smelt Appendix). Baxter (2015) reported that increased water temperatures are expected to shorten the spawning period for Longfin Smelt, with warmer winter and spring water temperatures increasing the metabolic demand among larvae, and without a likely corresponding increase in food availability. Baxter further stated that summer and fall water temperatures will reduce habitat quality of the upper Estuary in general, and that runoff reductions, particularly in spring, will cause a negative effect on Longfin Smelt recruitment. The critical role of outflow for this species and its vulnerability to climate change impacts is supported by the central role of outflow on the distribution of larvae, recruitment success and abundance across their entire estuary's range (see Longfin Smelt appendix). Moreover population trends of several pelagic species, including Longfin Smelt, were associated to winter-spring salinity increases due to water diversions (Castillo et al. 2018). Considering that juvenile-adult Longfin Smelt caught in the upper Estuary predominate within the LSZ (3.33 ± 2.18 ; mean \pm sd) at intermediate turbidities (77.8 ± 34.2 NTU (mean \pm SD) and that their salinity habitat component shifts further upstream with X2 (Castillo et al. 2018), the observed and projected increased frequency of droughts and sea level rise (NRC 2012) could result in further upstream shift of the LZS, and potentially include narrower, riprapped river channels making fish potentially more vulnerable to entrainment by upstream water diversions. Moreover, the proliferation of aquatic macrophytes since the late 20th century could further decrease turbidity and open waters habitats, further degrading Longfin Smelt habitat in the estuary.

Plankton

Plankton are important members of open water food webs. Plankton cannot actively swim against a current, making them subject to water movement. However, some plankton have the ability to migrate vertically in the water column, allowing them to access the full water column and in conjunction with tide, adjust their location. Plankton are broadly categorized into photosynthetic plankton (single-celled photosynthetic organisms), bacteria, and zooplankton. Zooplankton feed on photosynthetic plankton, bacteria, other zooplankton, or even detritus. Since 1999, freshwater photosynthetic and planktonic bacteria, called cyanobacteria, have formed toxic blooms known as harmful algal blooms in the estuary (HABs, Lehman et al. 2021). These HABs can negatively affect fish health (Acuña et al. 2012), change species composition in the lower trophic levels of the food web (Lehman et al. 2010; Ger et al. 2018), and have adverse impacts on humans and their pets. HABs are discussed in more detail separately within this functional group. A third group of plankton include microscopic organisms that can be mixotrophic (both photosynthetic and heterotrophic, e.g., dinoflagellates) or non-photosynthetic, such as protists (e.g., ciliates) that are understudied in the estuary and not discussed further.

Photosynthetic plankton

Status

Photosynthetic plankton in the estuary are microscopic unicellular or colonial organisms that float in the water column and move with streamflow, wind, and tide. They form the base of the aquatic food web because through photosynthesis they convert raw materials (energy from the sun, carbon dioxide from the air and inorganic nutrients in the water) into the sugars (food) used by the rest of the food web. In the San Francisco Estuary they consist of bacteria in the phylum Cyanophyta (cyanobacteria) and phytoplankton in the phyla Bacillariophyta (diatoms), Dinoflagellata (dinoflagellates), Chrysophyta (chrysophytes), Cryptophyta (cryptophytes), and Chlorophyta (green algae). Each phylum has its own general response to hydrology, salinity, and water temperature, which vary with climate change.

Elevated chlorophyll *a* concentration often occurs in the Delta and Suisun Bay at low streamflow, which allows photosynthetic plankton to accumulate (Conomos et al. 1979; Cloern et al. 1985; Peterson et al. 1989; Lehman 1992a, 1996; Jassby 2008). Small diameter green algae can form high chlorophyll *a* concentrations in backwater sloughs where residence time is long, while large diameter diatoms often occur in open water where vertical mixing is high (Lehman 2007; Stumpner et al. 2020). Since 2000, low streamflow, high nutrient concentration and elevated water temperature throughout the summer and fall have been associated with an increase in chlorophyll *a* concentration due to cyanobacteria (Lehman et al. 2017, 2020).

Moderate streamflow will flush chlorophyll *a* from the Delta into Suisun Bay (Lehman 1996; Jassby 2008) and often contributes diatom cells to seaward reaches (Lehman 2004; Jassby 2008). However, chlorophyll *a* concentration in Suisun Bay has been low since the mid-1980s due to grazing by the invasive clam *Potamocorbula amurensis* (Nichols et al. 1990; Alpine and Cloern 1992; Kimmerer 2004; Dugdale et al. 2016; Lucas et al. 2016). Diatoms are particularly susceptible to grazing by these clams in the shallow waters of Suisun Bay due to their rapid sinking rate (Nichols et al. 1990; Alpine and Cloern 1992; Kimmerer 2004; Dugdale et al. 2016; Lucas et al. 2016). High ammonium concentration caused by wastewater treatment plant discharge may contribute to the loss of diatoms due to the slower growth rate of diatoms when grown on ammonium compared with nitrate (Wilkerson et al. 2006; Dugdale et al. 2007; Parker et al. 2012).

Streamflow influences the load and concentration of the major nutrients, nitrogen, phosphorus, and silica, needed for photosynthetic plankton growth in the upper estuary (Peterson et al. 1985; Cloern et al. 2020). Nitrate concentration varied inversely with streamflow between the 1970s and 2000 (Peterson et al. 1985; Lehman 2004). Increased ammonium load from wastewater treatment plants in the early 2000s affected the conservative nature of the nitrogen in the estuary, but streamflow remained an important driver of total nitrogen concentration (Wilkerson et al. 2006; Dugdale et al. 2007). Phosphate concentration also varies inversely with streamflow (Lehman 2000a, 2004) and increases with turbidity which is caused by both high streamflow and resuspension of sediment (Lehman 2004; Schoellhamer et al. 2013). Silica enters the estuary from riverine sources upstream (Lehman 2000a, 2004; Kimmerer 2005). These three major nutrients are currently not limiting to phytoplankton growth (Cloern et al. 2020). In contrast, it was hypothesized that ammonium ($> 4 \mu\text{M/L}$) may reduce chlorophyll *a* concentration by reducing the nitrate uptake of diatoms, which grow better on nitrate (Wilkerson et al. 2006; Dugdale et al. 2007; Parker et al. 2012).

Response to Climate Change

Predictive models developed for chlorophyll *a* concentration measured between 1975 and 1987 demonstrated a positive correlation between elevated water temperature and chlorophyll *a* concentration in the Sacramento and San Joaquin River (Lehman 1992b). In contrast, there was a negative correlation between chlorophyll *a* concentration and water temperature in Suisun Bay, where water temperature is usually cool due to tidal flow and chlorophyll *a* concentration is associated with large volume marine species (Lehman 1992b). The influence of water temperature on biomass is dependent on the net growth rate. Although elevated water temperature may increase the growth rate, it can also increase respiration which decreases the net increase in biomass. The effect of these opposing forces on net growth rate was demonstrated for field studies in Yolo Bypass where a combination of both high growth rate and high respiration rate at warm water temperature led to net negative growth (Lehman et al.

2008b). Water temperature can also increase the net loss of biomass through its impact on herbivores. Both clams and zooplankton, which consume photosynthetic plankton, grow faster and consume more biomass at warmer temperature (Thompson et al. 2008).

Increased water temperature will also alter photosynthetic plankton community composition. Elevated water temperature favors some green algae and cyanobacteria, particularly the toxic cyanobacteria *Microcystis*, *Dolichospermum* and *Aphanizomenon* (Lehman et al. 2017, 2021). Pennate diatoms, green algae and cryptophytes also increased with water temperature during drought years (Lehman and Smith 1991; Lehman 2000b, 2004, 2007). Time series analysis indicated water temperature was negatively correlated with diatom carbon in the Delta but positively correlated with diatom carbon in Suisun Bay between 1975 and 1993 (Lehman 2004). Enhanced cyanobacteria populations that occur with warm water temperature (> 20 °C) may further alter community composition through allelopathy (Lehman et al. 2021). Abundance of the cyanobacterium, *Microcystis* was negatively correlated with the abundance of diatoms and green algae, at least in part due to allelopathy (Lehman et al. 2010, 2013, 2017, 2021). Unlike cyanobacteria, diatoms often grow better at low water temperature. Net productivity of diatoms decreased when water temperature exceeded 20 °C (Lehman et al. 2008a). Laboratory bioassays confirmed the increased growth of diatoms at cool water temperature (Glibert et al. 2014). Water temperature may have differing effects on diatom genera, however. Elevated water temperature was associated with increased abundance of centric diatoms such as *Aulacoseira granulata* and *Skeletonema potamos* but a decrease in the abundance of pennate diatoms, including *Asterionella*, and *Nitzschia* (Lehman 2000b). These changes in community composition can affect upper trophic levels by affecting the size structure and nutritional value of available food (Lehman 2000b; Kimmerer and Thompson 2014; Kayfetz and Kimmerer 2017; Cloern 2018).

The increased frequency and intensity of hydrologic extremes (e.g., flood and drought) due to climate change may also affect plankton location throughout the upper estuary. At low streamflow, chlorophyll *a* concentration in the Delta and Suisun Bay can increase due to accumulation (Conomos et al. 1979; Cloern et al. 1985; Peterson et al. 1989; Lehman 1992b, 1996; Jassby et al. 2002; Jassby 2008). Although some increase in chlorophyll *a* concentration may be beneficial, elevated levels may cause low dissolved oxygen concentration (Sutula et al. 2017). At high streamflow, plankton can be flushed seaward out of the upper estuary. Intermediate streamflow can flush chlorophyll *a* from the Delta into Suisun Bay, distributing biomass throughout the upper estuary (Cloern et al. 1985; Lehman 1992b, 1996; Jassby et al. 1995; Jassby and Cloern 2000; Kimmerer 2002; Lopez et al. 2006; Jassby 2008; Kimmerer and Thompson 2014). Between 1971 and 1993 chlorophyll *a* concentration across the upper estuary was significantly higher during normal (11%) than wet (8%) years compared with the long-term mean (Lehman 1996). Recent studies suggest transport from the upper Colusa drain into the

Cache Slough Complex is also possible (Frantzich et al. 2018). Chlorophyll *a* transport is further affected by water diversion. Modeling studies suggested a significant portion of the chlorophyll *a* in the Delta or Suisun Bay could be removed by water diversion (Jassby 2008; Hammock et al. 2019). As a result,, chlorophyll *a* concentration at any given time or place in the upper estuary can be a function of the water year type which affects both streamflow and diversion flows (Lehman 1996, 2000a).

Dry and critically dry years would be expected to contain a greater percentage of cryptophytes, green flagellates, and miscellaneous flagellates and a lower percentage of diatoms compared with wet and normal years (Lehman 1996, 2000a; Lehman et al. 2017, 2020). Low streamflow in dry and critically dry years reduces vertical mixing in the water column, which enables motile phyla, like Cryptophyta, Chrysophyta, Dinoflagellata and flagellated Chlorophyta to remain within the upper water column where light is available (euphotic zone) for growth. These phyla contrast with Bacillariophyta (diatoms) which are large, not motile and heavy due to their silica shell which causes them to rapidly sink out of the euphotic zone and to the bottom where removal by clam grazers is more likely (Cloern et al. 1983; Lehman 2007; Lucas et al. 2016). Pennate diatoms appear to be more easily sedimented by low streamflow than centric diatoms which commonly form chains, providing a large surface area for floatation (Lehman 2000a). However, some epibenthic diatoms, like *Aulacoseira granulata*, increase during drought conditions near the bottom (Cloern et al. 1983; Lehman 2000a). Such changes in community composition can have significant impacts on the food web because the loss of diatoms reduces the number of large cells and the largest source of omega-3 fatty acids available to the upper trophic levels (Galloway and Winder 2015; Cloern 2018).

Wet year conditions are associated with an increase in the percent carbon and biovolume of diatoms and green algae (Lehman and Smith 1991; Lehman 1996, 2000a, 2004). The diatoms *Cyclotella*, *Stephanodiscus* and a suite of pennate diatoms (*Asterionella*, *Cymbella*, *Fragilaria*, *Tabellaria*, *Rhoicosphenia*, *Gomphonema* and *Nitzschia*) were common during wetter years (Cloern et al. 1985; Lehman 2000a). The amount of streamflow partially influences the photosynthetic plankton composition through transport, with high streamflow flushing more diatoms and green algae downstream in normal and wet years (Lehman 1996). Diatom carbon was positively correlated with streamflow between 1975 and 1993 in the western Delta, Suisun Bay and the low salinity zone. In the low salinity zone, high streamflow increases the exchange of diatom cells from the shoals to the channel, increasing the diatoms in the water column (Peterson et al. 1975; Arthur and Ball 1979; Cloern et al. 1983).

Peak biomass may shift to earlier in the season as water temperatures warm (Winder and Sommer 2012; Merz et al. 2016). However, this may be balanced by increased grazing by consumers (Crauder et al. 2016). Shallow, littoral areas often have lower photosynthetic plankton biomass than deeper areas because of the access of grazers to the plankton within the

full water column (Lucas et al. 2009). This contrasts with deep channel areas where clam grazing is only effective near the bottom (Dugdale et al. 2016; Lucas et al. 2016).

Sea level rise will increase the amount of open-water habitat as well as the salinity in the Delta. Increased salinity may not have a negative impact on biomass or net productivity because community composition may merely shift to the large diameter marine diatoms (Cloern 2018). However, increased salinity will probably increase grazing by the invasive clam *Potamocorbula amurensis* which grows well in brackish water (Nichols et al. 1990b; Alpine and Cloern 1992; Kimmerer 2004; Lucas and Thompson 2012). Increased salinity may even cause an increase in the clam *Mya*, which was responsible for the loss of chlorophyll *a* concentration in Suisun Bay during the 1976 and 1977 drought (Nichols 1985). In contrast, increased salinity will affect the grazing rate of freshwater zooplankton which contribute significantly to the loss of chlorophyll *a* concentration in the low salinity zone (Kimmerer and Thompson 2014).

Future conditions are also likely to result in more variable turbidity. An increase in the frequency and severity of storms will increase the suspended sediment load and resuspension of bottom sediment (Stern et al. 2020). Elevated turbidity favors diatoms (Lehman 1996, 2004; Cloern 2018), which grow better at low light (Glibert et al. 2014). In addition, vertical mixing from storms enables diatoms, which sink quickly due to their weight, to remain suspended in the water column where light is available for growth (Lehman 2000a, 2007; Lucas et al. 2016). Laboratory incubation studies also indicated diatoms had an increased nitrate uptake rate at low light levels (Glibert et al. 2014). Conversely, the predicted increased frequency and intensity of drought and the associated quiescent water would favor sedimentation of suspended material and an increase in flagellated plankton and cyanobacteria (Lehman et al. 2017).

High outflow associated with flood events could also increase nutrient load (Ball and Arthur 1979; Conomos et al. 1979; Cole and Cloern 1984, 1987; Peterson et al. 1985). However, because nutrient concentrations are currently in excess, the importance of nutrient load on plankton communities will depend on management (Jassby et al. 2002; Jassby 2008). A negative correlation between diatom carbon and both nitrate and soluble reactive phosphorus concentration supported the current lack of nutrient controls on plankton (Lehman 2004). However, more subtle processes than load may be important. It is hypothesized that high nitrate to phosphate ratios favor cyanobacteria over diatoms, even at the high concentrations in the estuary (Glibert et al. 2011). Further, high ammonium concentration ($> 4 \mu\text{M}$) can reduce the uptake of nitrate by diatoms, which use nitrate more effectively for growth (Wilkerson et al. 2006; Dugdale et al. 2007; Parker et al. 2012).

Changes in salinity due to the wax and wane of marine water intrusion upstream with wet and dry conditions, as well as sea level rise will also change plankton communities. Phytoplankton species throughout the estuary were found to vary along a salinity gradient (Cloern 2018).

However, because the salinity range of most species was wide, large changes in salinity may be necessary to significantly change community composition.

Lastly, increased depth with sea level rise could lead to lower net photosynthetic plankton growth due to a decrease in the euphotic zone depth (1% light level) to total depth ratio (Cloern 1987; Lucas et al. 2016). Net growth rate decreases and can become negative as this ratio becomes smaller due to the presence of more depths where respiration exceeds oxygen production. A deeper water column would also reduce the loss rate of plankton cells due to sinking, and therefore, grazing from clams on the bottom (Lehman 2007; Lucas et al. 2016).

Zooplankton

Status

Zooplankton in the estuary is also highly diverse, with different taxa having different responses to hydrology and temperature. The bulk of zooplankton biomass in the current estuary is calanoid copepods, cyclopoid copepods, and (in fresh water) cladocera. Rotifers may be numerically abundant in some areas, but have much lower biomass than the crustaceans listed above. Mysid shrimp were once dominant, but have declined greatly over the past 40 years.

Zooplankton are the dominant food source for pelagic fish in the estuary. Like phytoplankton, zooplankton are largely at the mercy of currents for movement around the estuary. However, zooplankton can control their horizontal movement to some extent by exploiting countervailing vertically-stratified currents (Kimmerer and McKinnon 1987; Kimmerer et al. 2002). Therefore, zooplankton biomass is closely linked to salinity, seasonality, hydrologic, and climatic factors.

The salinity field, in particular, has the greatest impact on zooplankton distribution, more so than geography per se. High outflow years have little impact on fresh water zooplankton, however they can increase abundance of at least one species of freshwater zooplankton (*Pseudodiaptomus forbesi*) in Suisun Bay and the Low Salinity Zone by transporting them to these regions (Kimmerer et al. 2018). Freshwater regions of the estuary have great abundance of cladocerans and certain calanoid copepods (including *P. forbesi*), while brackish regions have more copepods, barnacle nauplii, and crab zoeae. Because the water column in the upper estuary is usually fairly well mixed, the zooplankton community tends to be similar between the shallow, littoral area and deeper open-water areas (Kimmerer and Slaughter 2016), (Grimaldo et al. 2009b), though epiphytic and epibenthic invertebrates may dominate over zooplankton in total invertebrate biomass in littoral or vegetated areas (Grimaldo et al. 2009b; Hartman et al. 2019).

Overall zooplankton biomass is typically higher in the summer, with dominance of the calanoid copepod *Pseudodiaptomus forbesi*, however other taxa dominate in winter and spring. The native copepod *Eurytemora affinis* is most abundant in spring, however the peak of abundance

has shifted earlier than it was historically, partially due to the invasion of *P. forbesi* (Merz et al. 2016).

The zooplankton community has almost completely turned over from species invasions since the 1970s. Native species of zooplankton that were the traditional food for native fishes have been replaced by invaders mostly East Asian in origin (Winder and Jassby 2011). Some of these invasive species are now critical food sources for many native fishes (e.g., *Pseudodiaptomus forbesi*), while others contribute little to fish (e.g., *Limnoithona tetraspina*; (Slater and Baxter 2014). The invasion of Asian clams (*Potamocorbula* and *Corbicula*) which decreased phytoplankton biomass have had a similar effect on zooplankton, both through a reduction in food supply and direct consumption of early life stages (Kimmerer et al. 2005; Kimmerer and Lougee 2015).

Response to Climate Change

Zooplankton are particularly sensitive to climate change due to their short generation times and high physiological sensitivity to temperature (Richardson 2008). Furthermore, as free-floating animals, they have no access to shelter or physical refuges that would be available to benthic or terrestrial species. This high sensitivity may make zooplankton useful indicator species for climate change impacts (Richardson 2008).

Most research on the impact of climate change on zooplankton has occurred either in freshwater or in the ocean, not in estuaries, so precise changes will be difficult to predict. Increased temperatures will cause an increase in growth rate (when food is not limiting), decreased body size, and potentially changes to phenology and community structure. Studies of increased temperature on other zooplankton communities found shifts towards lower body size within a species, or shifts toward species with smaller sizes overall (Garzke et al. 2015; Rice et al. 2015). For example, an extreme heat wave in Australia caused a shift in zooplankton community composition from larger to smaller taxa and an overall decline in biomass (Richardson et al. 2020). In the SF Estuary, this may be partly why the small cyclopoid copepod, *Limnoithona tetraspina*, has dominated over the larger calanoid copepods in recent years (Bouley and Kimmerer 2006). It may also be why the smaller mysid *H. longirostris* is dominating over the larger *N. mercedis* (Avila and Hartman 2020).

Changes to zooplankton size structure may be due to plasticity, rapid evolutionary adaptation, or change in community structure. Studies of multiple copepod species in the Atlantic found little evidence for thermal adaptation. Instead, species shifted their range to adapt to changing conditions (Beaugrand et al. 2002; Hinder et al. 2014)). However, studies on populations of the copepod *Acartia tonsa* from Florida, USA to New Brunswick, CA found evidence for thermal adaptation in local populations, as well as high variability in thermal tolerance that could provide the requisite fodder for rapid adaptation (Sasaki and Dam 2019). Low latitude

populations had the highest thermal tolerance but they also had the least thermal plasticity, which may expose them to increased risk from rapidly rising temperatures or extreme events. Adaptive evolution is a balance between gene flow (genetic exchange among populations) and selection. If there is too much gene flow, selection must be very strong to make an impact on top of the continual input of new individuals and genes to the populations. If there is too little gene flow, genetic variation may be too low such that more favorable alleles are not present for selection to promote (Blanquart et al. 2013). In an estuary, populations may be isolated by salinity barriers (i.e. the Pacific Ocean blocking exchange of fresh or brackish water species with other estuaries) and gene flow may be dependent on the same vectors of invasive species introduction that first brought the presently dominant species here.

Changes to zooplankton community structure in response to climate change will be contingent on new community members with tolerances appropriate to the new environment being present. The current suite of invasive species likely rose to dominance because of their wide salinity tolerance that helped them thrive in drought conditions, different feeding modes that were more effective in conditions with lower quality and quantity of phytoplankton prey, and better escape behaviors against benthic clams (Winder and Jassby 2011). In the ocean, new species can be introduced via range shifts, whereas freshwater systems are more disconnected, making colonization less likely. In the estuary, rapid invasions, such as those facilitated by global shipping (Simkanin et al. 2009), may increase the likelihood of zooplankton community turnover more than in freshwater, but not as much as in the open ocean.

Like phytoplankton, zooplankton may also experience changes to phenology. Peak abundance of zooplankton taxa has also shifted earlier in the past 40 years (Merz et al. 2016). It is unclear if the observed phenological shift for plankton is linked to climate change, but continued increases to temperature earlier in the year, and potentially earlier spring run-off may cause this shift to continue. Decoupling of timing between trophic levels have led to reduction in zooplankton availability in other systems (Winder and Schindler 2004), so if taxa shift at different rates there may be food limitation or other stresses from changing community structure.

Harmful Algal Blooms (HABs)

Status

Toxic freshwater cyanobacteria blooms (Cyanophyta) have occurred each year in the freshwater reaches of the upper estuary since 1999. These blooms are dominated by *Microcystis* spp., but the abundance of other toxic cyanobacteria species including *Dolchospermum* and *Aphanizomenon* have increased since 2014 (Lehman et al. 2021). The current bloom is a cocktail of cyanobacteria species with multiple toxins that affect both the liver (microcystin) and the nervous system (anatoxin *a* and saxitoxin). These blooms occur in

the summer and fall, and can be detrimental to photosynthetic plankton, including other cyanobacteria (Lehman et al. 2010, 2017), zooplankton (Ger et al. 2009), and native fishes (Acuña et al. 2012; Kurobe et al. 2018). The abundance and duration of the blooms are directly correlated with water temperature and residence time and can last from July through December (Lehman et al. 2008a, 2013, 2017). *Microcystis* first appears in the water column when water temperature reaches $\geq 19^{\circ}\text{C}$ (Lehman et al. 2008b, 2013), increases in abundance until water temperature reaches 25°C , persists until water temperature declines to $\leq 15^{\circ}\text{C}$, and then settles out of the water column to the sediment to await the next season (Lehman et al. 2017, 2020). The cyanobacteria HAB bloom is larger during dry (i.e., low freshwater outflow) years and peaks when the X2 index is 85 km or more. Other freshwater HABs in the upper estuary include the haptophyte *Chrysochromulina* and the green alga *Euglena*, but large blooms of these species have not occurred.

In the brackish water reaches of the upper estuary near Suisun Bay, eukaryotic phytoplankton in the phyla Dinoflagellata and Bacillariophyta periodically produce small HABs. These blooms usually contain neurotoxins that cause paralytic and amnesic shellfish poisoning. Dinoflagellata HABs contain dinoflagellates like *Alexandrium*, *Karlodinium* and *Peridinium*, which contain the paralytic shellfish poison saxitoxin (Sutula et al. 2017; Peacock et al. 2018). Bacillariophyta HABs contain the diatom *Pseudo-nitzschia*, which contains the amnesic shellfish poison domoic acid.

Response to Climate Change

It is expected that as water temperature increases with climate change the date of cyanobacteria bloom initiation will be earlier and the duration will be longer (Lehman et al. 2017, 2020). It is also expected that the magnitude of *Microcystis* blooms will increase with warmer water temperature because warm conditions favor growth of *Microcystis* over most photosynthetic plankton (Paerl and Huisman 2009). Because toxin production is linearly correlated with growth rate, increased temperature may also cause increased microcystin toxin production (Harke et al. 2016). It is further likely that as water temperature increases more species of toxic cyanobacteria will bloom in the estuary. The toxic cyanobacteria, *Dolichospermum* and *Aphanizomenon*, and their associated neurotoxins (saxitoxin and anatoxin a) have increased during the *Microcystis* bloom season since 2016 (Lehman et al. 2021).

The variation of wet and dry conditions with climate will have a significant impact on HABs in the upper estuary. High residence time associated with dry conditions enables HAB cells to accumulate and avoid being flushed downstream (Harke et al. 2016). This is especially important for the HAB *Microcystis* because it has a slow growth rate (Lehman et al. 2008b; Lee et al. 2015). High residence time is needed for blooms to develop and to reach a broad spatial distribution (Lehman et al. 2017, 2020). Since 1999, *Microcystis* blooms have been larger during

dry and critically dry years compared with wet years (Lehman et al. 2013, 2017, 2018, 2020). Water temperature and the X2 index, an index of salinity intrusion and associated residence time, were able to explain 78% of the surface and 58% of the subsurface *Microcystis* abundance (Lehman et al. 2020). Maximum *Microcystis* abundance occurred when the X2 index was above 85 km (Lehman et al. 2020). The bloom will persist, even in extreme wet years, as long as environmental conditions are favorable for some period of time, because cells are always present in the sediment (Lehman et al. 2017, 2020). A *Microcystis* bloom occurred late in 2017, even though 2017 was the wettest year on record since 1906 (Lehman et al. 2020). Wet and dry conditions will also affect the water quality conditions that influence HAB development. Flushing of ammonium from wastewater treatment plants downstream into the Delta during wet years will favor the growth of *Microcystis* which grows rapidly on ammonium (Lee et al. 2015; Lehman et al. 2015) and is more abundant when ammonium comprises a greater percentage of the total nitrogen at a given location (Lehman et al. 2015). Flushing of herbicides into the Delta during wet years or high application of herbicides to prevent aquatic weeds in dry years may also enhance *Microcystis* abundance. In laboratory studies, *Microcystis* had a lower mortality than diatoms when exposed to the herbicide fluridone (Lam et al. 2020).

Wet and dry conditions along with sea level rise will affect the salinity of the water column which will affect the type of HABs in the upper estuary. Low salinity conditions will favor freshwater cyanobacteria (e.g., *Microcystis*, *Dolichospermum*), haptophytes (e.g., *Chrysochromulina*) and green flagellates (e.g., *Euglena*). High salinity conditions will favor toxic dinoflagellate (*Alexandrium*, *Karlodinium* and *Peridinium*) and diatom (*Pseudo-nitzschia*) species (Sutula et al. 2017; Peacock et al. 2018). In the shallow waters of Suisun Bay these blooms may eventually cause low dissolved oxygen concentration (Sutula et al. 2017; Peacock et al. 2018).

Benthos

Benthic organisms are a major component of the estuarine food web, as exemplified by the introduction of *Potamocorbula* during the 1980s that caused a cascading effect (Nichols et al. 1990; Kimmerer 2006; Kimmerer and Thompson 2014). For the purpose of this article, we included epiphytic algae and invertebrates associated with aquatic vegetation under the benthos category. We split the benthic community into the following: benthic and epiphytic algae, epibenthic and epiphytic invertebrates, and benthic invertebrates. We also highlight a couple of species that have had a sizeable role in altering the estuary's food web: *Potamocorbula* and *Corbicula*, as well as one understudied taxon that may have had a substantial impact in the littoral habitat: crayfish.

Benthic and epiphytic algae

Status

Benthic algae are understudied, and existing studies have highly variable results. One analysis showed benthic algal production to be an order of magnitude lower than water-column phytoplankton production (Cohen et al. 2014), but other assessments show it can be quite important in shallow, littoral habitat (Cloern et al. 2016). However, it is likely that benthic algae in seasonal wetlands are much less important in the current Delta than historically (Cloern et al. 2016). However, recent analyses show that benthic diatoms are often the dominant plankton in river water (Kraus et al. 2017).

While not traditionally considered major parts of the estuarine food web in the Estuary, epiphytic algae and invertebrates may have extremely high biomass in areas dominated by aquatic weeds. Epiphytic algae are an important source of production for many taxa in aquatic weed beds, since they are more bioavailable than the vascular plants themselves (Klumpp et al. 1992). While epiphytic algae are understudied in the Delta, they are thought to be less important to the total system productivity in the current delta because of the loss of emergent vegetation (Cloern et al. 2016).

Response to Climate Change

Increased temperature could increase the productivity of some benthic and epiphytic algae. Decreased turbidity from sedimentation in slow moving waters, especially in aquatic weed beds, could increase production of benthic versus pelagic photosynthetic plankton due to increased light availability near the bottom. However, shade produced by aquatic vegetation may limit the available light (Yarrow et al. 2009). Lastly, sea level rise could decrease the extent of littoral habitat, enhancing benthic production (Swanson et al. 2015).

Epibenthic and epiphytic invertebrates

Status

Invertebrates associated with vegetation can also be extremely productive. Studies have found that abundances of amphipods, isopods, snails, and insect larvae, in particular, may be an order of magnitude higher in submerged vegetation than in open water or emergent wetland vegetation (Hartman et al. 2019). However, the value of vegetation as invertebrate habitat varies with the identity of the plants, with native plants often providing more habitat for native invertebrates and better foraging opportunities for fish than invasive plants (Toft et al. 2003; Boyer et al. 2013). Epibenthic and epiphytic invertebrates have become more important in diets of listed fish in recent decades since the productivity of phytoplankton and zooplankton has decreased (Slater and Baxter 2014).

Response to Climate Change

Epiphytic invertebrate communities may also change with increased temperature, shifting in abundance, community composition, size, and/or phenology. Amphipods have not been studied extensively in the Estuary, so it is unclear how they will respond to climate change. One study of amphipods in the genus *Gammarus* found congeners to have highly different phenotypic plasticity in response to temperature (Rastrick and Whiteley 2011), so some species in the Delta may adjust to rising temperatures, whereas others may be replaced by new invaders. Temperature thresholds for the dominant epifaunal taxa in the Delta (*Hylella*, *Gammarus*, *Crangonyx*), are high enough to withstand warming waters in the near-term (Ginn et al. 1976), however increased temperature may reduce *Hylella*'s ability to cope with pesticides and salinity (Hasenbein et al. 2018; Fulton et al. 2021).

Crayfish

Status

The largest invertebrates in the vegetation community are crayfish. Crayfish are omnivores, grazing on both the vegetation and smaller epiphytic invertebrates (Momot 1995). There are two species of crayfish in the Delta, the native signal crayfish (*Pacifastacus leniusculus*), and the invasive red swamp crayfish (*Procambarus clarkii*). They are major components of striped bass, pikeminnow, and largemouth bass diets (Weinersmith et al. 2019; Stompe et al. 2020b). Comparison of Largemouth Bass diet studies between the 1960s and 2000s may indicate that *P. clarkii* has become more prevalent than *P. leniusculus* (Turner and Kelley 1966; Nobriga and Feyrer 2007; Weinersmith et al. 2019), but their overall trends and ecosystem importance are not well understood.

Response to Climate Change

Neither crayfish species is considered especially vulnerable to climate change (Hossain et al. 2018), and both have been introduced around the world, where they may have sweeping ecosystem impacts. Prolonged heat waves may switch *P. clarkii* diet from majority carnivorous to majority herbivorous, and may decrease growth and survival (Carreira et al. 2017), but *P. clarkii* is found globally at higher temperatures than *P. leniusculus*, so it may dominate the Delta in the future (Zhang et al. 2020).

Benthic invertebrates

Status

Benthic invertebrates, with the exception of invasive bivalves (Asian clams *Corbicula fluminea* and *Potamocorbula amurensis*), are understudied in the estuary. Benthic invertebrate

community structure is typically driven by salinity and substrate type, and is relatively stable across seasons and years in comparison to the zooplankton community (Thompson et al. 2013). Besides bivalves, the community is primarily comprised of amphipods such as *Americorophium* spp., *Hylella*, and *Gammarus daibari*, the cumaceans *Nippoleucon hinumensis*, and annelid worms such as *Varichaetadrilus angustipenis* and *Manayunkia speciosa* (Watkins and Wells 2020). Precise species composition is driven by salinity, with more salt-tolerant species in the brackish-water reaches of Suisun Bay and Suisun Marsh, and freshwater species in the Delta.

Invasive bivalves *Potamocorbula* and *Corbicula* have had an outsized effect on the estuary food web, severely grazing down the standing stock of phytoplankton biomass (Kimmerer and Thompson 2014). Native bivalves, such as the mussels *Anodonta* spp. and native clams *Psidium* spp. and *Macoma* spp. have lower reproductive rates and lower grazing rates, so were not thought to have controlled the pelagic food web historically (Nichols et al. 1990; Howard and Cuffey 2006). Shallow-water habitat is particularly impacted by benthic grazers because clams can filter the entire water column quickly.

Response to Climate Change

It is unclear how rising water temperature will affect the benthic invertebrate community of the estuary, however, it will likely increase the grazing rates of bivalves in addition to changing species composition. Because the benthic communities are aligned fairly well along the salinity gradient (Thompson et al. 2013), we expect that increased salinity intrusion due to sea level rise would lead to a more truncated distribution for the tidal freshwater species (e.g., *C. fluminea*, tubificid oligochaete worms, *G. daibari*) and further inland distribution of the brackish-water species (*P. amurensis*, *Marenzelleria viridis* polychaete worm, *N. hinumensis*). A more dynamic salinity field in the estuary may also mean that dispersal mechanism will become more important in determining community clusters. Benthic invertebrates with planktonic larval stages may be better able to shift their distribution with salinity.

Potamocorbula amurensis (Overbite clam)

Status

The overbite clam, *Potamocorbula amurensis*, has had sweeping impacts on the aquatic ecosystem of Suisun Bay and the brackish regions of the estuary since it was introduced in 1986. These clams have extremely high grazing rates and reproductive rates that outpace native grazers and phytoplankton production, leading to low phytoplankton biomass and associated declines in pelagic organisms further up the food web (Greene et al. 2011; Winder and Jassby 2011; Crauder et al. 2016). *Potamocorbula* can also directly consume zooplankton and was implicated in substantial reductions of zooplankton in the estuary (Kimmerer et al. 1994). *Potamocorbula* competes with other benthic infauna, including native clams and

mussels, and alters benthic dynamics through substrate destabilization, alteration of suspended sediment load of near-bottom water, and change of sediment surface redox balance (Carlton et al. 1990). They are a source of prey for benthic feeding birds and fishes (Linville et al. 2002; Poulton et al. 2002; Zeug et al. 2014), however their ability to bioaccumulate selenium may cause toxic effects further up the food web (Stewart et al. 2004). Adult *Potamocorbula* can tolerate salinities from 0.1–32.0 PSU (Carlton et al. 1990; Werner and Hinton 2000) but cannot recruit into the population at salinities below 2PSU (Nicolini and Penry 2000), so *Potamocorbula* is the dominant clam species in the salinity range of 1–18 ppt in the Estuary (Crauder et al. 2016). They occur in all sediment types except hard rock surfaces, are tolerant of very low dissolved oxygen, and may occur in any water depth, including the intertidal zone (Thompson and Parchaso 2012).

Response to Climate Change

Potamocorbula can survive temperatures up to 36 °C, but are reproductive at lower temperatures (6-23 °C), so increased temperatures may shift the spawning window, increasing reproduction during the winters and decreasing during the summers. Filtration rate will increase with temperature, up to some threshold, though this relationship has not been experimentally tested in *Potamocorbula* (Thompson et al. 2008; Kimmerer and Thompson 2014). In shallow water, where the benthic community can more effectively filter the entire water column, this increase in filtration rate may offset any increase in pelagic phytoplankton production (Lucas et al. 2009).

Shifts to flow and the salinity regime is predicted to have the largest impact on *Potamocorbula*. Higher outflow will shift the low salinity zone westward, causing lower recruitment in the Confluence and Suisun Bay, whereas droughts and sea level rise will allow *Potamocorbula* to colonize further up the Sacramento River (Nichols and Thompson 1985; Nichols et al. 1990; Peterson and Vayssieres 2010). If the shifts in salinity occur rapidly, overall population of *Potamocorbula* may decrease. *Potamocorbula* larvae are pelagic, so recruits do have the ability to move with shifting conditions, however populations will not shift as quickly as zooplankton or fishes since benthic adults are unable to move.

Corbicula fluminea (Asian clam)

Status

The Asian clam (*Corbicula fluminea*) is another bivalve introduced from Asia and now common in the upper Estuary. *Corbicula* were introduced in the 1940s, and while they can impact pelagic productivity, their grazing rates are four times lower than *Potamocorbula*. Therefore, they have not caused the extreme declines seen in other parts of the estuary occupied by *Potamocorbula* (Thompson and Parchaso 2013). Other systems have seen reductions of chlorophyll with

invasion of these clams (Phelps 1994; McMahon 1999), and high clam abundance has been linked to lower productivity in local areas of the Delta (Lopez et al. 2006), but not the sweeping ecosystem changes seen in Suisun Bay. *Corbicula* are an important food source for benthic fishes and birds. They do not bioaccumulate selenium and other toxic contaminants in as high a concentration as *Potamocorbula*, but their hard shells make them less digestible than other benthic organisms.

Response to Climate Change

Corbicula is very tolerant of high temperatures and may benefit from climate change. The temperature range for adults is typically 0-34 °C, with a lethal limit of 38 °C (Nascimento et al. 1996), much higher than typically seen in today's Estuary. Like *Potamocorbula*, higher temperatures will increase filtration rates, with rates increasing up to a threshold of between 24 and 30°C. (Mattice and Dye 1975; Lauritsen and Mozley 1989). However, if higher temperatures are accompanied by low dissolved oxygen, growth rates may be reduced and large-scale die-offs can occur at very low DO (Cherry et al. 2005; Ilarri et al. 2010). *Corbicula*'s distribution will also change with shifting flow and salinity regimes. Their abundance and range will be positively influenced by higher outflow years and negatively influenced by dry years (Peterson and Vayssieres 2010; Castillo 2019), because their larvae are restricted to salinities of <2 PSU (Foe and Knight 1985). Adults may survive at salinities up to 10 PSU, so brief periods of high salinity may not negatively impact the population. However other studies show *Corbicula fluminea* can occur at salinities up to 17 PSU (Lucy et al. 2012)

The overlap in salinity tolerance between *Corbicula* and *Potamocorbula* results in dominance of *Corbicula* in the confluence and Suisun bay after high-outflow periods and *Potamocorbula* dominance after periods of low-outflow. *Corbicula* larvae are not pelagic, and instead move with movement of sediment, so have somewhat less ability to shift their range with changing conditions. However, small adults can use secreted mucous threads to float and disperse with water movement (Prezant and Chalermwat 1984) and this behavior has been triggered by temperature increases (Rosa et al. 2012), so climate change may trigger increased dispersal in this species.

Conclusion

The amount of open-water habitat has essentially doubled since the mid-19th century and today it is the dominant aquatic habitat in the estuary (SFEI-ASC 2014). Climate models project increased air temperatures as well as more frequent floods and droughts in California. Meanwhile, sea level rise will lead to further encroachment of salinity into the Delta for large parts of the year, and lower snowpack levels will mean reduced late-spring and early-summer flows. These climate change impacts will alter the dynamics of the open water habitat in the

estuary and impact the organisms that inhabit it in both direct and indirect manners. The multivariate and interacting nature of these environmental drivers result in much uncertainty regarding the trajectory of this habitat; however, some larger overarching trends were evident from our literature review. For all functional groups, we expect a shift in phenology and increased prevalence of brackish-water or salinity tolerant assemblage in the upper estuary. A considerable number of non-native and cosmopolitan species tolerant of high temperatures are predicted to be resistant to or benefit from climate change consistent with their upward trends in the estuary (e.g., *Microcystis*, *P. amurensis*, *Egeria* etc.). In contrast, climate change impacts are expected to be detrimental to some fish species of conservation concern in the estuary that utilize the open waters such as Delta Smelt, Longfin Smelt, and Chinook Salmon. Other native species may become more prevalent (e.g., Tule Perch, *Stuckenia* spp.). The answer to the question of what the estuary exactly would look like under different climate change scenarios remains elusive, but the conceptual model framework we present in this paper can be used to highlight key uncertainties ripe for future research.

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Appendices

Appendix A: Supplemental Information on Delta Smelt

Distribution and responses relevant to climate change

Because field data enables interpreting laboratory experiments in a more integrated ecological context, field data are a critical complement to evaluate potential fish responses to climate change impacts. For example, based on otolith analyses, growth rate of Delta Smelt is reduced at temperatures $>20^{\circ}\text{C}$ and when salinity is greater than 2 ppt (Hobbs et al. 2019). Variability in spawning success and larval survival for Delta Smelt is induced by climate and other environmental and anthropogenic factors that operate between winter and mid-summer (Bennett 2005, Nobriga et al. 2008, Castillo et al. 2018). In addition, considering that reductions in freshwater flows during fall has been linked to long-term habitat degradation and reduced abundance of this species (Feyrer et al. 2007, Castillo 2019), increased drought frequency under climate change could exacerbate habitat degradation during fall. Unger (1994) used the 10th and 90th percentiles of salinity distribution to estimate the ranges of optimal salinities for Delta Smelt and nine other estuarine species, including fishes and invertebrates. Based on these analyses, Delta smelt exhibited the narrowest optimum salinity range (0.3 - 1.8 ppt) at the larval and juveniles stages. For juvenile stages alone however, Bennett (2005) reported that $>90\%$ of the catch occurred under 6 ppt. The low salinity range for larvae and juvenile could also apply to subadult and adult Delta Smelt. Bennett showed $>90\%$ of subadult Delta Smelt are caught at salinities <6 ppt; while adult Delta Smelt predominated at a salinity of 1.32 ± 1.94 ppt (mean \pm sd) (Castillo et al. 2018). Bennett showed 50% and 100% of juvenile Delta Smelt were respectively caught at temperatures of c.a. 21.5°C and 26°C . In contrast, 50% and 100% percent of subadult Delta Smelt were respectively collected at water temperatures of c.a. 16°C and 22.5°C . Moreover, adult Delta Smelt predominated at a temperatures of $11.17 \pm 2.38^{\circ}\text{C}$ (mean \pm sd) and turbidities of 44.9 ± 25.9 NTU (mean \pm sd) (Castillo et al. 2018). Feyrer et al. (2007) modeled subadult Delta Smelt presence/absence as a function of EC, temperature and Secchi depth. Their models showed EC and Secchi depth were more important than temperature. While no absolute thresholds for “suitable” abiotic habitat were evident, fish occurrence increased exponentially as Secchi depth below 1 m while occurrence reached a peak at EC $\sim 5000 \mu\text{S cm}^{-1}$. Predicted fish occurrence declined progressively at EC $> 12000 \mu\text{S cm}^{-1}$ compared to EC $< 5000 \mu\text{S cm}^{-1}$. Nobriga et al. (2008) modeled juvenile delta smelt presence/absence as a function of EC, temperature and Secchi depth, and found all these covariates were important, with highest probability of occurrence at EC 1000-5000 (c.a. 0.6-3 psu), Secchi <40 cm and temperatures less than 24°C .

Experiments relevant to climate change impacts:

Laboratory tests using wild fish showed juvenile Delta Smelt 38-47 mm acclimated to 17 °C were generally sensitive to temperatures >24°C and had a critical thermal maximum (CT_{max}, loss of equilibrium endpoint) of 25.4°C (Swanson et al. 2000). Juvenile Delta Smelt acclimated to 11.9, 15.7 and 19.7 °C had CT_{max} of 27.1, 28.2 and 28.9 °C, respectively (Komoroske et al. 2014). Evaluation of cellular processes, sublethal thresholds and effects of thermal acclimation on acute stress responses (Komoroske et al. 2015) showed that Delta Smelt had limited capacity to modify the expression of some genes and cellular mechanisms key to coping with acute thermal stress. Sublethal critical thresholds of Delta Smelt were 4–6 °C below upper tolerance limits and their limited thermal plasticity may be partially due to an inability to achieve new homeostasis at higher temperatures, leading to chronic thermal stress (Komoroske et al. 2015). Similarly, by exposing larval Delta Smelt to 14°C and 20°C Jeffries et al. (2016) examined the transcriptome-wide responses using RNA sequencing by exposing fish to elevated water temperature. At 20°C they noted increases in both metabolic rate and expression of genes involved in metabolic processes and protein synthesis.

Based on a survival test reflecting the natural daily temperature cycle in the south Delta during summer, Castillo et al. (2012) found that exposure of juvenile Delta Smelt to peak daily ambient water temperatures above 27 °C over consecutive days significantly reduced survival. Although a fraction of Delta Smelt was able to survive repeated exposure to temperatures comparable to CT_{max} estimates from lab experiments, the extent to which Delta Smelt could selectively adapt to higher temperatures has not been experimentally evaluated and such capacity can vary greatly among species (e.g., Klerks et al. 2019).

Komoroske et al. (2014) reported that short-term (96 h) survival of late-larval Delta Smelt, juvenile and adults was not influenced by salinities of 0.4 to 18 ppt. Additional tests for juvenile and adult showed survival at salinities of 34 ppt was 81.5% for adults and 64.5% for juveniles. Although Delta Smelt can osmoregulate in response to rapid salinity changes in estuarine environments, body condition was reduced at high salinities (Komoroske et al. 2016).

Comparative physiological studies of Delta Smelt and introduced fish species:

These studies provide additional insights on potential implications of climate change on habitat overlap, fish interactions, environmental protection and habitat restoration efforts. Use of the same, or similar, experimental conditions can be particularly useful to compare stressors among fish.

Comparison between Delta Smelt and Wakasagi: Swanson et al. (2000) compared the tolerances of Delta Smelt and Wakasagi to temperature, salinity, and water velocity, three factors that vary spatially and temporally in the estuary and could be greatly influenced by climate change. For fishes acclimated to 17°C and fresh water (0 ppt), they measured CT_{max},

CT_{min}, chronic upper salinity tolerance limits, and critical swimming velocities. Wakasagi had higher CT_{max} (29.1 °C vs 25.4 °C), lower critical thermal minima (2.3 °C vs. 7.5 °C), higher upper salinity tolerances (26.8 ppt vs. 19.1 ppt), and swam faster (43.3 cm s⁻¹ vs. 28.2 cm s⁻¹ for fish 6.0-6.9 cm SL fish). Given the wide seasonal and year-to-year fluctuations of these habitat factors in the estuary, Swanson et al. (2000) concluded Delta Smelt may be at a physiological disadvantage. The lower abundance of Wakasagi in the estuary at that time suggested that Wakasagi eggs and larvae may be less tolerant to temperature, salinity, and flow. Alternatively, other unaccounted factors may determine Wakasagi distribution in the estuary.

Comparison among Delta Smelt, Mississippi Silverside and Largemouth Bass: To evaluate how environmental stressors (elevated temperature or salinity) are exacerbating climate change and drought-related impacts, Davis et al. (2019a) examined how single and multiple environmental stressors influence the physiology of Delta Smelt and compared that to the responses of two introduced fish species (Mississippi Silverside, *Menidia beryllina* and Largemouth Bass *Micropterus salmoides*). They determined CT_{max} after 0, 2, 4 and 7 days following single and multiple stressors of elevated temperature (16°C vs. 20°C) and salinity (2.4 vs. 8–12 ppt), introduced fishes had significantly higher CT_{max} than Delta Smelt (which also had increased hematocrit and decreased muscle tissue water content). Elevated salinity had little effect on CT_{max} but consistent with previous studies, a 4°C rise in temperature increased CT_{max}. Hence this study further suggests increased physiological disadvantage for Delta Smelt to climate change. It further suggested potential ecological disadvantages to cope with species interactions under climate change.

Turbidity effects:

Climate change projections suggest increases in suspended sediment in the estuary (Stern et al. 2020) but because turbidity is also influenced the same direction by organic matter, and phytoplankton and in opposite direction by macrophytes (e.g., Hestir et al. 2016), the direction of change for this key habitat component of Delta Smelt in response to climate change is unclear. Given that turbid conditions are important for feeding of larvae (Baskerville et al. 2004) and that long-term increase of Secchi depth (decreased turbidity) is linked to reduced habitat quality for subadult Delta Smelt (Feyrer et al. 2007), certain levels of turbidity increases could benefit Delta Smelt. Highest feeding rates for Delta Smelt occurred at low turbidity (12 NTU) but relatively persistent feeding rates occurred over a broad range of turbidities (12–120 NTU), (Hasenbein et al. 2013). In combination with salinity, turbidity can influence feeding performance and physiological stress and increasing turbidities could result in reduced feeding rates, especially at 250 NTU (Hasenbein et al. 2013). Yet, reduced predation pressure is more likely under more turbid conditions (Ferrari et al. 2014).

Climate Change Models:

Feyrer et al. (2011) modeled how a range of drier and wetter climate change scenarios could relate to estuarine outflow and a habitat index of subadult Delta Smelt. Results suggested all outflow scenarios would generally lead to further declines in Delta Smelt habitat across all water year types. However, the model did not account for expected increase in the extent and duration of stressful water temperatures in the estuary. Moreover, Brown et al. (2013) modeled changes in the position of the low salinity zone, turbidity, and water temperature from four 100-year scenarios of climate change. Their projections suggested water temperature increase would render waters historically inhabited by Delta Smelt near the confluence largely uninhabitable. In addition, the projected position of the low salinity zone in the fall and the habitat suitability index by the mid 21 century reached values only observed during the most severe droughts of their baseline period (1969–2000). Potential climate change influence on the spawning window of Delta Smelt has also been inferred. Bennett (2005) defined spawning season as the time when temperature is 15-20 °C based primarily on hatch success, with an optimal temperature of 15-17 °C. Results showed the end of spawning season was correlated with a climate change index (first principle component of sea surface temperature, sea level at Fort Point (entrance to the estuary at the Golden Gate Bridge and the Pacific Decadal Oscillation index). Based on the duration of fall temperatures <20 °C to allow for maturation of Delta Smelt, Brown et al. (2013) suggested this temperature window would occur earlier and decrease with climate change. Yet, the mean date of the spawning window seemed more responsive to climate change than the duration of the window. Brown et al. (2016) suggested a decrease in spawning duration only for the most extreme scenario and the beginning of spawning was expected 20-41 days earlier. Hobbs et al. (2019) suggested a temperature of 12 °C might be better indicator of spawning duration of Delta Smelt and 15 °C may be too conservative for the beginning of spawning. Hatching corresponded with temperature variability and 20 °C seems a threshold for the end of reproduction. They suggested that droughts could greatly accelerate hatching period, as seen during the last drought when water temperatures of 20°C in Suisun Bay and the Delta reach occurred earlier in the year.

Climate change influence on the position of the low salinity zone (LSZ):

More extreme hydrology under climate change (Knowles et al. 2018) suggests correspondingly more variable Delta Smelt responses could be expected. Given current and projected trends in sea level rise for the estuary (NRC 2012) a long-term upstream movement of the LSZ would be expected along the Sacramento and San Joaquin rivers. Reduced fall outflow (increased X2) is predicted to reduce abiotic habitat and abundance of subadults (Feyrer et al. 2011). Reduced fall outflow likely exposes Delta Smelt to more unfavorable press-perturbations enhanced by community interactions (X2 positions > 81 km) compared to community interactions when X2 ≤ 74 km (Castillo 2019). Population trends of Delta Smelt and other pelagic species were

associated to overall salinity increases due to water diversions (Castillo et al. 2018), suggesting this effect would be more prevalent under increased frequency of droughts and higher sea levels. Increased drought frequency would also greatly limit Delta Smelt recruitment given that lower February-June X2 is associated to higher relative abundance of larval-juvenile Delta Smelt (IEP 2015).

Appendix B: Supplemental Information on Wakasagi

Interactions with Delta Smelt: Evidence of hybridization between the two species seems to confirm spawning of Wakasagi also occurs in the freshwater portions of the estuary (Dill and Cordone 1997, Moyle 2002). Wakasagi larvae are also typically mixed with Delta Smelt and Longfin Smelt larvae (Wang 2007). Benjamin et al. (2019) showed the hybrids of these two congener species are not sterile, contrary to what was previously assumed (Trenham *et al.*, 1998). Benjamin et al. (2019) reported directional backcrossing between hybrids of these two species and Wakasagi; but no further introgression of Delta Smelt was detected in the Yolo Bypass. Benjamin et al. (2019) found very few hybrids and unidirectional gene flow. They stated that even if hybridization between Wakasagi and Delta Smelt does not cause introgression for Delta Smelt, hybridization can still reduce their genetic diversity and compromise their viability (e.g., through wasted reproductive energy, competition, or infectious diseases (Laikre et al. 2010). Benjamin et al. (2019) recommended additional genetic monitoring efforts to quantify hybridization rates over space and time in the estuary. Hence, Allee effects could significantly impact Delta Smelt if the Delta Smelt population declines further or if the Wakasagi population continues increasing in the estuary.

Appendix C: Supplemental Information on Longfin Smelt

Distribution in relation to abiotic habitat components:

Density of larval Longfin Smelt in the estuary seemed to peak between 8 and 12 °C (Grimaldo et al. 2017) but temperature did not explain model variance as well as salinity or Secchi depth, with salinity explaining best larval Longfin Smelt densities, and densities being negatively related to salinity less than 2 and above 12 ppt (Grimaldo et al. 2017). Secchi depth was second to salinity in explaining the model variance, with Longfin Smelt density peaking near 50 cm, while increasing Secchi depths were negatively related to larval densities. Catch weighted distribution of Longfin Smelt larvae and juveniles in the estuary (mean \pm sd) was associated salinities of 3.13 ± 2.93 ppt; turbidities of $64.6 \text{ NTU} \pm 35.5$; and temperatures of 15.97 ± 1.60 °C from March to July (Castillo et al. in prep.). Interestingly, the temperature (mean \pm sd) at which most larvae and juvenile Longfin Smelt are collected is only a degree higher than the average temperature at which most juvenile and adult Longfin Smelt were caught from January to May in the upper estuary (14.9 ± 1.91 °C; Castillo et al. 2018). Based on this, the extent to which

maturation and spawning success of Longfin Smelt could be impacted in warmer waters under climate change projections seems a relevant question.

Response to outflow:

Distribution of larval and post-larval Longfin Smelt across the salinity field in estuary areas west of the confluence during 2016 and 2017 was upstream during the low outflow year 2016, overlapping with spawning habitats. In contrast, during the high outflow year 2017 they were distributed downstream, including smaller tributaries and shallow habitats of San Francisco Bay (Grimaldo et al. 2020). These findings are consistent with the ideas that recruitment success in San Francisco Bay is limited to years of high Delta outflow, in spite of the potential for spawning in all water year types (Lewis et al. 2020). Similarly, high outflow is also conducive to higher recruitment in the upper estuary (Kimmerer 2002, Nobriga and Rosenfield 2016). Yet, mechanisms influencing juvenile survival could be more prevalent in mesohaline or marine environments than in freshwater or low-salinity-zone waters (Nobriga and Rosenfield 2016). Delta outflow and X2 are also significantly associated to Longfin Smelt's abundance in the upper estuary (Stevens and Miller 1983; Kimmerer 2002b), Suisun Marsh and across the estuary (Rosenfield and Baxter 2007).

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Chapter 3: Tidal Marshes and Climate Change

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Introduction

Tidal marshes provide refuge, foraging, and spawning habitat for a variety of fish and wildlife species in the upper San Francisco Estuary (Estuary) Sacramento-San Joaquin Delta (“Delta”) and Suisun Marsh (Sherman et al. 2017b). Historically (~200 years ago), tidal marshes were the dominant landscape feature, covering 61% of total habitat area (Robinson et al. 2014). Larger sloughs branched into dendritic channel networks lined with extensive swaths of emergent vegetation (e.g. tules and cattails) and transitioned to uplands with riparian forests, oak woodlands, and seasonal creeks (Whipple et al. 2012). Spatial patterns of biological communities shifted as a function of the salinity gradient, with brackish marshes supporting more salt-tolerant species (e.g. pickleweed, marine transient fish) in downstream areas such as western Suisun Marsh (Moyle et al. 2014) and the Delta supporting less salt-tolerant species (cattails, freshwater resident fish).

In the present-day Delta, the spatial extent of tidal marshes has been drastically reduced, with 98% of freshwater emergent marshes lost to land conversion (Robinson et al. 2014). Suisun Marsh has lost 87% of emergent tidal marshes (Moyle et al. 2014). Widespread diking and draining of tidal marshes for agriculture and hunting disconnected large expanses of marsh plains from sloughs, which fragmented the landscape, dampened hydrologic variability, decreased physical access to vegetated marsh edges, and disrupted aquatic-terrestrial linkages supporting diverse and productive food webs. It also resulted in widespread oxidation of peat soils and elevation deficits (e.g. an estimated 5-30 mm per year subsidence rate in farmed Delta islands; (Deverel and Leighton 2010).

Remaining tidal marshes in the upper estuary are composed of a few large undiked patches (e.g. Rush Ranch, Browns Island), small patches of fringing marsh along diked channel banks, and restored marshes resulting from levee failure (e.g. Liberty Island, Sherman Lake) or intentional levee breaching/removal (e.g. Wildland’s [Liberty Island Conservation Bank](#), [Blacklock Restoration Project](#)). Several restoration programs are currently planning to restore tidal marshes, and a few restoration projects are being implemented (California Natural Resources Agency 2016, Robinson et al. 2016b, California Natural Resources Agency 2017). However, successful restoration and maintenance of tidal marshes is challenging because it is dependent on site-level factors such as hydrology, elevation, and sediment supply. Rising sea levels pose an additional challenge for the persistence of tidal marsh because increased hydroperiod must be compensated by sediment accretion, organic matter accumulation, and/or upland transgression to avoid marsh erosion and collapse (Kirwan et al. 2010, Knowles 2010).

In this conceptual model, we provide an up-to-date summary of how climate change will impact tidal marshes of the Delta and Suisun Marsh. We synthesize information on various climate

change impacts on the structure of tidal marshes and how these impacts are likely to alter ecosystem functions for fish, invertebrate, and plankton species.

Marsh Definition

To limit the scope of our review, we are using the following definition of “marsh”: Tidal marshes are ecotones where water and land meet in an intertidal vegetated zone, including both channels and the marsh platform.

- Marshes include an extended marsh platform. “Fringing marsh”, where a small line of emergent vegetation hugs a steep channel without a marsh plain is not included in this discussion.
- Marshes are perennially wet. Floodplains will be included in the Floodplains model, and other seasonal wetlands will not be addressed here.
- Tidal marshes must be connected to the tides and allow fish access. Managed wetlands cut off from the channel are not included.
- Marshes are dominated by emergent vegetation. Flooded lakes full of submerged vegetation are addressed in the Open Water model.
- Examples of marshes in the Delta and Suisun Marsh include: Liberty Island, the Lindsey Slough Restoration Site, Yolo Flyway Farms, Decker Island, the tip of Mandeville Island, Sherman Lake, Browns Island, Winter Island, Ryer Island (in Suisun Bay), Roe Island, Tule Red, Blacklock, the tip of Joice Island, Rush Ranch, and several areas on the southern coast of Suisun Bay (Figure 1, Figure 2).

Conceptual Model Structure

Like the Overview model, the Marsh sub-model is organized into tiers. At the top we have selected the environmental conditions within the marsh most likely to change given the global climate change effects discussed in the Overview model. These environmental conditions interact with the landscape, including human management and landscape change to influence the site-level environment. The focal groups (or “outcomes”) we have chosen to focus on are migratory fish (e.g., salmon), resident fish (e.g., Tule Perch), structural vegetation (e.g., tules and cattails), the benthic/epiphytic community (e.g., algae, amphipods), and the planktonic community (e.g., diatoms, copepods).

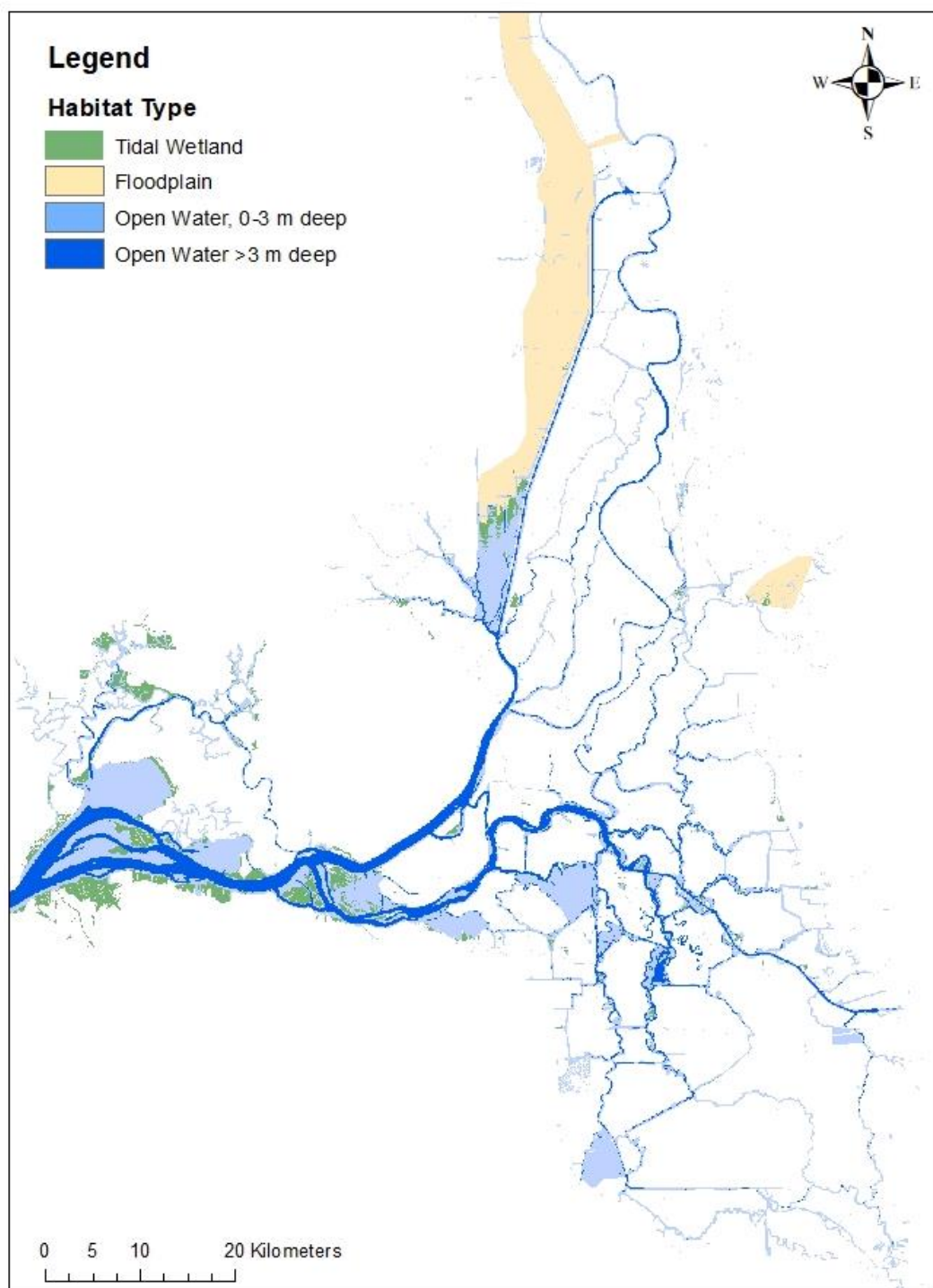


Figure 1. Map of habitat types in the Upper San Francisco Estuary. Tidal Marshes are in green. Delta floodplain and tidal marshes come from SFEI's Delta Landscape Scenario Planning tool (San Francisco Estuary Institute (SFEI) 2020). Suisun habitat types come from the California Aquatic Resource Inventory (San Francisco Estuary Institute (SFEI) 2017). Bathymetry comes from (Fregoso et al. 2017).

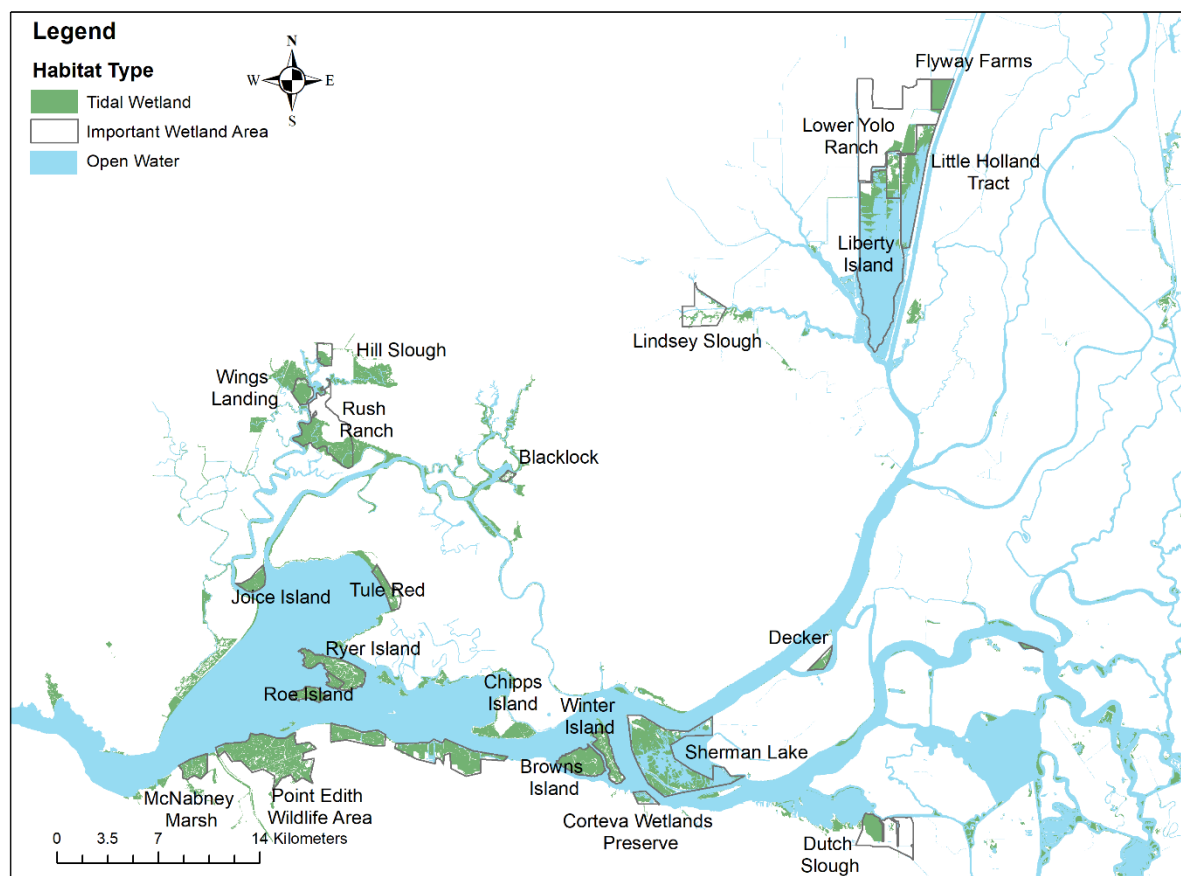


Figure 2. Map of important tidal wetland areas in the Delta and Suisun Marsh.

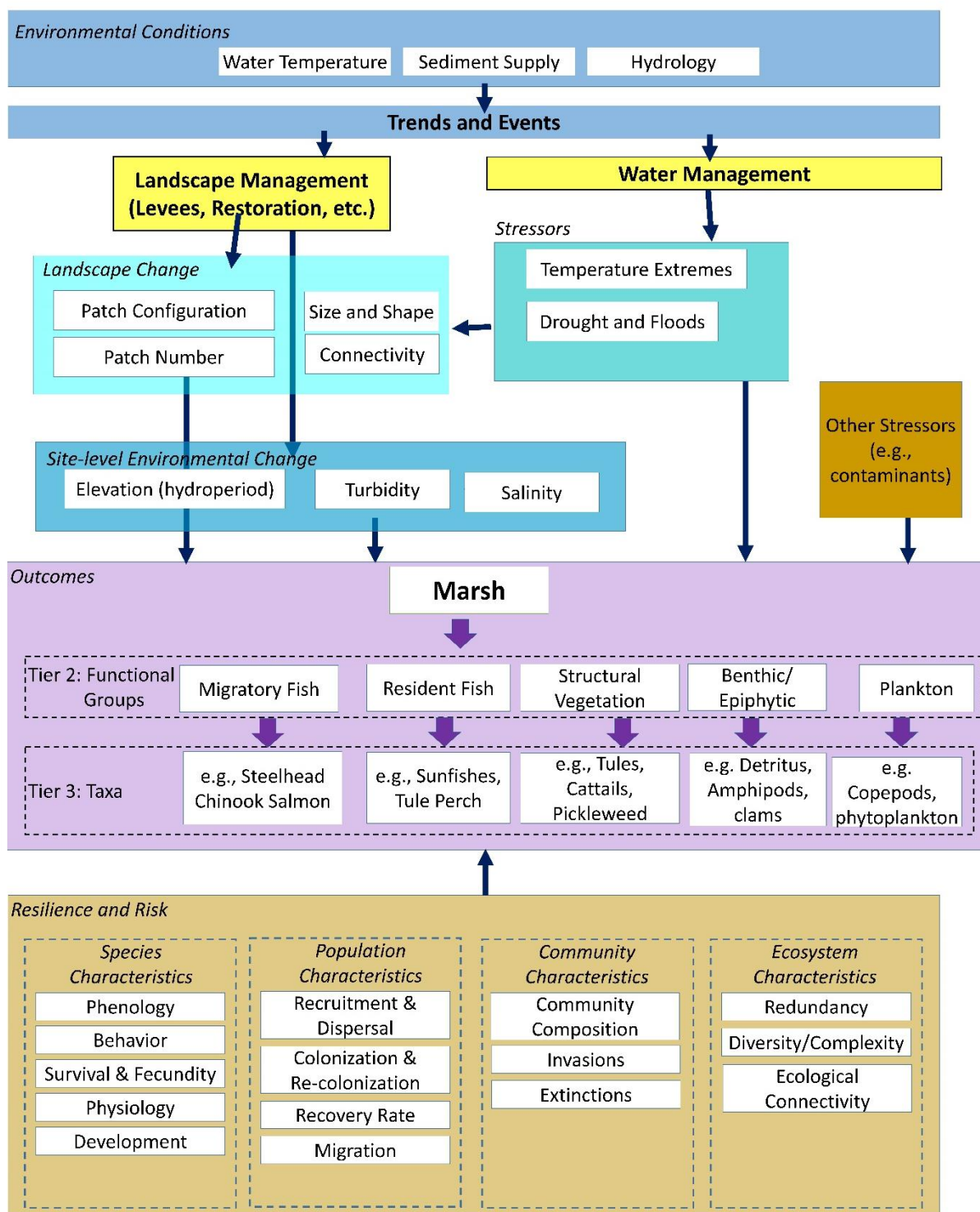


Figure 3. Model diagram for climate change impacts on tidal marsh.

Environmental conditions

Water Temperature

Water temperature variability in tidal marshes of the Delta and Suisun Marsh is driven by several factors, including atmospheric and tidal forcing. Shallow-water marshes have high surface-area-to-volume ratios so are more sensitive to changes in air temperature than deeper habitats (Shellenbarger and Schoellhamer 2011). Tidal flooding of the marsh plain during nighttime high tides can facilitate evaporative cooling and provide cool water that is exported to adjacent sloughs on outgoing tides (Enright et al. 2013). Climate change scenarios predict more extreme maximum temperatures during daytime, a phenomenon that is likely to be more pronounced in the interior marshes in the northern Delta (e.g. the Cache Slough Complex) and northern Suisun Marsh, which are further from cool tidal waters brought in from the Pacific Ocean (FLOAT-MAST 2020). Marshes on islands in Suisun Bay may be less subject to extreme temperature swings.

Vegetation can also have a cooling impact on water in marsh channels. In particular, the shade provided by emergent vegetation can decrease water temperature when compared to areas colonized by submerged vegetation (Miller and Fujii 2010). Water temperatures deeper in the marsh were found to be cooler than temperatures near the mouth of marsh channels (Crepeau and Miller 2014). Because marshes are shallow, they will not benefit from any thermal refugia found in deep channels, but most channels have relatively little stratification in the Estuary (Vroom et al. 2017).

Sediment Supply

The amount of sediment transported onto a tidal marsh is determined by an interaction between hydrology and upstream supply. Suspended sediment concentrations have been decreasing over the past 30 years due to depletion of the erodible sediment pool left over from the hydraulic mining era and upstream dams cutting off new sediment supply (Schoellhamer 2011). Episodic floods further deplete the erodible sediment pool from below the dams (Hestir et al. 2013). From 1957 to 2001 the sediment load from the Sacramento River decreased nearly 50% (Wright and Schoellhamer 2004), and this resulted in sedimentation rates in tidal marshes of the estuary decreasing as well (Canuel et al. 2009). There is also evidence that the increase in submerged aquatic vegetation contributes to decreases in suspended sediment and blocks sediment from reaching tidal marshes (Hestir et al. 2015, Drexler et al. 2020).

The future of sediment supply in the SFE is unclear. Cloern et al. (2011) predict that suspended sediment concentrations will decline slightly under the assumption that sediment supply remains constant, but concentrations may decline greatly if the current declining trend in available sediment continues. However, Stern et al. (2020) predict an increase in sediment

supply due to increases in peak stream flow. The future of sediment supply will determine whether marshes can increase in elevation fast enough to keep pace with sea level rise, particularly for marshes cut off from upland transition zones.

Hydrology

There is still uncertainty as to whether California will experience an overall increase or decrease in precipitation, however, it is agreed that spring floods will occur earlier in the year and a greater proportion of precipitation will fall as rain, rather than snow (Swain et al. 2018). There will also be increase in extremes – both wet and dry: more severe, longer droughts and stronger, wetter storms (Cloern et al. 2011). Floods may affect tidal marshes through their impact on local hydrology, causing an increase in water levels (see Site Level Environmental Change, below). Floods may also exacerbate the impact of sea level rise by threatening levee stability.

Within a marsh, the action of the tides impose greater control on the hydrology than freshwater inflow. Tidal flows may be orders of magnitude greater than net flow, and the daily, monthly, and annual cycles of the tides control temperature, water quality, productivity, and fish movement within the marsh (Enright et al. 2013, Sloey et al. 2015, Colombano et al. 2020a). On the estuary-wide scale, sea level rise may cause an increase in tidal amplification, if shorelines are armored and levees remain intact (Holleman and Stacey 2014). However, if sea level rise causes flooding of low-lying areas or marsh restoration increases flooded areas then tidal amplification will decrease (Holleman and Stacey 2014). Because the force of the tides is critical to site-level marsh geomorphology (see below) and for transporting productivity, changes in tidal amplitude will affect sediment accretion and marsh function in the future (Ganju et al. 2013, Lehman et al. 2015).

Stressors

The key climate change stressors affecting tidal marshes are temperature and salinity extremes such as heat waves, and hydrologic extremes (floods and droughts). Storms causing coastal flooding and other extreme climactic events may also affect marshes.

Temperature Extremes

Increased average temperature (discussed above) will result in gradual changes to the marsh community. However, increases in the maximum and minimum temperatures may have greater effects on the marsh community, even as the average rate of change remains constant. Heat waves are prolonged periods of high temperatures, which will become longer, more intense, and more frequent under climate change (Dettinger et al. 2016). Because tidal marshes can reduce temperatures by allowing water to cool quickly when spread out over the marsh plain at night (Enright et al. 2013), heat waves where temperatures stay high during the night may

reduce the potential for marshes to act as thermal refugia. Projections of air temperature in California predict heat waves will become more frequent and nighttime temperatures will increase more than daytime temperatures (Zhao et al. 2020), reducing the benefit of marshes as cooling systems.

Extreme Droughts and Floods

Droughts are also predicted to become more extreme and more frequent under many climate change scenarios (Dettinger et al. 2016, Swain et al. 2018). Droughts and sea level rise may lead to increased salinity intrusion. Increased salinity in the marsh may change vegetation communities, reduce primary productivity, and change consumer communities (see Functional Groups, below). Water management is expected to respond to minimize salinity intrusion, but the extent to which this will be possible remains to be seen (Knowles et al. 2018), particularly if the response requires maintaining larger outflows for longer periods of time.

In addition to the gradual changes associated with sea level rise, increases in storms and flood flows will affect terrestrial species and birds that use the marsh, making the tidal-terrestrial transition zone important as a refuge from high waters due to extreme storm surges, waves, and flow events (Tsao et al. 2015). Like tidal marshes, transition zones shift upslope as sea level rises which will require additional accommodation space in most cases. Marshes without adjacent transition zones will be more vulnerable to both storm events and sea level rise. Large storms, which (like droughts) are expected to become more frequent under climate change, may scour away vegetation at the marsh edge (Zedler 2010). If this occurs frequently, storm scour may interact with sea level rise to increase rate of marsh loss.

Water Management

Water flow through tidal marshes is driven primarily by tides, with riverine net flows dominating marshes only during very high flow events. Therefore, large-scale water management conducted by the State Water Project and Central Valley Project (Projects) will chiefly affect tidal marshes via their impact on salinity regimes. Freshwater outflow is the chief driver of salinity in the estuary, and Project operation is a key driver of freshwater outflow (Shellenbarger and Schoellhamer 2011). The Projects have decoupled long-term trends in annual mean outflow and salinity from long-term trends in climate forces, but climate still has primary control over variability in outflow (Enright and Culberson 2009). Overall, diversions decrease Delta outflow, increasing salinity intrusion.

Local diversions and water operation may have some influence on water quality within a given marsh. For example, drainage water from a managed marsh may provide a subsidy of productivity to a nearby tidal marsh (Brown et al. 2016), or it may cause a local drop in dissolved oxygen levels (Siegel et al. 2011).

On a slightly larger scale, operation of gates and barriers, such as the operation of the Suisun Marsh Salinity Control Gates (Sommer et al. 2020) and the Emergency Drought Barrier (Kimmerer et al. 2019) may locally decrease salinity. The Suisun Marsh Salinity Control Gates, in particular, have the potential to mediate the impact of salinity intrusion on tidal marshes in Suisun Marsh by tidally pumping fresh water into Suisun Marsh.

Predictions of water management in California are beyond the scope of this paper, but there are likely to be many changes. Various proposed changes to water operations may decrease the impact of the Projects on salinity in the Delta, but increases in the human population of California, and potential for increased drought frequency may increase the demand for water. Some changes have already been made with the recent update to the Projects' Biological Opinions and Incidental Take Permit, including summer operation of the Suisun Marsh Salinity Control Gates (USFWS 2019, CDFW 2020).

Land Management

Restoration

Tidal marsh restoration has the potential to increase the total area of tidal marshes, increase the number of marsh patches, patch connectivity, and resilience to sea level rise. Most restoration projects in the Delta rely on breaching levees surrounding farmland or managed marshes at appropriate elevations, excavating "starter channels" into the marsh, and vegetation management. Recommendations for tidal marsh restoration include (Robinson et al. 2016):

- Tidal marshes should be as large as possible.
- Distance between tidal marshes should be minimized.
- The ratio of core to edge habitat should be maximized.
- The ratio of marsh to open water should increase.
- Tidal marsh-water edge length should be maximized through the development of interior channel networks.
- Tidal channels should be embedded within tidal marshes.
- The ratio of blind channel length to flow-through channel length should increase.

In order to ensure new restoration sites are sustainable in the long-term, restoration sites also need to include gentle, sloping upland transitions to provide space for marshes to move inland with sea level rise. Accelerating the pace of restoration efforts that harness the biophysical interactions that create and maintain tidal marshes may be one of the most effective means of promoting marsh resilience to sea-level rise (Knowles 2010). Planners and land managers may also identify areas that are currently upland, but will fall within tidal marsh elevations under future conditions.

There is limited area in the Delta at appropriate elevations for restoration (Durand 2017). Because much of the Delta is highly subsided, breaching levees may result in tidal lakes, rather than marshes (see the Open Water Model for details). Furthermore, increasing the area of flooded land within the Delta will decrease the tidal range and has the potential to increase regional salinity intrusion (Resource Management Associates 2013).

The largest effort to restore marshes in the upper Estuary is the [California EcoRestore Program](#)¹. The EcoRestore program aims to protect, enhance and restore at least 9,000 acres of tidal marsh throughout the legal Delta. Several of these projects have already been completed, with more planned in the next few years (Figure 4). Predicting restoration projects beyond the ones planned under California EcoRestore is beyond the scope of this report, however future restoration may help mitigate impacts of climate change.

¹ <http://files.resources.ca.gov/ecorestore/>

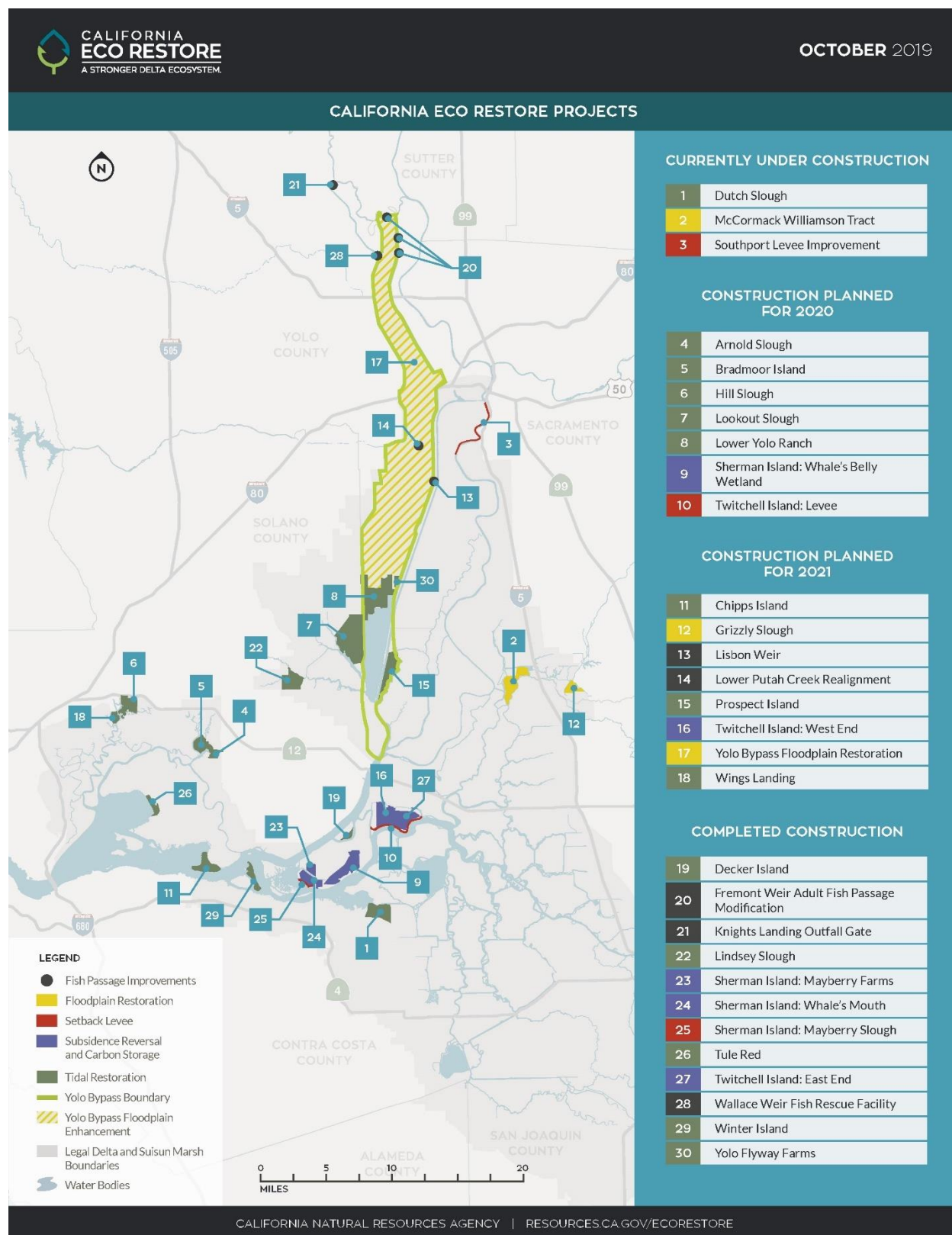


Figure 4. Map of California EcoRestore projects (October 2019).

Levee Infrastructure

Increased flooding and sea level rise may increase accidental levee breaches, but the timing and location of these breaches is impossible to predict. What can be expected, however, is that impacts of floods on levees in the Delta will not be uniform. Federally-maintained flood control project levees will almost certainly be invested in for many years (Suddeth et al. 2010). Other levees are less well-maintained and may be allowed to fail if sea level rise and increased floods cause the cost of maintenance to outweigh the benefits (Suddeth et al. 2010, Deverel et al. 2016). Where leveed islands are at appropriate elevations, levee breaches may cause “accidental restorations” that may increase the marsh area (such as occurred at Liberty Island in 1997). However, the exact placement of these breaches will be difficult to predict, and ongoing levee maintenance and repairs may mitigate their occurrence.

In Suisun Marsh, more frequent levee overtopping will cause flooding of managed marshes. Unless controlled, this may cause the slow erosion of the levees and restore the tidal connection of the marshes (Moyle et al. 2014). Even restored tidal marshes are still surrounded by levees; the connection to the tides is only restored in the few places where the levee has been breached. More frequent overtopping of these levees will alter the hydrologic dynamics of the restored tidal marshes.

Landscape change

Patch size, number, configuration, and connectivity

The 95% decline in marsh area in the Delta and Suisun Marsh resulted in small and isolated patches of tidal marsh (Robinson et al. 2014). Whereas the Delta of 200 years ago consisted mostly of marshland interlaced with tidal channels, it is now dominated by leveed open water and agriculture. In Suisun Marsh, most of what once was a continuous tidal marsh has been converted into diked, managed marshes, but some tidal marsh patches remain, including the 2070-acre Rush Ranch preserve (Moyle et al. 2014). The average size of tidal marsh patches today is several hundred times smaller than it was historically, and these small, remnant patches are surrounded by large areas of open water, built levees, and agriculture (Robinson et al. 2014). There are differences in connectivity between marshes in the different regions of the Delta. Between Liberty Island and Sherman Lake (the largest existing patches in the Delta in 2016, Figure 2), there are a few marshes that can serve as stepping stones for transiting wildlife. In the Central Delta, remaining patches are small and isolated from large patches. Large areas of the south and north Delta today lack tidal marshes. The small size and isolation of existing marsh patches severely limit marsh-dependent wildlife populations, and these problems will be exacerbated as sea level rise decreases patch size and increases distance between patches.

Changes to patch size, number, configuration, and connectivity will be chiefly impacted by land management and sea level rise. Where space is available, tidal marshes can expand at the edges of the Delta and Suisun Marsh, migrating onto adjacent higher areas. In the current landscape, however, many remaining marshes cannot move landward due to the presence of extensive levees, roadways, and other infrastructure (Orr and Sheehan. 2012, Dettinger et al. 2016). Marsh islands, such as Browns Island and Ryer Island (Figure 2), are completely cut off from upland transition zones, and may be lost as sea level rise continues. Restoration to allow landward migration of marshes with sea level rise will increase sustainability of the landscape.

Site-level Environmental Change

Elevation and Hydroperiod

Decreasing sediment supply will make it more difficult for marshes to keep pace with sea level rise. A healthy, stable marsh will slowly increase in elevation through sediment accretion and peat accumulation (Reed 2002, Culberson et al. 2004). If this process occurs at a slower rate than sea level rise, the marsh will “drown”, with emergent vegetation dying from constant inundation and/or increased salinity (Schile et al. 2014). If the marsh is bordered by gentle, sloping transition zones, the marsh may progress inland as sea levels rise, but if the marsh is bordered by steep banks, levees, or open water, the habitat will be lost.

Multiple models have assessed the likelihood that marshes can increase in elevation fast enough to keep pace with sea level rise in the SFE, but results have been mixed. Schile et al. (2014), found marshes only occurring in former upland areas in several scenarios, with differences between more productive, brackish-water marshes and less-productive, higher-salinity marshes (Figure 5). A global model of marsh sustainability found marshes may be sustainable under low sea-level rise scenarios, but not higher ones, and only if sediment supply is adequate (Kirwan et al. 2010). One estimate suggested that the San Francisco Bay and Suisun Marsh (excluding the Delta) would require over 150 million cubic meters of sediment to counter a 50 cm increase in sea level (Knowles 2010). Estimates of current sediment supply are in the range of 1.5 to 3.8 million cubic meters per year, with only 10% of that depositing on wetlands (Wright and Schoellhamer 2005).

While sediment supply is an important factor in marsh sustainability, rate of sea-level rise is even more important. Swanson et al. (2015) found sea level rise to be the primary driver of future marsh elevation. Most marshes included in the study were predicted to be sustainable with 88 cm of sea level rise by 2100 in even moderate sediment supply models, but were only sustainable with the highest sediment supply models when sea level rise was increased to 133 or 179 cm (Swanson et al. 2015).

As part of the Delta Stewardship Council's climate change vulnerability assessment, the habitat evolution projections for all tidal marshes in the Delta and Suisun Marsh was modeled using the Marsh Accretion Rate Model of Ecosystem Resilience (Delta Stewardship Council 2021). For mid-century (2050) sea level rise scenarios, high marsh tidal marshes are predicted not be at risk of habitat transitions or drowning under one foot of sea level rise. Under two feet of sea level rise, tidal freshwater marshes in the Delta are predicted to be at risk of transitioning to low marsh, but brackish tidal marshes in Suisun Marsh will persist and keep pace with sea level rise. For late-century (2085) scenarios, tidal marshes will not be at risk of transitioning to low marsh under two feet of sea level rise but will be at risk of transitioning under 3.5 feet of sea level rise. Under the more extreme end-of-century scenario (6 feet sea level rise by 2100), all tidal marshes in the Delta and Suisun Marsh are at risk of drowning. Similar to Swanson et al. (2015), sensitivity of model results to differences in sediment supply model parameters was low.

Marsh surface elevation regulates hydroperiod, which is defined as the frequency, duration, timing and amplitude of tidal flooding. Brackish marshes that possess elevation gradients typically feature more salt-tolerant plant species (e.g. *Salicornia*) at low elevations (Grewell et al. 2014). Due to accelerated sea-level rise and storm surges, marsh plain inundation may become more frequent and/or occur at higher elevations. Potential outcomes are replacement by more salt-tolerant plant species or a combination of plant senescence, soil erosion, and channel expansion (Schile et al. 2014).

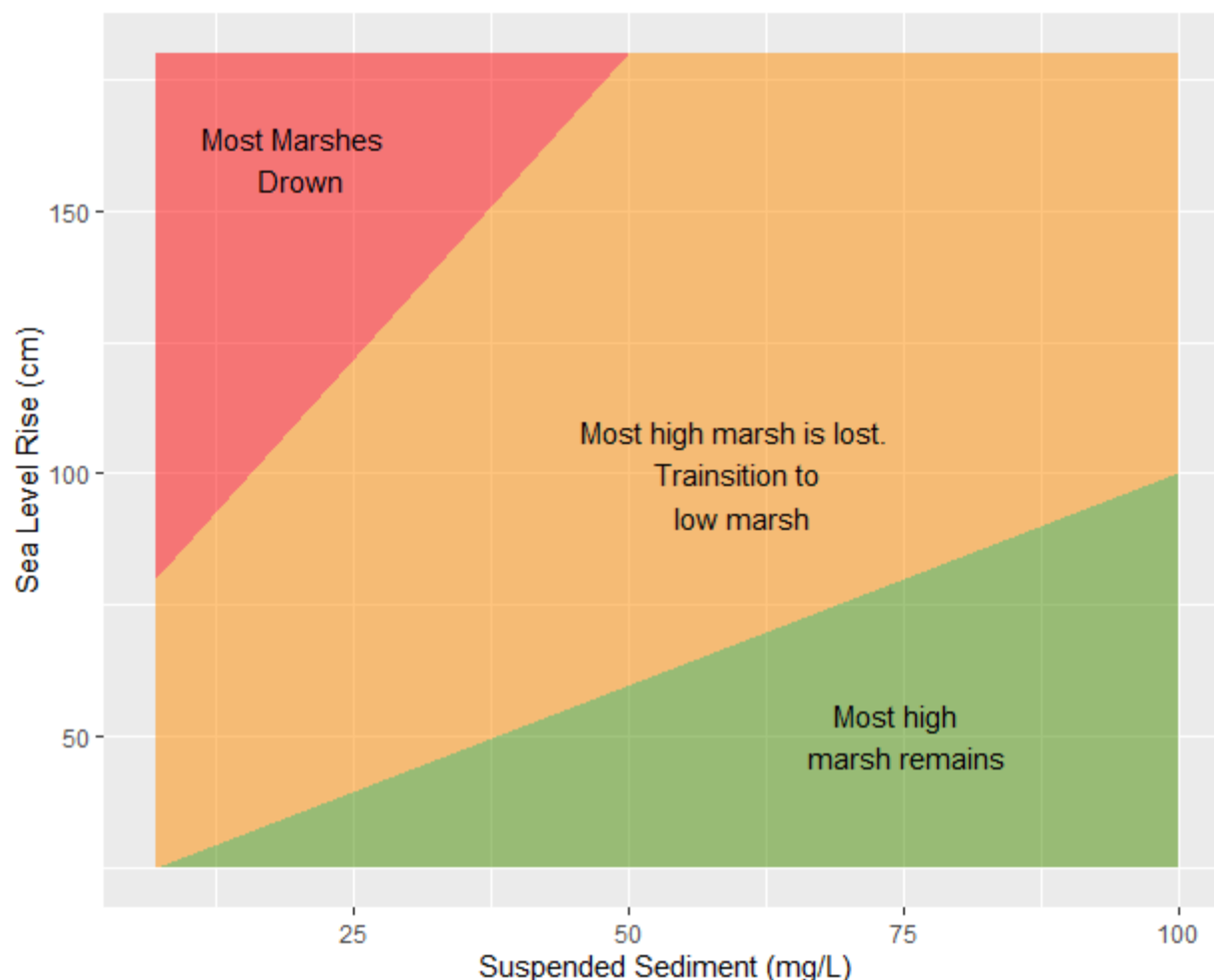


Figure 5. Combinations of sediment supply and sea level rise scenarios for marsh sustainability through 2100. The likelihood that a particular marsh will avoid being drowned will depend on vegetation present and the long-term trajectory of sediment supply. Modified from Schile et al. 2014.

Turbidity

Changes in turbidity in marshes depend on multiple factors such as sediment supply, wind speed, and invasive submerged vegetation spread (Cloern et al. 2011, Hestir et al. 2015, Bever et al. 2018). As mentioned above, it is not clear whether sediment supply will increase or decrease in the next few decades (Cloern et al. 2011, Stern et al. 2020), but if sediment supply decreases, turbidity may decrease as well. Winds that mix the water column and pick sediment up off the bottom will increase turbidity, but wind speed has been dropping and submerged aquatic vegetation (SAV) extent in the Bay-Delta is rising. Already, observed declines in both wind speed and sediment supply over the past 20 years have resulted in reduced turbidity in the San Francisco Estuary from October through January (Bever et al. 2018). Many remaining marshes in the Bay-Delta are increasingly surrounded by SAV in the shallow subtidal region.

This leads to sediment dropping out of the water column into the SAV mat before it even gets on to the tidal marshes. A couple of recent studies illustrate how SAV acts as a sink for sediment and for carbon, hampering the movement of sediment onto the marsh (Drexler et al. 2020, Work et al. 2020). Thus the combination of decreasing wind and increasing SAV may continue the trend of decreasing turbidity in the estuary even if sediment supply increases (Hestir et al. 2015, Bever et al. 2018).

Salinity

Salinity in a tidal marsh at the site level is driven primarily by the marsh's proximity to the ocean. If not adequately controlled via water management, sea level rise may cause an increase in salinity on the marsh (see general model). However, landscape-level salinity fields interact with site-level factors such as marsh surface elevation, hydroperiod, groundwater, and sedimentation/accretion rates. High evapotranspiration in the vegetated marsh plain often results in pockets of higher salinity water in the upper marsh, particularly in isolated pannes or ponds. Inflow from freshwater creeks, agricultural drainage, or draining of managed wetlands may also cause local changes to salinity. According to Watson and Byrne (2009), if sedimentation keeps up with sea level rise and salinity intrusion continues unabated, salinity will rise throughout the marsh plain since the pockets of isolated high salinity water in high marsh pannes will remain. If sea level rise is more rapid, the marsh will drown, causing salinity in lower marsh to increase, but causing the high marsh pannes to be flooded more regularly and equalizing salinity throughout the marsh.

Functional Groups and Species

Table 1. General predictions for the impact of climate change on major taxa within the marsh.

Functional Group	Species	Effect of Increased Temperature	Effect of Greater Salinity Intrusion	Sea level Rise
Resident Fishes	Sunfishes	Minimal impact	Shift further upstream	Reduced marsh habitat
Resident Fishes	Tule Perch	Minimal impact	Minimal impact	Reduced marsh habitat
Migratory Fishes	Steelhead	Lower survival, thermal stress, shift in migratory timing	Less rearing in downstream marshes	Reduced marsh habitat

Migratory Fishes	Chinook Salmon	Lower survival, thermal stress, shift in migratory timing	Minimal impact	Reduced marsh habitat
Plankton	Phytoplankton	Increase in cyanobacteria.	Shift to more marine species	Shift to shallower water
Plankton	Zooplankton	Shift to smaller species, peak abundance earlier in the year.	Shift to more marine species	Unknown
Benthos	Epibenthic algae	Unknown	shift to more marine species	May decrease productivity as water depth increases
Benthos	Amphipods	Unknown	Shift to more marine species	Minimal impact
Benthos	<i>Potamocorbula amurensis</i>	Minimal impact	Shift upstream	Minimal impact
Benthos	<i>Corbicula fluminea</i>	Minimal impact	Shift upstream	Minimal impact
Structural Vegetation	Tules (<i>Schoenoplectus</i> spp.)	Decreased germination	Expansion of <i>S. americanus</i> contraction of other species	May replace cattails as the distribution moves to higher elevations
Structural Vegetation	Cattails (<i>Typha</i> spp.)	Decreased germination	Range contraction	Shift to higher elevations
Structural Vegetation	Pickleweed (<i>Sarcocornia pacifica</i>)	Minimal impact	Minimal impact	Shifts upslope, range contractions

Resident Fishes

Current Status

Present-day tidal marshes support a variety of native and nonnative resident fish species, those that complete their life cycles in relatively small home ranges. In freshwater tidal marshes, typical resident fishes include native Tule Perch (*Hysterocarpus traski*), Sacramento Sucker (*Catostomus occidentalis*), Hitch (*Lavinia exilicauda*), Sacramento Blackfish (*Orthodon microlepidotus*), and Prickly Sculpin (*Cottus asper*). Nonnative resident fish include the Redear Sunfish (*Lepomis microlophus*), Bluegill Sunfish (*Lepomis macrochirus*), Black Crappie (*Pomoxis nigromaculatus*), Golden Shiner (*Notemigonus crysoleucas*), Common Carp (*Cyprinus carpio*), and Yellowfin Goby (*Acanthogobius flavimanus*) (Moyle 2002). Fish community structure typically varies as a function of salinity (i.e. the marine-estuarine-freshwater gradient) and habitat (e.g. depth, vegetation type and structure). For example, Tule Perch are a deep-bodied livebearer commonly associated with emergent aquatic vegetation (EAV) and submerged aquatic vegetation (SAV). Recent studies have shown that Tule Perch are found in habitats with relatively high variability in flows, tides, temperatures, turbidities, and salinities (e.g. Sherman Lake, the Nurse-Denverton Complex, Rush Ranch), suggesting that they are adapted to rapidly changing conditions typical of shallow, complex estuarine habitats (Young et al. 2018, Colombano et al. 2020a, Colombano et al. 2020b). While their diets have been found to consist primarily of detritus, amphipods, and isopods in Suisun Marsh, stable isotope analysis of muscle tissues show that they derive energy from both detrital and pelagic food web pathways in the North Delta (Young et al. 2021). In contrast, slow-moving backwater habitat in freshwater tidal marshes of the interior Delta are more likely to have stable, clear, warm conditions, which often harbor invasive SAV species such as Brazilian waterweed (*Egeria densa*) and SAV-associated fishes (e.g., Largemouth Bass, Redear Sunfish) (Conrad et al. 2016, Young et al. 2018, Young et al. 2021).

Effect of Climate Change

Climate change effects on fish community structure, and in particular the composition of resident species, are likely to be driven by both gradual increases in mean temperature and salinity but also the frequency and duration of extreme events such as heatwaves and droughts. A major climate-related stressor in the upper estuary is elevated summer and fall salinities, which will increasingly compress the spatial extent of freshwater and brackish habitat available to fishes (Cloern and Jassby 2012). Coupled with increased temperatures, the frequency and severity of warm, saline conditions are likely to have both direct and indirect effects on fish assemblages. Because resident species occupy smaller home ranges, they are subjected to direct effects of local changes in environmental conditions, which under climate change, may exceed critical thresholds such as physiological tolerances (e.g. thermal tolerances) (Jackson et al. 2016). Indirect effects may occur due to shifts in physical structure

(e.g. an increase in hydroperiod may reduce the availability of intertidal habitat and/or vegetated interstitial spaces that provide refuge from predators), food web pathways (e.g. a shift from detrital- to phytoplankton-dominated pathways due to EAV loss), and/or mismatches with prey availability (e.g. invertebrate prey responding differently to changes in habitat availability or environmental conditions than predators) (Colombano et al. 2021b). In addition, non-consumptive species interactions such as competition for food and cover may have stronger (i.e., localized) effects on resident fishes because they are not as adapted to moving around in search of optimal conditions for foraging, growth, and survival compared to migratory fishes.

Migratory Fishes

Current Status

Several native and nonnative migratory fish species use tidal marshes during one or more life stages. The most prominent examples of naïve migrants include the Sacramento Splittail (*Pogonichthys macrolepidotus*), Pacific Lamprey (*Entosphenus spp*), and Chinook Salmon (*Oncorhynchus tshawytscha*). Non-naïve fishes include Striped Bass (*Morone saxatilis*) and Yellowfin Goby (*Acanthogobius flavimanus*).

However, there is substantial variation in the degree to which migratory fish species rely on tidal marshes vs. use them opportunistically for food and refuge. For example, Sacramento Splittail is a large-bodied, semi-anadromous, benthic minnow that spawns on riverine floodplains (e.g. Yolo Bypass) during winter months, after which the young-of-the-year (YOY) eventually migrate downstream to brackish tidal marshes of the West Delta, Suisun Bay, and Suisun Marsh (Moyle et al. 2004, Baerwald et al. 2007). Juveniles reside in tidal marshes for 1-2 years before becoming sexually mature (Moyle et al. 2004). During this time, small YOY are strongly associated with shallow, dendritic marshes (e.g. Rush Ranch) early upon arrival in the low salinity zone (Feyrer et al. 2005, Colombano et al. 2020a), however, all life stages of splittail may be found in shallow (<1.5m) tidal marsh habitats (Baxter 1999). Furthermore, recent evidence suggests that splittail exhibit site fidelity to tidal marshes, as was shown by several individuals that frequently used an intertidal channel in Rush Ranch over the span of two years and possibly before/after spawning migrations (Colombano et al. 2020a). Splittail ≤100mm have been shown to consume detritus and nematodes in tidal marsh habitat whereas splittail >100mm have been shown to consume detritus, nematodes, clams, amphipods, and isopods (Colombano et al. 2021a). Collectively, splittail associations with brackish waters, shallow vegetated intertidal and subtidal marsh channels, and benthic invertebrates demonstrate a reliance on tidal marshes, especially in juvenile life stages. In contrast, the degree to which migratory fish species such as juvenile Chinook Salmon use tidal marshes in this estuary remains a topic of debate. While juvenile outmigrating Chinook Salmon are regularly captured in springtime beach seine samples in Montezuma Slough, a migratory corridor connecting the

Sacramento River to tidal marshes of Suisun Marsh (O'Rear and Moyle. 2017), the extent to which there is a “resident” life history that rears in tidal marshes for extended periods (as is commonly observed in tidal marshes of the Pacific Northwest) is unknown (Aha et al. 2021).

Effect of Climate Change

Similar to resident fishes, migratory fishes that use tidal marsh habitat seasonally or opportunistically may be impacted by local changes to habitat suitability/ environmental conditions (e.g., warm temperatures that exceed physiological tolerances during drought). They may also be vulnerable to regional climate-driven shifts in the timing, duration, and magnitude of seasonal environmental conditions that are linked to important phenological events such as spawning, migration, recruitment, or peak abundance (Renner and Zohner 2018). Examples include the outmigration timing of juvenile Chinook Salmon from tributaries in the upper watershed (Satterthwaite et al. 2014, Munsch et al. 2019) and the upstream migration of adult Striped Bass, both of which may increasingly overlap in tidal marshes in spring if warming trends continue (Goertler et al. 2021). Overall, climate change impacts to tidal marsh habitat and environmental conditions may diminish their ecological functions for migratory fishes, including rearing, foraging, and avoiding predators, which in turn may impact growth, survival, and/or recruitment (Colombano et al. 2021b).

Structural Vegetation

Current Status

Currently, the largest continuous tracts of marsh in the upper estuary are located in the Suisun region and the Liberty Island – Cache Slough complex. Most of the tidally active marsh in Suisun is restored marsh which consists mainly of native tule (*Schoenoplectus acutus*, *S. californicus*, and *S. americanus*) and cattails (*Typha angustifolia*, *T. latifolia* and their hybrids) and the invasive common reed (*Phragmites australis*). In more saline regions of Suisun, there are brackish species such as pickleweed (*Salicornia virginica*), alkali bulrush (*Bolboschoenus maritimus*), saltgrass (*Distichlis spicata*) (Watson and Byrne 2009). Many invasive species are also found in the marsh such as yellow starthistle (*Centaurea solstitialis*), perennial pepperweed (*Lepidium latifolium*), pampas grass (*Cortaderia selloana*), and giant reed (*Arundo donax*). The freshwater tidal marsh in the northwest Delta is mainly a tule marsh. Tules in recently flooded islands have naturally expanded their extent over the past two decades (Hester et al. 2016). However, in recent years, water primrose (*Ludwigia peploides* ssp. *peploides* and *L. grandiflora* ssp. *hexapetala*), a floating-leaved invasive plant, and submerged vegetation dominated by invasive water milfoil (*Myriophyllum spicatum*) have been increasing in cover in the region (Khanna et al. 2015, Khanna et al. 2018).

Even without climate change, there are challenges to the health of these marshes. The submerged and floating vegetation mats that surround the marsh in the Cache Slough Complex

block sediment from reaching the marsh compromising the ability of the marsh to keep up with sea level rise (Drexler et al. 2020). Furthermore, invasive species such as water primrose have been expanding into the marsh and replacing marsh vegetation such as tule and cattails (Khanna et al. 2018).

Effect of Climate Change

Changes in temperature may shift vegetation communities, or alter plant-herbivore interactions, e.g., (e.g. Borgnis 2013, Reddy et al. 2019). In recent years, droughts and higher temperatures have aided spread of invasive species, especially those that originate in tropical regions (Kimmerer et al. 2019, Durand et al. 2020). Tules and cattails are sensitive to high temperature during germination (Watson and Byrne 2009). While plant survival might not be threatened directly, increasing temperatures may affect germination and reproduction.

Sea level rise interacts with sedimentation and organic processes to determine the risk that a marsh will be drowned by sea level rise, and whether the salinity regime within the marsh will change. As discussed above, if sedimentation keeps up with sea level rise, salinity will increase over the entire marsh plain and the vegetation community will change accordingly (Watson and Byrne 2009). If sea level rise is more rapid, salinity in lower marshes will increase, but will decrease in higher marshes (Watson and Byrne 2009). Because salinity, not absolute elevation, drives plant communities in brackish marshes, plant communities will be driven by this salinity change in Suisun Marsh and westward. If we ignore the impact of sea level rise on salinity for the moment, we expect tules (*Schoenoplectus* spp. and *Scirpus californicus*) that grow at lower levels, to shift their distributions to slightly higher elevations replacing cattails (*Typha* spp.). Cattails, in turn, would shift to elevations higher than they are currently occupying, likely encroaching on willow habitat. Whether any of these species increase in cover or decrease will depend on the amount of habitat available.

Increase in salinity due to both sea level rise and more severe and frequent droughts may already be impacting marsh vegetation in the SFE, causing shifts to more salt-tolerant species (Watson and Byrne 2012). It can also cause a reduction in dissolved organic carbon transport in the estuary and change nitrogen transport from organic to inorganic forms, greatly increasing ammonium loading (Ardón et al. 2013, Ardón et al. 2016). Severe droughts and higher salinities will also impact restorations planned in the SFE, especially in the Suisun region. Chapple and Dronova (2017) found growth rates of marsh vegetation in drought years to be much lower than in wet years in restoration sites. This effect was much more pronounced in higher salinity marshes compared to freshwater tidal marshes found in the Delta. Among tule species found in the Delta, *S. americanus* is more tolerant of high salinity than the other two tule species, hence this species might increase in cover while the other two species ranges will contract (Watson and Byrne 2009).

Submerged aquatic vegetation makes up a larger proportion of carbon contributing to fish diets in the summer than the spring (Young et al. 2021). Increases in submerged aquatic vegetation caused by warmer temperatures (such as seen during the summer) may mean a larger proportion of fish carbon coming from submerged aquatic vegetation as well, though this remains an area in need of additional research.

Benthos

Current Status

Due to the shallow water and high coverage of structural vegetation characteristic of tidal marshes, benthic and epiphytic processes have a much larger influence on ecosystem function than they do in deeper, open-water systems. An analysis of sources of primary production found that benthic and epiphytic algae had an order of magnitude higher production in the historic Delta than in the modern Delta, mostly due to the large extent of tidal marshes in the historic Delta (Cloern et al. 2016). Both epibenthic/epiphytic algae and vascular plant detritus are important sources of productivity for consumers in marshes. The diet of epibenthic invertebrates, such as amphipods, insect larvae, clams, and oligochaete worms may consist of 10-50% benthic microalgae, and up to 90% vascular plant detritus, though these values vary regionally and seasonally (Schroeter et al. 2015, Young et al. 2021).

Benthic infauna, in particular the filter-feeding clams *Potamocorbula amurensis* and *Corbicula fluminea*, also have a larger effect on the ecosystem in shallow water than in deep water. Both modeling and empirical studies have found that clams can more effectively reduce overall phytoplankton production when water is shallow (Thompson et al. 2008, Lucas and Thompson 2012). Therefore, tidal marshes with extended shallow areas may be particularly vulnerable to invasion by these clams. However, surveys have found fewer clams in the small sloughs of Suisun Marsh than larger sloughs (Baumsteiger et al. 2017) (DWR unpublished data), meaning the small sloughs of tidal marshes may be somewhat resistant to invasion.

Other benthic and epiphytic invertebrates, such as amphipods, isopods, oligochaete worms, polychaete worms, and insects also occupy an important part of marsh ecosystems. Density and biomass of invertebrates associated with vegetation is much higher than density and biomass of open-water invertebrate communities (Hartman et al. 2019). Benthic and epiphytic invertebrates compose a larger proportion of fish diets in marshes than in open water. For example, the Estuary-endemic and endangered Delta Smelt (*Hypomesus transpacificus*) caught by open-water surveys consume very few amphipods, and almost no insects (Slater and Baxter 2014), but Delta Smelt caught near shallow marsh habitat regularly consume insects and other epibenthic invertebrates (Whitley and Bollens 2014).

Effect of Climate Change

The potential for decreased turbidity may increase the importance of benthic algae in marshes, since shallow water will allow light to penetrate to the bottom. Benthic and epiphytic algae are already more important in marsh habitat than open-water habitat (Robinson et al. 2016a), so decreases to turbidity may further extend this importance in both marshes and open-water habitat.

Benthic grazers, particularly invasive bivalves, may benefit from climate change. Both *Potamocorbula* and *Corbicula* tolerate broad temperature ranges, with a maximal thermal tolerance of 28°C and 34°C, respectively (Rodgers et al. 1977, Kamenev and Nekrasov 2012). Therefore, marshes are unlikely to be impacted by a loss of clams due to high temperatures. Rather, higher temperatures greatly increase clam filtration rates, potentially reducing phytoplankton blooms further and decreasing the availability of food for other benthic invertebrates and zooplankton (Hartman et al. 2017). Sea level rise and the shifting salinity field will also change the bivalve community. As salinity moves inland, *Potamocorbula* may move further upstream. Because *Potamocorbula* may filter four times as much phytoplankton out of the water column as *Corbicula*, this could reduce available productivity in marshes in the Delta.

Other benthic and epiphytic invertebrates have salinity tolerances that may impact their future distribution. Communities throughout the estuary can be grouped into assemblages based mainly on salinity and substrate type (Thompson et al. 2013). Shifts in the salinity gradient may change the identity and relative abundance of the major constituents of the benthic community. While we do not have data on temperature tolerances for many species, some taxa may shift timing of peak abundance or reproduction earlier in the year or have reduced abundance in high-temperature areas.

Plankton

Current Status

The phytoplankton community within tidal marshes is not as productive as the vascular plant community, however phytoplankton carbon is more readily available than vascular plant carbon (Jassby et al. 2003). Shallow water marshes, where the water depth is less than the point where respiration outpaces photosynthesis can provide an important source of productivity to the nearby planktonic environment (Lucas et al. 2009, Sherman et al. 2017a). Dead-end sloughs, such as those found in marshes, frequently have much higher chlorophyll-a (a proxy for standing stock of phytoplankton) than larger, distributary channels (Montgomery et al. 2015, Stumpner et al. 2020).

Zooplankton, including copepods, cladocera, and mysids, are important primary consumers in the tidal marsh food web, and may be exported to the nearby open-water habitat. Early study of food webs in the estuary found zooplankton primarily consumed phytoplankton (Mueller-

Solger et al. 2006), however, recent research has found that they rely more on carbon produced by marsh plants than previously believed (Schroeter et al. 2015, Kimmerer et al. 2018a, Harfmann et al. 2019), especially in recent years as pelagic productivity has decreased (Brown et al. 2016). Zooplankton carbon sources can shift greatly between regions, with zooplankton in marsh-dominated regions relying primarily on benthic algae and vascular plants, whereas zooplankton in open-water habitat rely more on phytoplankton (Young et al. 2021).

Zooplankton in tidal marshes in the SFE have not been studied as extensively as zooplankton in open-water habitat. The few studies that have been conducted have found the total abundance to be similar, however community composition may be different, with more calanoid copepods in marsh habitat, particularly *Eurytemora affinis* (Bollens et al. 2014, Grimaldo et al. 2020).

Effect of Climate Change

Phytoplankton productivity is tied to light and temperature, both of which may change. The potential for decreased turbidity may change the proportion of production from pelagic versus benthic algae and increase overall productivity (Cloern 1987, Robinson et al. 2016a, Stumpner et al. 2020). Because marshes have extensive shallow areas and high proportions of benthic productivity to begin with, increased water clarity could further shift production to benthic algae.

Increased temperatures may increase productivity, but also change phytoplankton community structure, shifting biomass away from large diatoms and toward smaller pico- or nano-plankton (Hare et al. 2007, Marañón et al. 2012). Increased temperatures will also impact zooplankton growth and physiology and may impact community composition. Phytoplankton blooms and the peak abundance of several zooplankton taxa have shifted to earlier in the season over the past 40 years, mainly due to the effect of invasive clams (Merz et al. 2016). However, peak abundances are closely tied to warming temperatures (increasing productivity), and hydrology. With increased temperatures earlier in the season and an earlier peak in the hydrograph, peak abundances may shift even earlier.

Zooplankton abundance and diversity may also be impacted by climate change. For example, an extreme heat wave in Australia caused a shift in zooplankton community composition from larger to smaller taxa and an overall decline in biomass (Richardson et al. 2020). Other studies have found similar shifts in community compositions (Rice et al. 2015, Dam and Baumann 2017). While few of these studies have occurred in tidal marshes, we expect these impacts to be similar in marsh habitat and open water habitat, because zooplankton communities within the SFE tend to be similar in tidal marshes and deeper waters (Grimaldo et al. 2004).

If the salinity field moves inland, location-specific community composition will change. The relationship between flow and community composition will also change, especially for some of the most important calanoid copepods that serve as diet for endangered pelagic fishes

(Kimmerer et al. 2018b). Bollens et al. (2014) found zooplankton in fresher-water marshes to have higher abundance of the large, nutritious cladoceran *Bosmina*, whereas more saline marshes were more likely to contain the less-nutritious cyclopoid copepod *Limnoithona tetraspina*.

Conclusions

Tidal marshes of the Estuary have been dealt a bad hand over the past 150 years, declining in area by over 95%. The future of these habitats is unclear – with enough sediment supply, low-to-moderate sea level rise, and an increased emphasis on restoration, tidal marshes could become an important part of the future ecosystem, providing increased productivity, nursery habitat, and thermal refuges into the future. However, the assemblage of species in the marshes will almost certainly be different due to changes in temperature and salinity. If sediment supply is insufficient, and development continues to encroach on the shores of the estuary, existing marshes may drown with sea level rise and the Estuary will continue to lose this important habitat and many marsh-obligate species.

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Chapter 4: Floodplains and Climate Change

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Introduction

Floodplains are landscape features that are periodically inundated by water from adjacent rivers (Opperman et al. 2010). Ecologically, functional floodplains are characterized by three primary elements: connectivity, flow regime, and spatial scale. Water quantity flowing over floodplains can vary greatly. Based on a flood's effects on the floodplain, three flood categories have been defined: floodplain-activation floods, floodplain-maintenance floods, and floodplain-resetting floods (Box 1). Several physical parameters determine the types of ecosystems on floodplains and the species they will support; these include temperature, water depth, water velocity, and hydrologic connectivity (Opperman et al. 2010). Natural ecosystems commonly found on floodplains include annual vegetation, forests, seasonal wetlands, and permanent ponds or wetlands (Whipple et al. 2012). Floodplains provide many valuable ecosystem services: attenuation of flood flows which reduces flood risk, filtration of surface water, recreation, fisheries, agriculture, biodiversity, food availability, and groundwater recharge, which contributes to more-sustained and cooler dry-season flows (Opperman et al. 2010).

Box 1

Floodplain-activation flood

A small magnitude flood that occurs relatively frequently and produces characteristic ecological benefits such as food-web productivity and habitat creation for native fish spawning and rearing.

Floodplain-maintenance flood

A higher magnitude flood that, in addition to providing ecological benefits, results in geomorphic changes including bank erosion and deposition on the floodplain.

Floodplain-resetting flood

A very high-magnitude flood that occurs rarely and results in extensive geomorphic changes, such as the scouring of floodplain surfaces and changes in channel location due to avulsion.

Overview of changes that have occurred to the Delta as it relates to floodplains

Ninety percent of Europe's and North America's floodplains have been developed for human use, primarily for agricultural production (Tockner and Stanford, 2002; Corline et al. 2017). In California's Central Valley, most floodplains have been disconnected from their rivers by levees and altered for agriculture and other human uses (Jeffres et al. 2008). Only 5% of functional

floodplains remain, and these are mostly bypasses constructed as flood-control measures to divert water away from urban areas during high-flow events (Opperman et al. 2010; Hanak, 2011; Corline et al. 2017). These bypasses are graded to efficiently drain floodwaters, which decreases the time water remains on the floodplain compared to historical conditions (Corline et al. 2017; Sommer et al. 2001). In addition, natural flood flows are greatly reduced or completely eliminated by dams, which reduces the magnitude of inundation of the remaining floodplains (Opperman et al. 2010; Whipple et al. 2012).

Floodplains included in this review

Two different floodplains, the Yolo By-Pass (hereafter referred to as “Yolo Bypass”) and Cosumnes River floodplain, contribute the majority of floodplain habitat remaining in the Sacramento-San Joaquin Delta (hereafter referred to as “the Delta;” Figure 1). The Yolo Bypass is an extensive historical floodplain of the Sacramento River, though it has been highly altered for flood control via a system of levees and weirs. Presently, the bypass can fully flood only when the river exceeds a specific stage height (32 ft) and is able to overtop a weir series located at the northern end of the bypass. When not flooded, the northern portion of the bypass consists of a 1500-acre wildlife area and agricultural fields used for a variety of crop types; the middle portion of the bypass consists of a large wildlife preserve, wetlands, and agricultural land managed for waterfowl; the southern portion includes agricultural land and established and restored tidal habitats (Sommer et al. 2001). The Cosumnes River floodplain, conversely, is smaller in scale but less modified and managed. Because the Cosumnes River does not have any large dams, during even small rain events, the river is able to spill into the floodplain without having to overtop a weir. The floodplain supports natural floodplain vegetation. While both floodplains have been modified and differ substantially from the dynamic landscape of historical river floodplains (Florsheim and Mount, 2002), they still provide some of the key ecological services characteristic of floodplain habitats (Sommer et al. 2001).

Other floodplains exist upstream of the Delta (e.g., the Sutter By-Pass, hereafter referred to as “Sutter Bypass”) and along the San Joaquin River; however, the conceptual model should be applicable to all Central Valley floodplains.

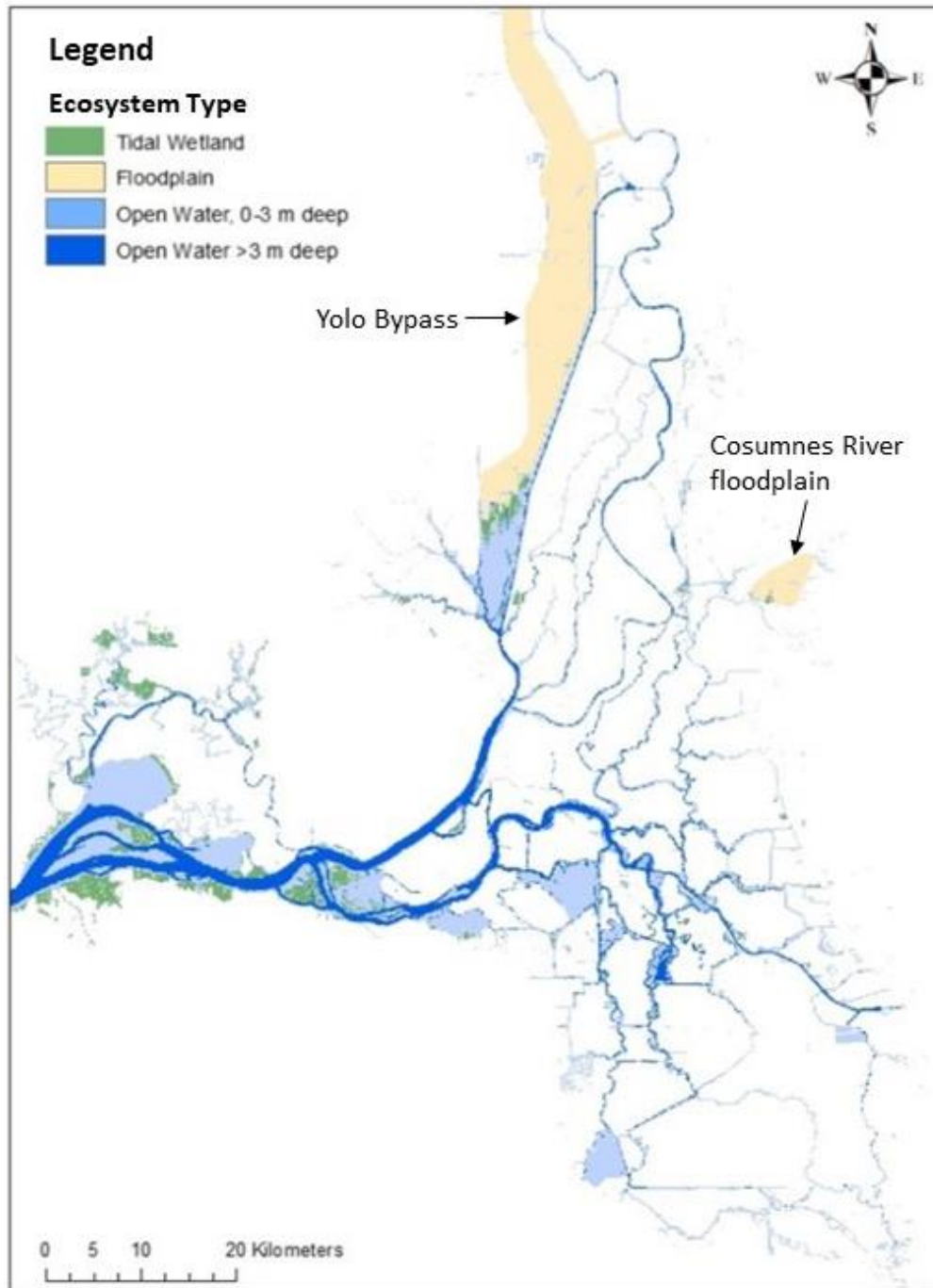


FIGURE 1. Map of ecosystem types in the Upper San Francisco Estuary. Tidal wetlands are in green. Delta floodplain and tidal wetlands come from SFEI's Delta Landscape Scenario Planning tool (SFEI, 2022a). Suisun ecosystem types come from the California Aquatic Resource Inventory (SFEI, 2022b). Bathymetry comes from (Fregoso et al. 2017)

Yolo Bypass

The Yolo Bypass extends over 59,000 acres in the northern Delta. During periods of high Sacramento River flow (~56,000 CFS), water from the river enters the northernmost point of the Yolo Bypass by spilling over the Fremont and Sacramento Weirs. The capacity of the bypass is about five times the capacity of the river channel, and the bypass has been successful in protecting the urban development on either side, including the City of Sacramento. Currently, the Yolo Bypass is inundated when the Sacramento River stage exceeds 33.5 feet, causing it to overtop Fremont Weir. This has occurred in more than 70% of years since the installation of Fremont Weir (Sommer et al. 2001; 2008). The Sacramento Weir, located just downstream from the Fremont Weir, provides an additional location for river water to enter the Yolo Bypass. However, unlike the Fremont Weir, where the river can volitionally overtop the weir, the Sacramento Weir requires staff to pull boards to fully allow water to access the floodplain. This occurs in fewer years than Fremont Weir overtopping but is a valuable flood control tool during extremely large storms and/or wet water years. Even during flood years when the weir is left in place, water tends to spill through gaps in the boards, allowing for some hydrologic connectivity to the floodplain. In addition to the weirs, local tributaries are capable of flooding parts of the Yolo Bypass during storm runoff events. These runoff contributions usually result in bank overtopping of the bypass's perennial channel, the Toe Drain, and some flooding of connected tidal wetland habitats. A proposed gated notch in the Fremont Weir will soon allow inundation of the Yolo Bypass more frequently and for longer durations.

The hydrology, vegetation, and topographic variability of Yolo Bypass differs from the historical landscape that included seasonally flooded perennial wetlands and a landscape of extensive seasonal marshes and some permanent water bodies (Whipple et al. 2012). This ecosystem was extremely productive and exported large quantities of organic matter to the Delta. Currently, the levees, built to redirect floodwaters from cities, reduce connection to the adjacent river to only periods of high flows. The floodplain surface is also leveled for multi-benefit purposes like agriculture, managed wetlands, migratory bird habitat, and flood carrying/draining capacity. There are fewer distributary channels than would likely be present in a natural floodplain ecosystem. Sediment deposition and erosion are mostly limited to periods of flooding. Natural vegetation is confined in scope because of other land uses, the most dominant of which is agriculture (Suddeth 2014). Agricultural crops grown in the bypass include rice, safflower, tomatoes, corn, sunflower, and irrigated pasture, with a growing season from spring through early autumn. However, natural vegetation is also present and can be found in the Fremont Wildlife Area, across the bypass's restored marshes (early successional community), and in and along channels of multiple sizes (Sommer et al. 2001; Robinson et al. 2014; Suddeth 2014; Goertler et al. 2018).

Despite the differences between the historical river floodplain and current flood bypass, the Yolo Bypass still provides important ecosystem services common of floodplain habitats. Inundation of the bypass provides floodplain habitat for spawning and rearing of native fishes; it is particularly important for spawning and rearing of Sacramento Splittail (*Pogonichthys macrolepidotus*) and rearing of juvenile Chinook Salmon (*Oncorhynchus tshawytscha*; Sommer et al. 2001; Moyle et al. 2004; Goertler et al. 2018).

The southern end of the bypass, the Cache Slough Complex, generates high levels of phytoplankton and zooplankton and contributes to the downstream food web during winter and spring high-flow events (Sommer et al. 2001; Corline et al. 2017). Additionally, the bypass connects the food-rich water exported by flooded agriculture and managed wetlands to the northern Delta to support native fishes, and exports plankton into adjacent streams (Frantzich et al. 2018; 2019). During flooding events, the bypass magnifies this benefit drastically, amplifying food resources and habitat for fish and wildlife, including juvenile Chinook Salmon and shorebirds, geese, and ducks, many of which migrate along the Pacific Flyway (Sommer et al. 2001; Moyle et al. 2007; Corline et al. 2017; Goertler et al. 2018; Suddeth et al. 2016).

Cosumnes River Floodplain

The Cosumnes River is the only river draining into the Delta that does not have a major dam. However, different types of levees, including low levees that do not prevent seasonal flooding, setback levees, and higher agricultural levees, constrain the floodplain in many places. The riverside levees and channel modifications have resulted in a single, incised river channel (Nichols and Viers 2017). Historically, the portion of the river flowing through the Delta consisted of multiple, shifting channels in a broad floodplain, which supported a mosaic of aquatic and terrestrial habitats, including riparian forest, valley oak woodlands, grasslands, seasonal and perennial wetlands, permanent sloughs, and seasonal floodplain lakes. Today, much of the original floodplain consists of farm fields protected by low levees that do not prevent seasonal high-water flooding.

Over the past few decades, there have been deliberate and accidental levee breaches along the river to improve floodplain connectivity, restore floodplain processes and function, and observe the change in plant communities with time (Florsheim and Mount 2002). Improved hydrologic connectivity resulted in sediment deposition, which increased floodplain topographic heterogeneity and promoted the establishment of early-stage successional riparian forests (Nichols and Viers 2017). Restoration of ecological processes has resulted in a mosaic of ecosystems that include oak and willow-cottonwood forests of various successional stages, uplands, sand bars, and a series of sloughs and ditches (Florsheim et al. 2006; Swenson et al. 2003). To date, lateral connectivity has only been restored to a small percentage of the current floodplain in the Cosumnes River Preserve, which extends over about 15,000 acres (Figure 11).

Ongoing and planned restoration projects in the Cosumnes River floodplain will further diversify and increase the area of the floodplain ecosystem in the future.

Conceptual Model Structure

Like the Overview model, the Floodplains sub-model is organized into tiers (Figure 2). At the top, we have selected the environmental conditions within the floodplain most likely to change given the global climate-change effects discussed in the Overview model. These environmental conditions interact with the landscape, including human management and landscape change to influence the site-level environment. The functional groups we have chosen to focus on are floodplain spawners, floodplain foragers, lower trophic organisms (plankton and benthos/insects), and structural vegetation (reeds, shrubs, and trees).

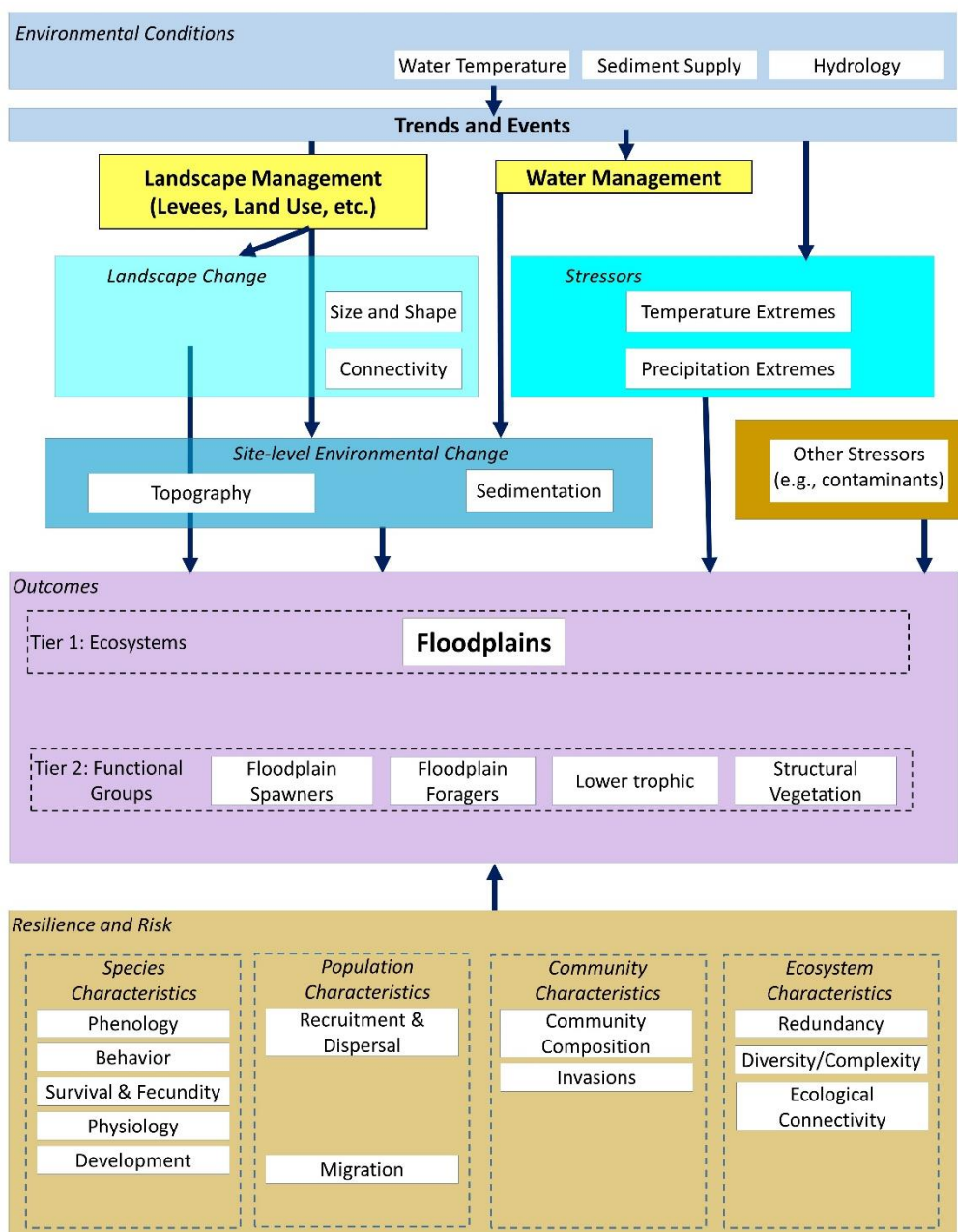


FIGURE 2. Model diagram for climate change impacts on floodplains.

Environmental Conditions

Water Temperature

Increased air temperature due to climate change will result in higher water temperatures within the shallow water of floodplains (Shellenbarger and Schoellhamer 2011). However, there can be complex interactions in shallow water bodies. For example, Enright et al. (2013) found that tidal cycles could generate cooling patterns when high tides coincided with night, cooler

temperatures, and breezy (evaporative) conditions. Aha et al. (2021) also documented a shallow water body that maintained lower temperatures with less diel fluctuation than nearby, deeper tidal sloughs. The general pattern for the Yolo Bypass is winter-spring water temperatures that are warmer on the floodplain than in the adjacent Sacramento River channel (Sommer et al. 2001; 2003). However, there are notable anomalies from this pattern. Specifically, high wind days in winter and spring can generate cooler temperatures in shallow flooded areas of Yolo Bypass, presumably because of strong evaporative cooling (Ted Sommer, 2021, DWR, written communication).

Projected spring and winter water temperatures during Yolo Bypass flooding events generally increased through the century (Figure 3, Wulff et al. 2021a). Water temperature was projected through 2099 using regression equations relating air temperature projection output from 10 downscaled global climate models (GCM) for two Representative Concentration Pathways (RCPs) for greenhouse gas concentrations (Knowles et al. 2018) to water temperature following Wagner et al. (2011) and Brown et al. (2016). Response was measured as the annual mean of the water-temperature projections during flood events for each combination of GCM and RCP annually from 2010 to 2099. Water temperature projections were also summarized into RCP 4.5 and 8.5 ensemble predictions for simplicity. Projected spring water temperatures exhibited little change for RCP 4.5 and increased slightly for RCP 8.5. Winter water temperatures were generally less than 15°C with occasional temperatures greater than 15°C after 2050 (Figure 3).

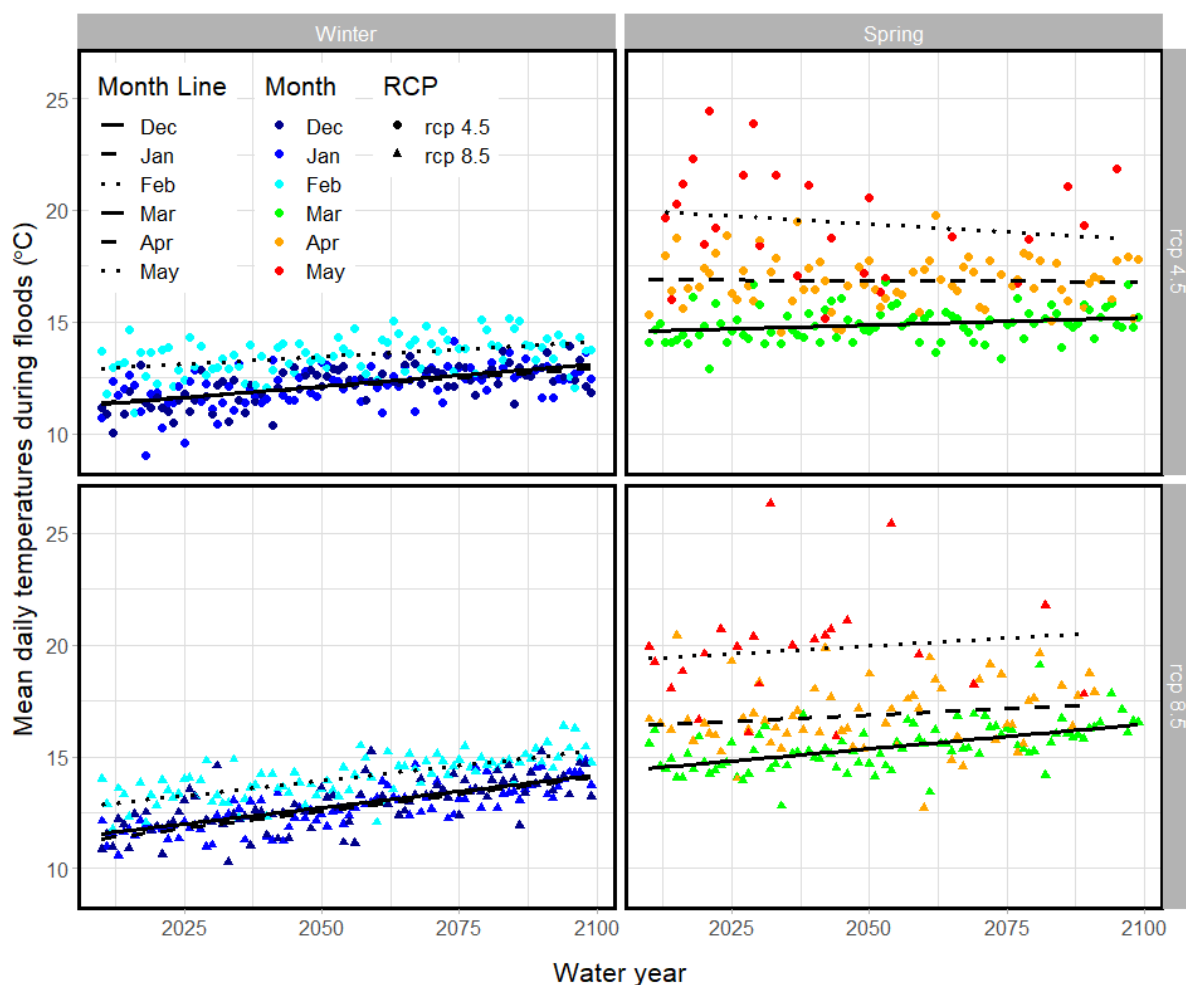


FIGURE 3. Mean daily water temperatures during flood events by month averaged across all climate scenarios for Representative Concentration Pathways (RCP) 4.5 (top) and RCP 8.5 (bottom).

Vegetation can reduce evaporation and have a cooling impact on water in floodplains. The shade provided by riparian forests and emergent vegetation, in particular, can decrease water temperature (Miller and Fujii 2010). However, warming air temperatures increase evapotranspiration rates which (1) cause stress on vegetation communities (Anderson et al. 2008), (2) likely dry floodplains faster, and (3) decrease soil moisture during the dry period.

Sediment Supply

The general pattern in the Bay-Delta has been a long-term decline in sediment availability because upstream dams block much of the sediment load from reaching downstream areas (Schoellhamer 2011). Moreover, Schoellhamer (2011) noted a potential regime shift around 1999 toward lower turbidity conditions. There is high uncertainty about changes in sediment availability in the Delta and Suisun Marsh with climate change. Some studies (Cloern et al. 2011; Hestir et al. 2013; Schoellhamer et al. 2013, 2018) predicted that sediment availability will

stabilize or decrease, but a recent modeling study forecasted increases in sediment load that may be caused by larger flood flows scouring upstream rivers and channels (Stern et al. 2020). A change in sediment supply will affect the dynamics of the Cosumnes River floodplain, and to a lesser degree the managed floodplains of the Yolo Bypass. A decrease in sediment availability would reduce topographic variability created during flooding events; an increase could result in the more frequent creation of sandbars and ecosystems dependent on that topography.

Hydrology

Floodplains and flood basins historically either received floodwaters through bank overtopping or through splays in natural levees. Floodwaters then receded off the floodplain and drained over the course of the dry season. This slow process extended the time the channels were connected to the floodplain, allowing for the exchange of water, sediment, and nutrients (Robinson et al. 2016).

Different aspects of hydrology are important for floodplain sustainability. Surface hydrology encompasses the sources that provide flows of water to a given river-floodplain system (Opperman 2008). The Sacramento River has the largest influence on surface hydrology of the Yolo Bypass, but the Cosumnes River determines the surface hydrology of its floodplain. River flow, in turn, is determined by regulated and unregulated discharges from the upstream watershed, which are affected by precipitation, runoff, and dam operations. Secondary hydrology encompasses hydrological inputs to the floodplain from sources other than the primary river, such as local precipitation, that add to the surface water, an elevated water table, groundwater inflows, other tributaries flowing into the floodplain, and human-constructed diversions. Secondary hydrology can influence the water quality on the floodplain, for example by contributing nutrients (Schemel et al. 2004; Opperman 2008). Groundwater hydrology is included in the secondary hydrology and influences the hydroperiod of floodplain wetlands, and, in turn, is influenced by the adjacent river, sediment characteristics, and groundwater pumping (Opperman 2008).

With climate change, river-flood hydrology, including inundation duration, frequency, magnitude, and timing, will change. In the Delta, projections show that high runoff events are likely to become increasingly concentrated in the core winter months, and the magnitude and frequency of these events will increase, while the duration of floods will decrease (Delta Stewardship Council 2021). Importantly, a more than threefold increase in overall frequency of extreme floods, that is, those events comparable to the ‘Great Flood of 1862,’ is predicted (Swain et al. 2018), in addition to the projected increase of severe drought events that may further reduce the already limited extent of existing Delta floodplain ecosystems by depriving them of riverine inundation. These whiplash conditions – rapid changes from one extreme to the other – are projected to increase by 25% to 100% (Swain et al. 2018). While runoff events

will affect floodplain hydrology in the Delta, moderate levels of sea level rise (up to 3.5 feet) are expected to have comparatively smaller impacts on the Yolo Bypass and Cosumnes River floodplain (Figure 4).

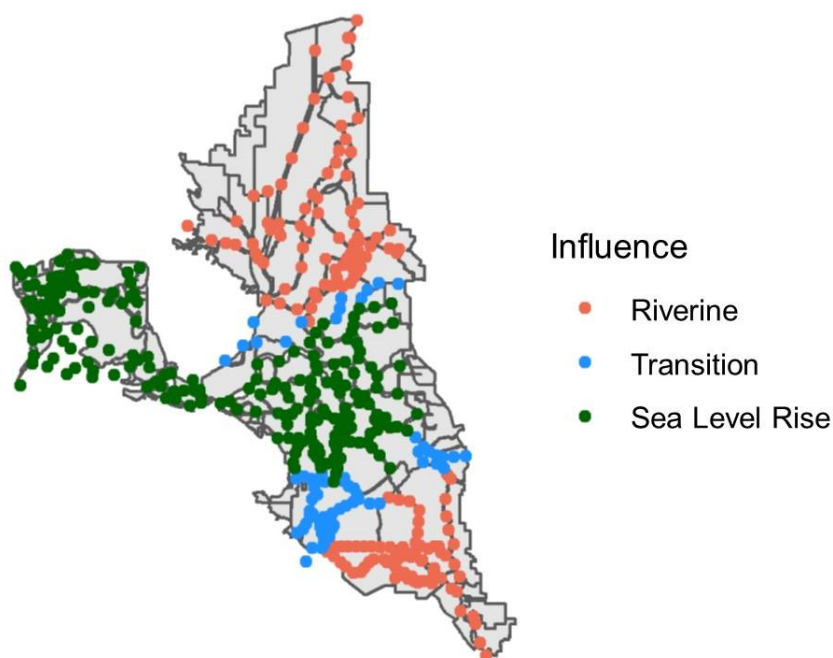


FIGURE 4. Primary climate change influence on peak water levels throughout the Delta (from Delta Stewardship Council, 2021).

Another prediction for climate change with substantial implications is longer, more severe droughts in California (He and Gautam 2016; Cayan et al. 2013). The 2012-2016 drought was one of the most severe droughts in California in the last 1200 years (Griffin and Anchukaitis 2014), and 2000-2020 is the second driest 19-year period since 800 CE (Williams et al. 2020). Long, severe droughts lead to loss of longitudinal, lateral, and vertical connectivity in river-floodplain corridors (Bond et al. 2008). During shorter periods of drought, inputs of direct precipitation, overland flow and shallow subsurface flow decrease, and deeper groundwater flows sustain surface flow. However, when the drought period lengthens, groundwater levels drop, and many streams lose surface water, resulting in the loss of longitudinal and vertical connectivity (Bond et al. 2008; Mosley et al. 2014). This in turn reduces allochthonous sources of dissolved organic carbon and other forms of organic nutrients, such as organic nitrogen and phosphorous, and enhances autotrophic processes relative to heterotrophic processes within remaining surface waters (Dahm et al. 2003; Bond et al. 2008). Groundwater drought is poorly understood, but it is critical to understand that when normal rainfall returns, surface water drought recovers faster than groundwater drought. In river floodplains, drought prevents seasonal inundation of floodplain wetlands and can extend the duration during which floodplains are not flooded, thus breaking lateral connectivity.

Hydrology of the Yolo Bypass

The hydrology of Yolo Bypass is complex, with multiple water sources including: 1) floodwaters from the Sacramento River, 2) tidal inputs from the lower Sacramento River, and 3) inputs from smaller tributaries (Knights Landing Ridge Cut, Cache Creek, Putah Creek (Sommer et al. 2008; Suddeth 2014; Frantzich et al. 2018). All these inputs are modified by flood infrastructure (e.g., weirs), small dams and barriers, agricultural operations, and local topographic features. By volume, the major input to the bypass is from the Sacramento River via Fremont Weir (Sommer et al. 2001), which occurs when the Sacramento River stage exceeds 32 feet and the Fremont Weir overtops (Figures 5, 6).

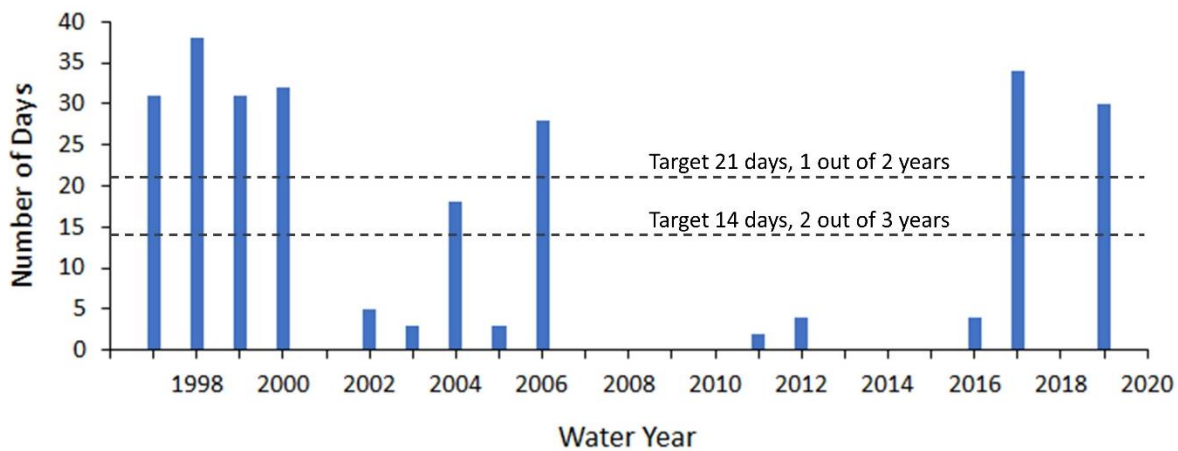
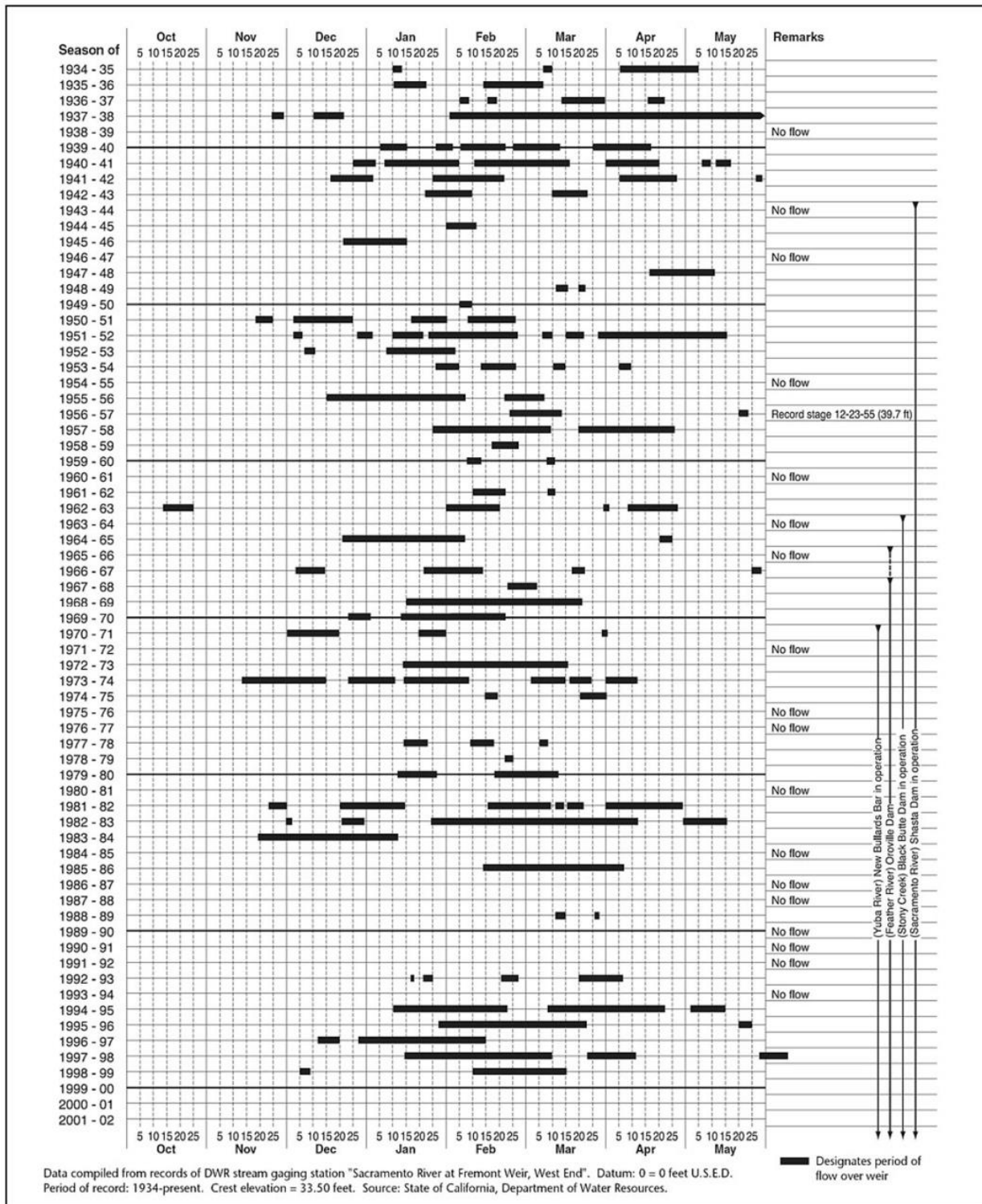


FIGURE 5. Number of consecutive days with Fremont Weir flows of at least 6,000 cubic feet per second (<https://viewperformance.deltacouncil.ca.gov/pm/functional-flows-yolo-bypass-inundation>)

A



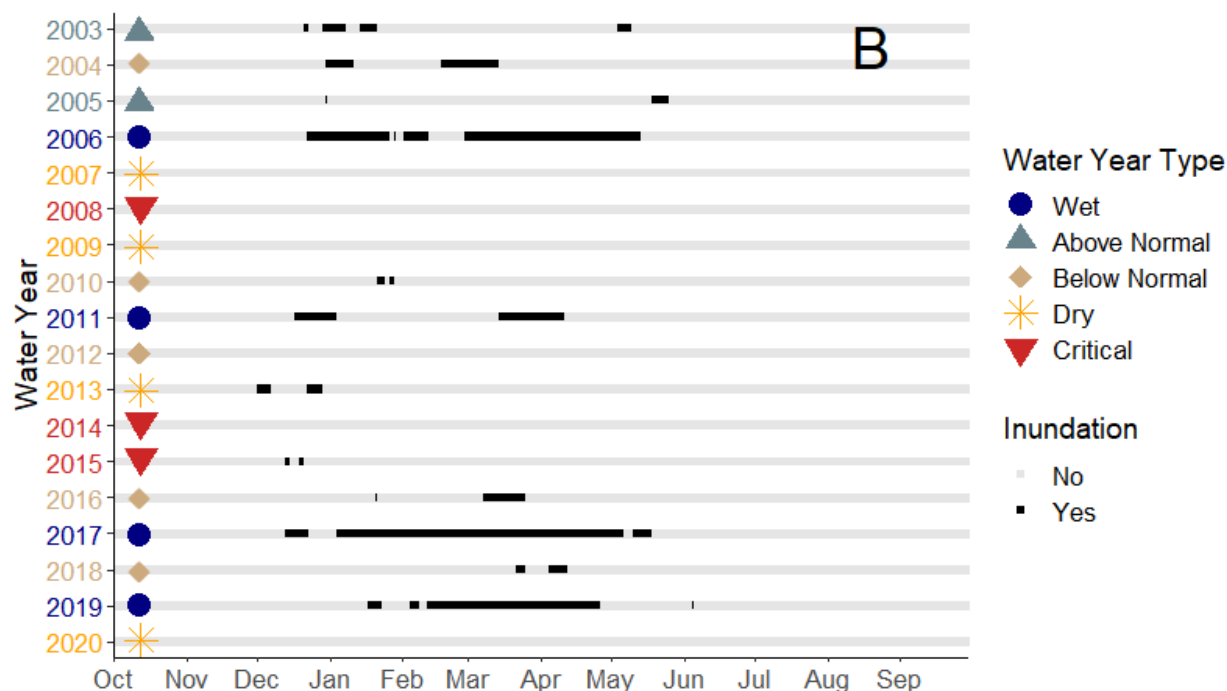


FIGURE 6. Periods of Overflow of the Yolo Bypass. A) Periods of Overflow of the Fremont Weir from 1935-1999. From Jones and Stokes 2001. B) Periods of Overflow from 2003-2020. Water-Year Type based on Sacramento Valley classification from <https://cdec.water.ca.gov/reportapp/javareports?name=WSIHIST>. Inundation data from Casby et al. 2021.

At very high flows, typically in about 1 out of 10 years, additional major flood flow enters via the Sacramento Weir. However, inputs from smaller westside tributaries contribute substantially to local flooding, resulting in complex lateral variability in water quality (Sommer et al. 2008) and thousands of acres of inundation even without inputs from Fremont Weir (Sommer et al. 2003). Tidal flows also create localized flooding and tidal currents at the southern end of the floodplain (Goertler et al. 2018) and provide a major source of water for agricultural distribution during summer and fall (Frantzich et al. 2018).

In the summer, the Toe Drain is the main water body in the Yolo Bypass. During the peak water diversion time in June through August, flows in the Toe Drain can be net negative, meaning that more water flows north than into the Delta due to tidal influences (Frantzich et al. 2018). When rice field drainage flows increase in late summer and early fall, the flow becomes net positive.

Potential effects of climate change on hydrology

Given the importance of Yolo Bypass flooding, understanding the influence of climate change on the frequency, magnitude, duration, and timing of flooding is critical for understanding the future value of the bypass to the Bay-Delta ecosystem (Box 2). For example, recently published

data (Wulff et al. 2021b) are being used to explore Yolo Bypass inundation patterns under 20 different climate-change scenarios. This analysis uses outputs from the Computational Assessments of Scenarios of Change for the Delta Ecosystem (CASCaDE II, <http://cascade.wr.usgs.gov/>) project (Knowles et al. 2018) to assess the effects of climate change on various flood metrics in the Yolo Bypass. Outputs from 10 global climate models (GCMs) under two Representative Concentration Pathway (RCP) trajectories for greenhouse gas concentrations were used to assess the effects of climate change on the frequency, duration, and timing of flood flows in the Yolo Bypass. Annual means of each flood metric were calculated for each GCM run. Ensemble trends were then determined over all years from runs that used each of RCP 4.5 or 8.5, with RCP 8.5 trending warmer and wetter than RCP 4.5. Yolo Bypass floods were designated as Fremont Weir flows > 4,000 CFS with the planned notched weir modification to Fremont Weir incorporated in the assessment (Bureau of Reclamation and California Department of Water Resources 2019). Analysis of the data (Wulff et al. 2021b) shows the notched-weir configuration provides more frequent flooding of longer duration compared to the existing no-notch configuration. These differences were maintained through the end of the century under both RCPs. There were few strong trends in projected flood metrics through the end of the century. Climate-change projections such as this suggest that the notch will increase the ecological value of Yolo Bypass to the fishes that use it for spawning and rearing and that these benefits will be maintained through the current century.

Cosumnes River floodplain:

Because there are no major dams, the Cosumnes River hydrology remains relatively natural (Jeffres et al. 2008). Streamflow is highly variable and mostly determined by rain events because much of the watershed lies below the snow line. In dry years, flow ceases by the end of the summer in the lower river reaches, exacerbated by severe declines in regional groundwater levels (Whipple et al. 2017).

Different flood types (Box 1) occur from fall to late spring in the lowland Cosumnes River (Figure 7, Whipple et al. 2017). From 1910 through 2014, the percent of annual volume of floodplain-resetting floods (which contributes to the total annual flow volume) increased by 14%; consequently, the percent of annual volume of the other flood types decreased (Whipple et al. 2017). After 1948 (the period of available data), all the very large events were associated with atmospheric river events (Dettinger et al. 2011; Whipple et al. 2017).

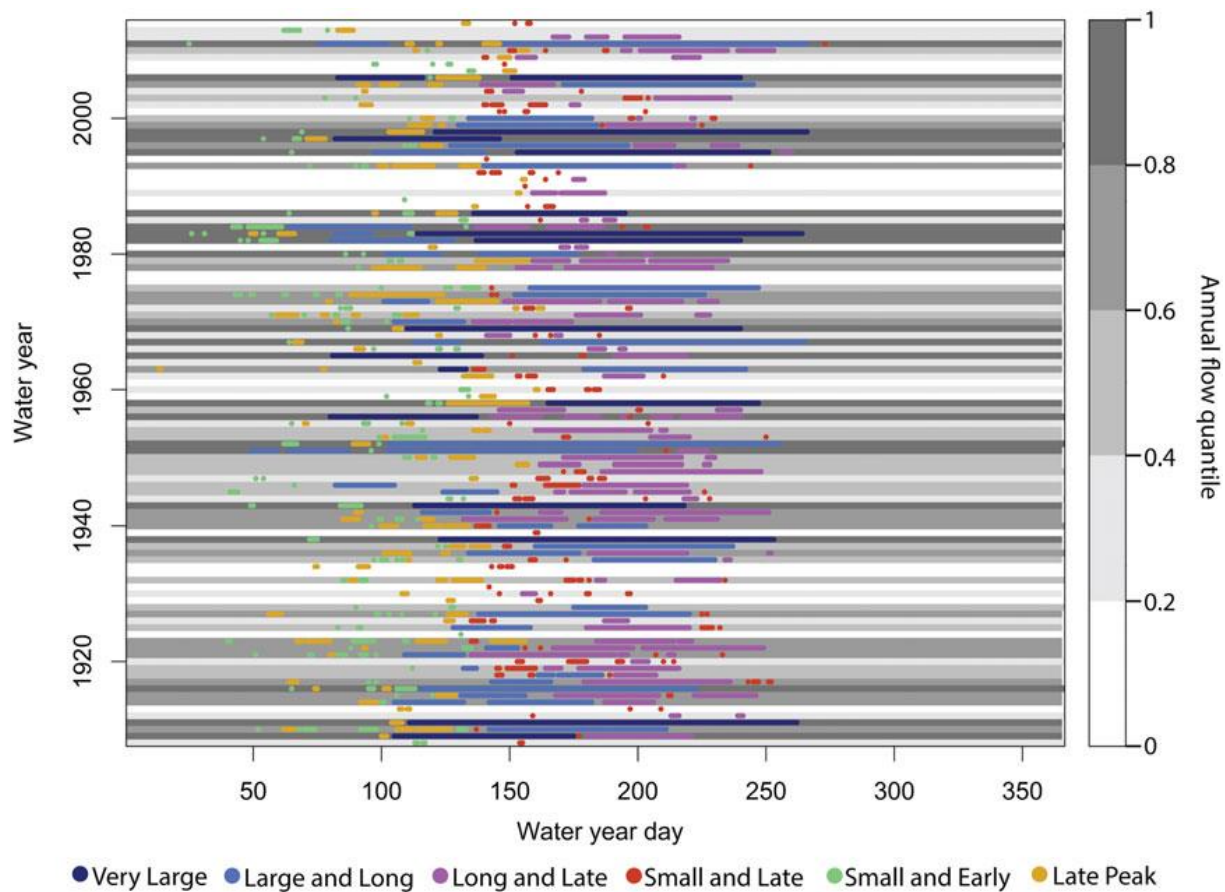


FIGURE 7. Each day of 532 individual flood events is shown over the period of record (from USGS gage 11335000; Cosumnes River above Michigan Bar CA, U.S. Geological Survey, 2022), colored by their flood type classification. To relate the events and their frequencies to climate conditions, the water year types based on annual flow quantiles are shown in the right part of the plot (wetter years are the darker shades) (From Whipple et al. 2017).

Understanding the influence of climate change on the frequency, magnitude, duration and timing of flooding and the effects on the ecological functioning of the Cosumnes River floodplains is important for the design of new restoration projects. Whipple (2018) compared floodplain inundation patterns predicted under four climate change scenarios, for both pre- and post-restoration conditions. The four scenarios spanned wetter to slightly drier future projections with respect to mean annual flow, and, to different extents, indicated higher extreme flood flows in winter and lower springtime flows for the period 2070-2099 compared to 1951-1980 (Figure 8). Floodplain inundation patterns were generally found to indicate these changes, although the magnitude and direction of change and variability differed across the metrics used (Figure 9). These results indicate that future changes in flow regime and floodplain inundations patterns may differ in relative magnitude and direction such that flow regime change alone may be inadequate to infer floodplain impacts. The analysis also showed that

restoration action reduced the effects of climate change in some scenarios, suggesting a potential for climate-change mitigation through floodplain restoration.

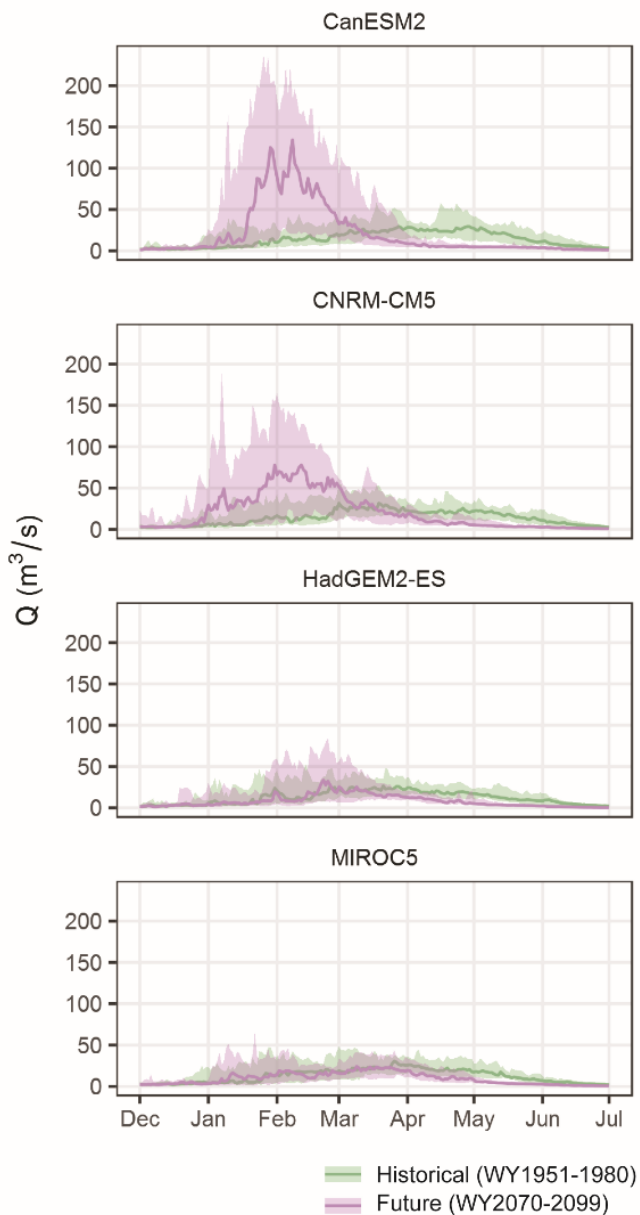


FIGURE 8. Median daily flow comparison for the water year (WY) 1951-1980 and WY 2070-2099 periods across high flow months for the four climate change scenarios. Shading shows the interquartile range. (From Whipple 2018)

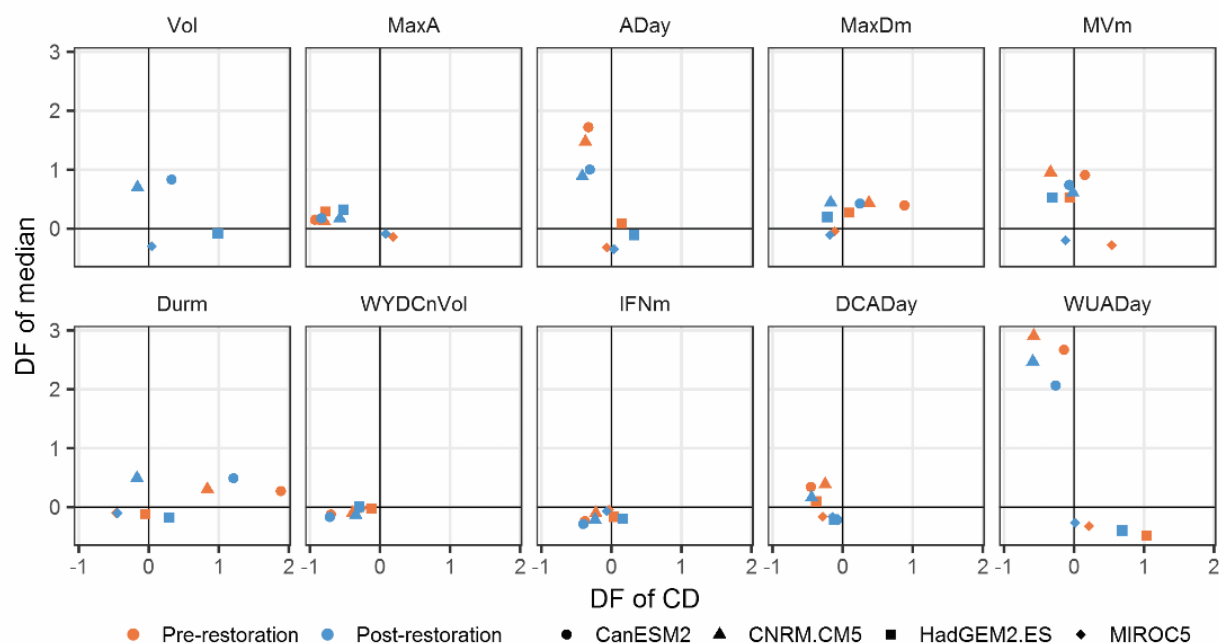


FIGURE 9. Change between water year (WY) 1951-1980 and WY 2070-2099. Deviation factors (DFs) of medians and coefficients of deviation (CD) for hydrospatial metrics comparing the WY 2070-2099 and WY 1951-1980 periods for each climate change scenario and restoration configuration. The upper left plot shows the DFs for the Cosumnes River water year flow volume projections for comparison purposes. Vol - flow volume; MaxA - Maximum daily inundated area in a water year; ADay - Daily inundated area summed over a water year; MaxDm - Spatial mean of maximum flood event depth, as mean for a water year; MVm - Spatial mean of mean flood event velocity, as mean for a water year; Durm - Mean water year spatial mean flood event duration; WYDCnVol - Water year day of centroid flood volume; IFNm - Mean water year spatial mean of flood event number of times inundated; DCADay - Daily disconnected inundated area summed over a water year; WUADay - Daily weighted usable area summed over a water year. (From Whipple 2018)

Box 2. Summary of potential effects of climate change on floodplain hydrology.

Throughout the 21st century, climate change is predicted to affect physical processes in the floodplains in the Sacramento-San Joaquin Delta as follows:

- The mean flood frequency will decrease.
- Under RCP 8.5, the frequency of large flooding events will slightly increase.
- A more than threefold increase in overall frequency of extreme floods, that is, those events comparable to the 'Great Flood of 1862,' is predicted (Swain et al. 2018).
- The average duration of floods will increase.
- Flooding will become increasingly concentrated in the core winter months.
- Severe drought events are projected to increase in frequency.

- Rapid changes from one extreme to the other are projected to increase by 25–100%.
- Water temperatures will increase.
- Higher air temperatures will cause increasing evapotranspiration rates.

In the Yolo Bypass, changing the configuration of the Fremont Weir will increase the frequency and duration of floods, and the date of first floods is predicted to move from mid-January to early January. Climate change will affect the new baseline of increased frequency and durations of floods in the Yolo Bypass. Under RCP 8.5, a slight decline in flooding frequency and an increase in mean flooding duration from about 22 to 26 days are predicted over the century.

Water and Landscape Management

Floodplain restoration will increase the total area of floodplains, the number of patches, and potentially decrease the distance between floodplains. Floodplain restoration projects in the Delta come in the form of flood bypass establishment or management with ecological objectives, or of projects breaching levees originally built to protect farmland from flooding by the adjacent river. Recommendations for floodplain restoration include (Robinson et al. 2016):

- re-establishing connectivity between streams and floodplains,
- increasing flows into the floodplain,
- ensuring that floodplains have connections to the river at both upstream and downstream ends, and
- restoring flooding regimes with a magnitude, timing, extent, and duration of inundation that supports desired ecological functions.

To increase the adaptive capacity of floodplains to climate change, management strategies can be effective. Examples are (1) modifications of weirs and levees as well as local changes to topography and habitat conditions to increase inundation frequency and duration, (2) ecological restoration to improve the quality and diversity of habitats (Sommer et al. 2020), and (3) improved fish passage projects (Bureau of Reclamation and California Department of Water Resources 2019).

Yolo Bypass

The EcoRestore program aims to restore or enhance 17,500 acres of floodplain ecosystem and is focusing on projects in the Yolo Bypass (Figure 10). Projects include restoration of local tributaries, fish passage and fish rescue projects, modifying the Fremont Weir, and increasing the area of the Yolo Bypass at the southern end by setting back levees (e.g., Lookout Slough restoration project; DWR 2022). There are several other companion projects to improve habitat conditions in the floodplain (e.g., Bureau of Reclamation and California Department of Water

Resources 2019; Sommer et al. 2020), and long-term enhancements to the flood management system are likely to lead to opportunities to further support and enhance ecological functions (DWR 2017).

The Yolo Bypass will also likely be a central component of flood-infrastructure improvements in the Sacramento Valley (DWR 2017). Potential changes include increases in floodplain area and a broader weir connection to the Sacramento River. The Department of Water Resources (DWR) and Bureau of Reclamation (Reclamation) are also planning major improvements to the Yolo Bypass landscape and hydrology to support fish rearing and migration (Bureau of Reclamation and California Department of Water Resources 2019). These changes are designed to increase the frequency and duration of inundation, reduce fish stranding, improve adult fish migration, and enhance downstream subsidies of food web organisms.

Local management changes to topography and land use that are being considered in the Yolo Bypass would support salmon rearing (Katz et al. 2017; Sommer et al. 2020). Studies of the suitability of seasonally flooded rice fields for providing rearing habitat for juvenile Chinook Salmon have been promising (Sommer et al. 2020). Connectivity of the fields would need to be established with adjacent channels so that salmon can reach them, use them for rearing, and then emigrate when the water level is declining. The availability of predator and temperature refugia may be another factor determining suitability of fields for salmon rearing.

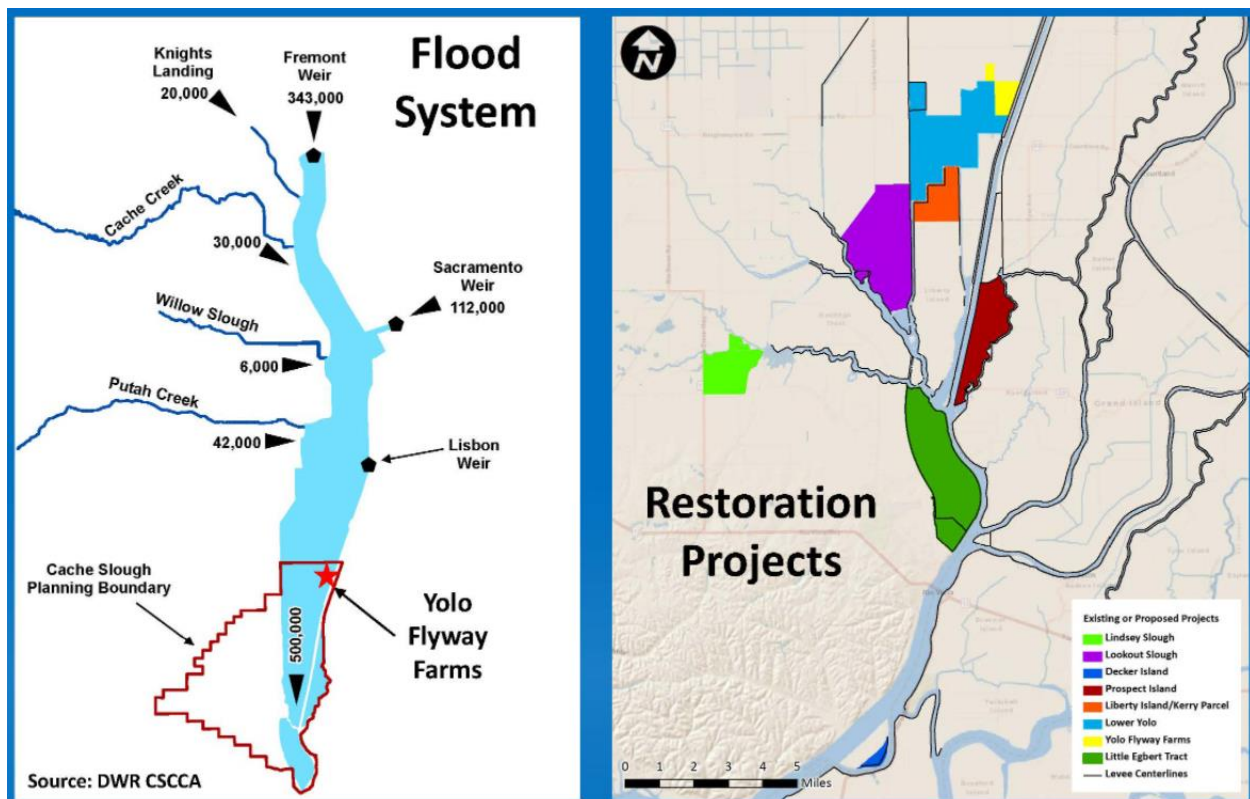


FIGURE 10. The Yolo Bypass with its tributaries (A) and existing and planned restoration projects at the southern end (B). (by Chris Campbell with CBEC Eco Engineering; <https://mavensnotebook.com/2019/02/14/bay-delta-science-conference-restoration-in-the-cache-slough-complex-the-yolo-flyway-farms-restoration-project/>)

Cosumnes River

Along the Cosumnes River, extensive groundwater pumping for agriculture and urban water supply for more than 50 years has disconnected the river from its aquifer and caused it to lose its baseflow from summer into mid-fall (Fleckenstein et al. 2004). A lower groundwater level also decreases the water available to vegetative communities on floodplains (Opperman 2008). Floodplain restoration can substantially recharge groundwater to benefit water users and natural communities. Groundwater management to reduce overdraft is important for maintaining river connectivity and providing a migratory corridor for fish.

Landscape management in the past years has included intentional levee breaks and setback levees, increasing the amount of floodplain along the Cosumnes River. Additional floodplain restoration projects along the Cosumnes River currently planned for the McCormack-Williamson Tract and Grizzly Slough will add nearly 2,000 acres of floodplain ecosystem along the downstream portion of the Cosumnes River Preserve (Figure 11).

More severe storms, sea-level rise, aging levees, and California's active seismic faults are likely to bring about unplanned levee breaches, which may lead to more floodplain area, but timing and location of these breaches is difficult to predict (Delta Stewardship Council 2021). The likelihood of more severe flooding may increase the motivation to restore more floodplains and decrease flooding risk in developed areas.

The need for water storage and flood protection will prevent re-establishment of the natural flow regime of most rivers. Instead, management of river flows will need to balance human needs with floodplain function.

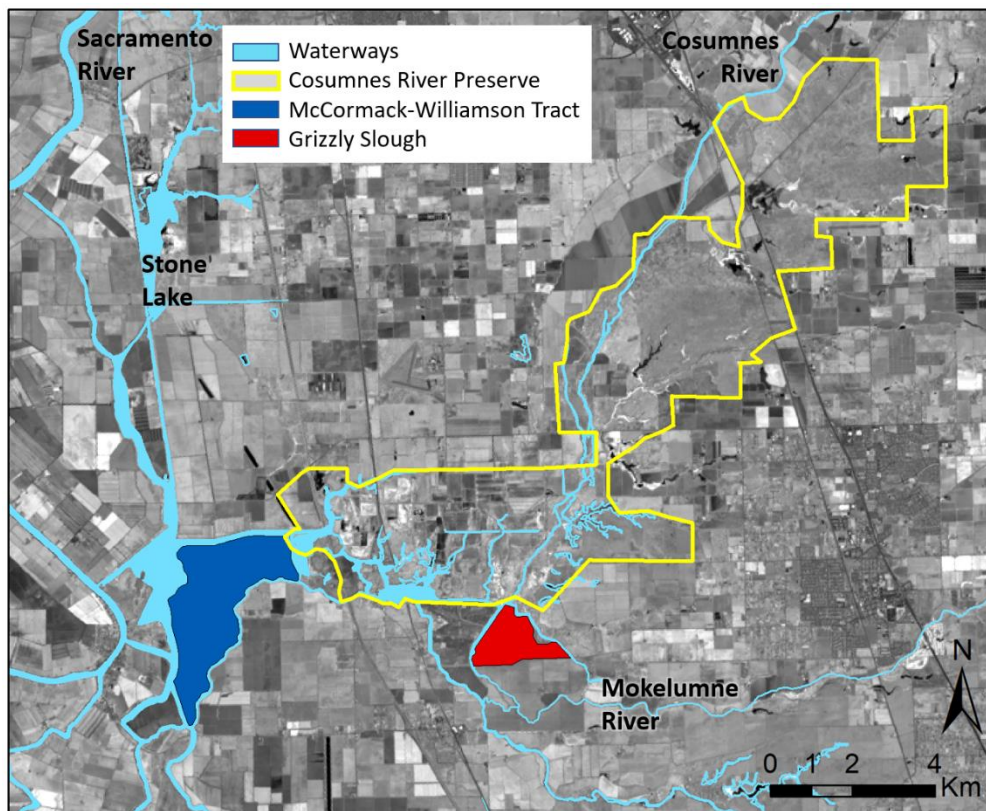


FIGURE 11. Location of the Cosumnes River Preserve and planned restoration projects to restore lateral connectivity to floodplains of the Cosumnes River.

Landscape Change

Patch Size and Shape, Connectivity

In an unimpeded river corridor, a river and its floodplain function as one integrated system, pulsing together to create a diverse environment that supports a highly diverse biota (Junk et al. 1989; Junk and Piedade 1997). The floodplain is spatially heterogeneous with multiple channels and deep alluvial deposits. It typically contains lotic, semi-lotic, and lentic bodies of water across the transect from the main channel (lotic) to the edge of the floodplain (lentic).

This transect is also stratified in terms of temperature and nutrients (Arscott et al. 2001). Lateral exchange among floodplain, river channel, and nutrient recycling within the floodplain have more direct impact on biota in the main river channel than any transport of nutrients from upstream (Junk et al. 1989). Many diverse terrestrial habitats on floodplains are created by the fluvial action of the river and its floods. These habitats include forested or bare islands, natural levees, sand bars, gravel bars, and piles of woody debris, each of which can potentially be in different seral, or secondary successional developmental stages. The spatially heterogeneous aquatic and terrestrial environments support a high degree of biodiversity offering varied niches to be exploited by the biota (Connell 1978).

Floods are the major structuring force responsible for maintaining spatial heterogeneity in the floodplain (Junk et al. 1989; Tockner et al. 2000). The floodplain slows down floodwaters and lowers peak flood levels by diverting water away from the main channel. Episodic floods may cause channel migration or avulsion, eliminate islands, sand, and gravel bars at some locations while forming new islands, sand, and gravel bars at others (Tockner et al. 2000). Vegetation colonizing these features follows a succession trajectory starting with flood-tolerant species and slowly moving toward more upland species as the feature stabilizes. Flooding resets succession in some regions while instigating succession in others. Large woody debris transported by a flood and stranded on the floodplain can serve as a nucleus for island formation. This leads to a diverse riparian community in various seral stages across the floodplain supporting a multitude of avian, amphibian, and invertebrate species. Water bodies also follow a similar process. Hence, the river floodplain is in a state of dynamic equilibrium between terrestrialization (between flooding events) and rejuvenation (during flooding events; Ward et al. 2001). Landscape elements, both aquatic and terrestrial, in the river-floodplain have a high turnover rate. Tockner et al. (2000) documented a 15% turnover for established islands and 83% for large woody debris and pioneer islands over just two years, 1984 to 1986, in the Tagliamento River of Italy. However, the average composition of different habitat types remains fairly constant (Arscott et al. 2001), ensuring habitat for diverse floodplain species at all times.

Habitat diversity is a function of both the water level and the location of the habitat on the lateral transect (Van Der Nat et al. 2002). At low water levels, connectivity is low; hence, shoreline length (edge habitat) is low. At mean water level, connectivity is moderate, and both shoreline length and habitat diversity are highest. As the water level increases further and waterbodies connect with each other, shoreline length decreases, and habitat heterogeneity decreases. Along the lateral transect, water bodies near the main river channel have the highest connectivity, and the water bodies near to the uplands have the lowest connectivity.

Ninety eight percent of the rivers in North America have some flow regulation for the purpose of navigation, agriculture, power generation, or flood-control (Vitousek et al. 1997). Levees and dams significantly alter flood regimes disconnecting the rivers from their floodplains, drastically

reducing spatial heterogeneity in the floodplain and the extent of the riparian corridor (Gergel et al. 2002). In the Yolo Bypass, lateral connectivity between the Sacramento River and the floodplain is non-existent and is minimal between the sloughs or the Toe Drain and the terrestrial ecosystems in most of the bypass. Only in the Cache Slough area at the southern end of the bypass have levee failures and restoration projects restored the potential for material exchange and species movements between aquatic and terrestrial ecosystems. In contrast, lateral connectivity along the Cosumnes River is much higher. While in the past, levees restricted lateral connectivity except during high flow events that caused overtopping, several levee breaches along the lower Cosumnes River have restored the potential for water to flow onto the floodplain (Nichols and Viers 2017). Planned restoration projects will increase lateral connectivity even more (see Water and Landscape Management section).

While lateral connectivity is key for floodplain processes, certain land uses adjacent to rivers can have harmful effects on organisms in floodplains and rivers by introducing pollution such as fertilizers and pesticides from agricultural areas and surface runoff from roadways (Wang et al. 2019; Tian et al. 2020, 2021).

Stressors

The main climate-change stressors affecting floodplains are temperature and precipitation extremes that result in extended droughts and extreme floods comparable to the 'Great Flood of 1862.' Organisms associated with floodplains are adapted to the natural flooding regime, which encompasses magnitude, frequency, duration, and timing of floods. In Mediterranean systems, organisms are also adapted to great variability in events, where long-lasting or extreme alteration of any component of the flood regime may threaten ecosystem functioning and species persistence. With climate change, events that were considered extreme in the past may become common (Cloern et al. 2011).

Extensive droughts can be detrimental to floodplains. They can lead to local biotic homogenization or loss of aquatic communities and can increase the time needed for natural communities to recover (dos Santos Bertoncin et al. 2019). In managed, agricultural floodplains that may be flooded even during drought conditions for crops or wildlife support, zooplankton densities can be high, but high temperatures and concentrated avian predators can cause fish mortality (Sommer et al. 2020).

Extreme floods, on the other hand, can be beneficial to floodplain ecosystems with a natural connection to the adjacent river. They cause strong natural disturbances that can reset aquatic and floodplain communities. Submergence of vast areas of land can stimulate the food web and create new fish habitat. Floodplain vegetation can be damaged and even lost during long periods of inundation but has the potential to re-establish quickly when floodwaters recede

(Hickey and Salas 1995). Managed floodplains like the Yolo Bypass are unlikely to experience floodplain-resetting floods, even with extreme flooding, unless infrastructure fails (e.g., levees and weirs).

Site-level Environmental Change

Topography

Floodplain ecosystems with a natural connection to the adjacent river (such as the Cosumnes River floodplain) may experience site-level changes in topography more frequently with climate change because of the increased frequency in storm events that cause floodplain-maintenance and floodplain-resetting floods.

More frequent and severe storms may bring sediment pulses. A daily rainfall runoff and transport model of the Sacramento River basin showed significantly increased sediment loads by the end of the century (Stern et al. 2020). With no major dams on the Cosumnes River, an increase in sediment supply would contribute to the more frequent creation of sandbars and ecosystems dependent on that topography on the Cosumnes River floodplain. Conversely, due to the dams above the Yolo Bypass, less sediment is available to affect the topography of the Yolo Bypass. Additionally, large expanses in the Bypass are constantly graded for agricultural purposes.

Groundwater

Groundwater declines caused by extended droughts and extensive pumping can decouple trees from soil moisture associated with the water table and result in high mortality in floodplain forests. Quantifying groundwater-depth thresholds and monitoring water-table trends will provide critical decision-support information for resource managers striving to conserve groundwater-dependent biodiversity (Kath et al. 2014; Mac Nally et al. 2014).

Other Stressors

Contaminants

Pesticide and fertilizer use may increase with climate change because of the longer growing seasons and because pest species (especially non-native species) may increase in abundance. Additionally, pesticides are a stressor that diminishes the resilience of organisms to additional stressors such as climate change. In the Yolo Bypass and Cosumnes River floodplains, organisms may be exposed to high levels of mercury, impairing the health and reproduction of fish, birds, and mammals (Henery et al. 2010; Alpers et al. 2014; Eagles-Smith et al. 2016).

Functional Groups

We considered the outcomes of climate-induced changes in environmental conditions, water and landscape management, and landscape configuration on different functional groups (Table 1). We separated the fish community into floodplain spawners and floodplain foragers and selected a few key species for detailed consideration. In the lower trophic category, we broadly considered the effects on plankton and benthic organisms. Finally, we contemplated the effects of climate change on vegetation and its structural properties.

Table 1. General predictions for the impact of climate change on major taxa in floodplains.

Functional groups and representative species	Decrease in Frequency of Flooding	Increase in Frequency of High-Magnitude Floods	More variable duration of flooding	Increase in frequency of drought conditions	Increased temperature
Floodplain spawners (fish)	More variable access to floodplains, higher variation in reproductive success (e.g., more boom-and-bust dynamics), unknown/mixed long-term impacts to populations dependent on life history and life span	Increase spawning and rearing habitat, more opportunities for adults to enter from river, likely positive impact on reproduction during years with these floods	Increased variability in access to spawning and rearing habitat; will have mixed impacts: negative if floods recede during spawning or rearing periods, positive if flooding allows for extended spawning or rearing seasons	Reduced access to floodplain habitat during droughts, negatively impacting spawning success	Depends on temperature preference and tolerance, but likely to benefit non-native species more than native floodplain spawners
Floodplain foragers (fish)	More variable access to floodplains, higher variation in reproductive success (i.e., more boom-and-bust dynamics), unknown/mixed long-term impacts to populations	Increase in foraging opportunities and connectivity to floodplains, which will likely have positive impacts of growth and survival for individuals that utilize this habitat during these floods	Increased variability in access to this habitat and will have mixed impacts, but could lead to increased chances of stranding (e.g., lower survival rates)	Reduced access to floodplain habitat during droughts, negative impacts on growth and survival if food resources in non-floodplain habitats are poor relative to floodplains	Depends on temperature preference, tolerance, and food availability, but likely to benefit non-native species more than native floodplain foragers

Lower trophic functional groups: Plankton, benthos, insects	Likely would lower plankton production and decrease abundance of benthic organisms, overall negative impacts to lower trophic levels	Increased abundance due to longer floodplain inundation, overall positive impacts during these events	Increased variation in production and abundance (shorter flooding causes lower abundance and longer flooding causing higher abundance)	Overall reduction in abundance and production of lower trophic levels on floodplains during flooding.	Generally increased production, changing species composition
Vegetation: reeds, shrubs, trees	Likely will lead to changes in community composition to favor higher successional shrub and tree communities	These floods will likely cause changes in floodplains that reset succession, lead to channel avulsion, etc. which would lead to more early successional communities	Increased duration of flooding will cause die-offs in species not used to longer flooding periods which helps species that are adapted to longer flooding	Increased frequency of severe drought will depress the water table and increase disconnection between the floodplain and the river, cause die-off or even extinction of some species, overall leading to a simpler less diverse riparian-floodplain community	Higher temperatures will stress native vegetation and encourage growth of invasive vegetation; most invasive species are from tropical regions and more adapted to hotter temperatures

Floodplain spawners

The narrative below focuses on native and nonnative species categorized as floodplain spawners by Moyle et al. (2007). This functional group of fishes uses floodplains for spawning and rearing. Adults use flooded vegetation as spawning substrate, and new hatchlings will often remain to rear in the floodplain and leave when water recedes (Moyle et al. 2007). Increased flood frequency and duration often improves recruitment for these fishes. Floodplain spawners can be classified as either obligate spawners who rely on floodplain habitat or opportunistic

spawners who could spawn successfully elsewhere but benefit from floodplain habitat. Because obligate spawners rely heavily on floodplains, they will likely be more impacted by changes to floodplain habitats, compared to opportunistic spawners. The following sections summarize various native and nonnative floodplain spawners present in the San Francisco Estuary and their associated climate-change risks.

Sacramento Splittail

Status quo

The Sacramento Splittail (*Pogonichthys macrolepidotus*), or Splittail for short, is a cyprinid fish native to California's Central Valley and the Napa River, primarily centered around the San Francisco Estuary (Moyle et al. 2004). It is a California Species of Special Concern and was delisted from the federal threatened species list by U.S. Fish and Wildlife Service in 2003 (Moyle et al. 2012; U.S. Fish and Wildlife Service, 1999). Splittail are considered obligate floodplain spawners. Adult Splittail usually migrate upstream in January and February and spawn on inundated floodplains in March and April (Moyle et al. 2004). Upstream migration is closely linked with flow events when floodplains are inundated (Garman and Baxter 1999; Harrell and Sommer 2003). Research has shown that healthy populations of Splittail need inundated floodplains in winter and spring, safe migration corridors between spawning and rearing habitats, and brackish shallow water rearing habitat (Moyle et al. 2004).

In the Sacramento River drainage, the Cosumnes River floodplain and Sutter and Yolo Bypasses are important spawning areas for Splittail. Splittail need at least 30 consecutive days of inundation for successful spawning and rearing, and both Sutter and Yolo Bypasses are inundated for long periods of time in wet years (Moyle et al. 2004; Sommer et al. 1997). Longer inundation periods have been shown to increase the number of larvae hatched in a given year, commonly referred to as year-class strength, of young Splittail (Moyle et al. 2004; Sommer et al. 2001).

Risks of climate change & associated impacts

Sacramento Splittail are generally considered to be tolerant of a wide range of environmental conditions, thus their long-term survival will be closely tied to access to, and availability of, adequate spawning and rearing habitat. Changes in frequency and intensity of droughts will negatively affect Splittail populations, particularly extended droughts (Moyle et al. 2004), but adults will successfully spawn if they are provided access to floodplain habitat in dry years (Sommer et al. 2003). Splittail reproduction could be improved through floodplain restoration, particularly if river-floodplain connectivity is improved in dry years (Sommer et al. 2003).

Over the century, projected changes in water temperatures during Yolo Bypass flooding events are relatively small (<2°C; Wulff et al. 2021a) and may have little effect on Splittail that are temperature tolerant and can survive temperature fluctuations (Moyle et al. 2004).

Other interacting effects

Managed inundation of a floodplain can be used to support Splittail populations and help mitigate climate-change effects. Wulff et al. (2021b) recently assessed a planned modification to the primary weir controlling flooding that will result in inundation of the Yolo Bypass at lower river flows. As intended, in the models, the notched weir configuration provided more frequent flooding of longer duration compared to the existing no-notch configuration. These differences were maintained through the end of the century under mitigated and business as usual climate scenarios. These climate change projections suggest that the notch will increase the ecological value of the Yolo Bypass to the fishes that use it for spawning and rearing and that these benefits will be maintained through the current century.

Sacramento Blackfish*Status quo*

Sacramento Blackfish (*Orthodon microlepidotus*), or Blackfish for short, are native to the San Francisco Estuary and spawn on submerged vegetation in floodplains but are not considered obligate floodplain spawners (Moyle et al. 2007). They are found in the Yolo Bypass and Cosumnes River floodplain later in the flooding season, and both adult and young-of-the-year (YOY) life stages seem to prefer conditions similar to those of nonnative species (Crain et al. 2003; Moyle et al. 2007). Adult Blackfish may occasionally enter the Cosumnes River floodplain from the adjacent river, and YOY Blackfish have been found in shallow water in the summer (Moyle et al. 2007). Small Blackfish prey on zooplankton and insects, while larger Blackfish increasingly rely on suspension feeding (Moyle 2002). While Blackfish are caught by the DWR Yolo Bypass Fish Monitoring Program (YBFMP) (Kwan et al. 2019; IEP et al. 2018), they are rarely caught in other surveys across the Delta (B. Mahardja, Bureau of Reclamation, written communication, 2021). Thus, little is known about the distribution and movements of Blackfish, especially compared with other fish species in the Delta.

Risks of climate change & associated impacts

Blackfish are highly adapted to extreme conditions, including high temperatures and hypoxia, and they have a range of feeding and respiratory behaviors that allow them to survive in extreme and changing conditions such as those associated with climate change (Campagna and Cech Jr 1981; Cech and Massingill 1995; Moyle 2002). In the floodplain environment, Blackfish exhibit preferences similar to those of nonnative species, associating with later flooding and warmer water temperatures, and have been classified as least vulnerable to climate change (Moyle et al. 2013). While climate change is likely to result in warmer temperatures and increased large floods, which are beneficial to Blackfish, it is also predicted that due to less snowpack and earlier snowmelt, flooding duration may be variable, and shift to earlier in the spring, which does not coincide with periods during which Blackfish spawn and use the floodplain (Moyle et al. 2007). Early season and increased large-magnitude flooding

opportunities may still provide benefits to Blackfish by providing greater connectivity to the river and by increasing productivity of the floodplain habitat (Harrell and Sommer 2003; Moyle et al. 2007); however, if the floodplain drains earlier in the season there may be greater stranding of Blackfish, unless there is sustained flooding during wetter years or due to water management. While shallow pond habitats are generally more favorable to nonnative species, Blackfish can benefit from these conditions and habitats as well (Moyle et al. 2007).

Impacts of water and landscape management

While the Yolo Bypass is currently managed primarily for flood control, water management and infrastructure may influence the timing and duration of inundation. Sustained inundation through late spring/early summer would be beneficial to Sacramento Blackfish, although this is unlikely to occur because of the benefits this would provide to non-native species.

Non-native species: Goldfish, Common carp

Status quo

Two non-native San Francisco Estuary species, Goldfish (*Carassius auratus*) and Common Carp (*Cyprinus carpio*), are considered opportunistic floodplain spawners (Moyle et al. 2007). Goldfish spawning generally begins in April/May and requires temperatures between 16-26°C. Common Carp begin moving to spawning groups in spring and early summer, once temperatures exceed 15°C (CalFish). Based on monitoring data from the YBFMP, Common Carp are more abundant in floodplain habitat than Goldfish. Carp are also one of the most frequently caught adult fish in the YBFMP fyke trap (Sommer et al. 2014; Interagency Ecological Program, 2018). YBFMP beach seine data also show that YOY carp tend to be more abundant during wet years, similar to the native Sacramento Splittail (Mahardja et al. 2017).

Risks of climate change & associated impacts

Generally, non-native species will benefit from climate change because of the same characteristics that made them successful invaders, including broad temperature tolerance and the ability to rapidly shift ranges (Hellmann et al. 2008). During various climate change scenarios, their invasive characteristics will help them outcompete native species (Mainka and Howard 2010). For example, changing conditions could increase survival and year-round occupation of previously inhospitable areas (Hellmann et al. 2008; Rahel and Olden 2008) or changing the timing of spawning and recruitment.

With increased temperatures due to climate change, Goldfish are likely to increase in abundance and range. Common Carp are one of the least vulnerable species and are likely to benefit from future conditions (Moyle et al. 2013). A study of Common Carp across North America compared fish located in warmer, southern latitudes to those in cooler, northern latitudes as a proxy for how climate change may affect the species. Common Carp in more northern latitudes were older and larger while fish in southern latitudes had 22% faster growth

but 31% higher mortality (Weber et al. 2015). This suggests that climate change could cause Common Carp to grow faster but have shorter life spans and smaller maximum sizes.

Increased flood duration is likely to increase spawning habitat availability for these two species, but the relationship between this habitat and goldfish is unclear due to low numbers of goldfish in the system. Winter flooding would likely be less beneficial than spring flooding because both species begin spawning around April. However, if water temperatures increase, these species could potentially extend their spawning windows into earlier months.

Floodplain foragers

The narrative below focuses on native and nonnative species categorized as floodplain foragers by Moyle et al. (2007). This functional group of fishes uses floodplains to forage; actively moving into flooded habitat to prey on abundant food resources (Moyle et al. 2007). This group typically uses the floodplain as juveniles or yearlings, generally displaying increased survival and growth rates relative to their counterparts which rear in non-flooded habitats. Climate change impacts to floodplains may alter these benefits and change the way these species use floodplain habitat. The following sections summarize the various native and nonnative floodplain foragers present in the San Francisco Estuary and their associated climate-change risks.

Chinook Salmon

Status quo

Floodplain habitats in the Delta serve as non-natal rearing habitats for juvenile Chinook Salmon as they migrate toward the ocean. In general, floodplains provide high-quality nursery habitat for juvenile Chinook Salmon and provide favorable conditions that promote fast growth (Sommer et al. 2001b; Jeffres et al. 2008; Limm and Marchetti 2009; Bellmore et al. 2013). Floodplains decrease water velocity, moderate water temperatures, and have higher prey availability than mainstem habitats (Beechie et al. 1994; Sommer et al. 2001b; Ebersole et al. 2003; Jeffres et al. 2008; Henery et al. 2010; Bellmore et al. 2013). Historically, access to floodplain habitats has been driven by precipitation (Nislow and Armstrong 2012; Merenlender and Matella 2013) and water management. As such, during high-water years, juvenile Chinook Salmon generally have access to both the Yolo Bypass and Cosumnes River floodplain. However, during average- and low-water years, access to floodplain habitat is generally limited, though restoration efforts to improve access through active management of the floodplain habitats are likely. A good example of this is the Cosumnes River floodplain, where these habitats commonly flood during precipitation events.

Risks of climate change & associated impacts

With the expected climate change effects (Box 2), we expect a mixture of effects on juvenile Chinook Salmon. In general, we expect to see more variability in the ability of juvenile Chinook Salmon to use floodplain habitats due to changes in flood frequency, the size of flooding events, duration of flooding, and frequency of drought periods. When floodplain habitat is accessible, we expect juvenile Chinook Salmon to utilize this habitat and experience benefits, such as higher growth rates over individuals that remain in mainstem habitats (e.g., Sommer et al. 2001b; Jeffres et al. 2008; Limm and Marchetti 2009; Bellmore et al. 2013). However, the magnitude of growth benefits might decrease if water temperatures on floodplains also increase. Changes in flood patterns that lead to abrupt within-season drops in water levels could lead to increased stranding and higher mortality of Chinook Salmon utilizing these habitats. Finally, changes in the duration and timing of floodplain inundation will likely influence which of the four Central Valley Chinook Salmon runs have access to floodplains within a given year (see Williams 2006 for description on Chinook Salmon runs). Collectively, we expect to see overall negative climate change impacts on juvenile Chinook Salmon within floodplain habitats.

Other interacting effects

We expect to see an increase in metabolic demand of juvenile Chinook Salmon in floodplains because of increased water temperatures. Therefore, individuals will need to forage more to maintain their base metabolism and high growth rates. As a result, they will need to have increased access to adequate foraging opportunities by finding areas of higher prey densities or increase the time spent foraging, both of which come at the cost of increasing predation risk (Walters and Martell 2004). Alternatively, increased water temperatures may cause a decrease in growth rates when sufficient prey resources are not available. Finally, we expect higher predation rates associated with increased water temperatures due to higher metabolic rates in predatory fish.

Sacramento Pikeminnow

Status quo

Sacramento Pikeminnow (*Ptychocheilus grandis*), or Pikeminnow for short, are river spawners that use the Yolo Bypass and Cosumnes River floodplain for foraging. Adult and yearling Sacramento Pikeminnow are associated with the early flows and flooding; they likely get washed in from adjacent waters (Harrell and Sommer 2003; Nobriga et al. 2006; Moyle et al. 2007). Immature Pikeminnow enter the Cosumnes River floodplain during late flooding between April and May. Pikeminnow, like most native fishes, generally leave the floodplains when inflow decreases, although juveniles may stay while water levels and temperatures remain favorable (Moyle et al. 2007). Young of year Pikeminnow consume amphipods, insects, and annelids, and shift to a more piscivorous diet as they grow (Nobriga and Feyrer 2007).

Risks of climate change & associated impacts

Although not as tolerant of extreme conditions as Blackfish, Pikeminnow can tolerate fairly high water temperatures and remain resilient through periods of extended drought (Cech et al. 1990; Moyle 2002). They exhibit moderate tolerance to climate change effects such as increased temperature and precipitation, and their habitat is not expected to be greatly affected. Therefore, Pikeminnow are considered less vulnerable to climate change (Moyle et al. 2013).

Increased early flooding would likely allow more opportunities for fish to enter the system from surrounding waters and increase food productivity and foraging opportunities for Sacramento Pikeminnow. Different life stages of Pikeminnow would benefit differentially from the habitat based on the timing of flooding.

Other interacting effects

While Pikeminnow are tolerant of higher water temperatures, their metabolic rate will increase with increasing temperatures, thus they will require more abundant prey. Increased prey abundance may be available with increased inundation periods. While high dissolved-oxygen concentrations are likely not a problem during inundation, in laboratory experiments, Pikeminnow sometimes died from sudden increases in water temperature if simultaneously exposed to low dissolved-oxygen concentrations (Cech et al. 1990).

Impacts of water and landscape management

Sacramento Pikeminnow respond positively to early season flows, and native fishes generally have increased survival when the floodplain is drained quickly and completely, as there are decreased stranding opportunities (Harrell and Sommer 2003; Moyle et al. 2007). Early season flows and the presence of continuous flood habitat benefit Sacramento Pikeminnow (Moyle et al. 2007).

Non-native species: Golden Shiner, Bluegill Sunfish, Redear Sunfish, Black Crappie, Black Basses

Status quo

Several non-native floodplain foragers, Golden shiner (*Notemigonus crysoleucas*), Bluegill Sunfish (*Lepomis macrochirus*), Redear Sunfish (*Lepomis microlophus*), Black Crappie (*Pomoxis nigromaculatus*), and Black Basses (Largemouth Bass *Micropterus salmoides*, Smallmouth Bass *Micropterus dolomieu*, and Spotted Bass *Micropterus punctulatus*) are present in the San Francisco Estuary (Moyle et al. 2007, Interagency Ecological Program, 2018). Golden Shiners are visual predators, targeting zooplankton, small insects, and occasionally small fish, mollusks, and aquatic insect larvae. Bluegill Sunfish prefer aquatic insect larvae but also will eat plankton, insects, snails, and small fish. Redear Sunfish target relatively abundant hard-shelled invertebrates, but will also consume benthic insect larvae, especially during the summer when

these prey items are more abundant. Black Crappie prefer zooplankton and small insect larvae as juveniles and switch to aquatic insects and fish as adults. The Black Basses generally start out consuming zooplankton and small insects, shift to targeting crustaceans and fish, adding in crayfish, tadpoles, and frogs once they are large enough to consume them (Moyle 2002). San Francisco Estuary floodplains provide higher zooplankton and insect densities (Corline et al. 2017; Frantzich et al. 2019) during inundation than the adjacent rivers, benefitting these opportunistic foragers. Based on YBFMP monitoring data, all these species are commonly found in the Yolo Bypass (IEP et al. 2018) and likely are present in other local floodplains as well.

Risks of climate change & associated impacts

Non-native species will likely be less impacted by climate change in relation to native species. The general reasoning for this is detailed in the non-native floodplain spawners section. The non-native species, which use floodplain habitat for foraging, will likely be no exception to this as they are distributed throughout the Delta and do not rely exclusively on floodplain habitat for foraging opportunities. All these species are expected to be the least vulnerable to climate change, while some may benefit (Moyle et al. 2013). Of the species listed, Golden Shiner and Largemouth Bass populations are the most likely to benefit from climate change. Increased flooding and flood duration could boost lower trophic productivity, benefitting non-native floodplain foragers. Timing of flooding will likely affect which life stage can take advantage of increased foraging opportunities.

Plankton

Status quo

Low water velocities, high water temperatures, and high residence times within the inundated floodplain support phytoplankton production, aquatic plants and attached algae. This primary productivity supports high productivity of zooplankton and aquatic invertebrates (Sommer et al. 2004; Opperman et al. 2010; Corline et al. 2017; Jeffres et al. 2020). Phytoplankton production increases with lower levels of turbidity and warmer water temperatures. Longer residence times increase phytoplankton production; increases in water temperature caused by higher air temperatures also increase plankton production (Durand 2008). While one study showed only a weak positive relationship between zooplankton productivity and average temperature (Grosholz and Gallo 2006), zooplankton should have higher growth rates in warmer water. Therefore, spring flooding (April and May) would likely result in greater productivity than winter flooding (January and February). The optimal temperature range for *Daphnia* spp. population growth is 15–20°C (Corline et al. 2017).

Zooplankton feed on phytoplankton and detrital carbon (Opperman 2008; Schroeter et al. 2015, Jeffres et al. 2020). Floodplains produce high concentrations of phytoplankton during the

draining stage, increasing the food resource for zooplankton (Opperman 2008; Frantzych et al. 2018).

Water on floodplains can support high zooplankton abundances (tens of thousands of individuals per square meter), 10-100 times higher than in the adjacent rivers (Grosholz and Gallo 2006; Corline et al. 2017, Jeffres et al. 2020). Inundated agricultural fields may support high population densities of *Daphnia pulex* with a detritus-based food web.

Risks of climate change & associated impacts

Even during drought years, the Cosumnes River has flooded every year since the levees were removed in 1995. Connectivity between the streams and floodplain is lower in the Yolo Bypass; however, as a managed system, there are mechanisms that may allow mitigating drought impacts to a small extent, such as purposefully flooding fields or seasonal wetlands. In flooded experimental fields, phytoplankton and zooplankton densities were higher than those measured when the fields were inundated during river flood events (Sommer et al. 2020). Because of shallower and therefore warmer water on the Yolo Bypass in drought years, the rate of plankton growth may be higher. The plankton communities are expected to respond to the floodplain conditions in every given year, but changes in the frequency and duration of flooding are not expected to have long-term effects.

Impacts of water and landscape management

Increasing the amount of floodplain as well as increasing the frequency and duration of floodplain inundation will benefit the plankton communities (Jeffres et al. 2020; Sommer et al. 2001a; Sommer et al. 2020).

Benthos/Insects

Status quo

A study on the effects of seasonal dynamics on the Cosumnes River floodplain examined the effects of changes in predation by seasonally abundant fish on the abundance and composition of invertebrates (Grosholz and Gallo 2006). Major taxa sampled were Coleoptera, Hemiptera, Diptera, Plecoptera, and Amphipoda. Benthic invertebrate biomass on the floodplain was 1-2 orders of magnitude greater than in the adjacent river. On the floodplain, most taxa increased in abundance in January, and then either slowly declined or maintained their numbers through the early spring. Some showed a second increase in abundance starting in March. By June, chironomids and other Diptera were low in abundance, but predators such as odonates, belostomatids (giant water bugs), and especially corixids (water boatmen) were common. Fish predation affected insect abundance, especially in Coleoptera and Diptera.

Sommer et al. (2004) observed that in the Yolo Bypass, the aquatic stages of Diptera were the most abundant group of organisms captured in drift samples and were an order of magnitude higher than in adjacent river samples (Sommer et al. 2001a). Species in the family

Chironomidae were the most common dipteran. In floodwater, the initial peak in invertebrate abundance was dominated by *Hydrobaenus saetheri* (Diptera: Chironomidae), which emerges from drought resistant cocoons in the floodplain sediments (Benigno and Sommer 2008). Throughout the season, the dominant chironomid taxa may change.

With respect to terrestrial invertebrates, 6 taxonomic orders dominated drift samples from the Yolo Bypass: Araneida, Auchenorrhyncha, Coleoptera, Collembola, Hemiptera, Hymenoptera (Sommer et al. 2004). Common aquatic taxa included Naididae and Enchytraeidae (oligochaete worms), Physidae (snails), and Hydridae (cnidarians) as the most common families observed each year. The density of Diptera was lower in a dry year compared with two wet years. Wet years can cause an immense production of macroinvertebrates in floodplain habitats (Gladden and Smock 1990). High phytoplankton levels, a large surface area, a lot of shallow water habitat, and warm water likely result in these high macroinvertebrate densities (Sommer et al. 2004).

Risks of climate change & associated impacts

A greater magnitude of flooding results in longer inundation time and increased macroinvertebrate abundance, while shorter floodplain inundation results in lower abundance. For example, peak abundance of chironomids generally occurs after two weeks of inundation (Benigno and Sommer 2008). Inundation lasting less than two weeks may not provide adequate time for the floodplain to become productive, whereas longer inundation may exhaust floodplain resources. A shift in timing of flooding will alter the timing of high abundances. If invertebrate abundance is decoupled from fish abundance, valuable floodplain resources may not be available for fishes of concern (Colombano et al. 2021). Increased water temperatures will likely change the species composition.

Severe droughts that result in a lack of floodplain flooding for long durations greatly deplete the invertebrate egg bank on the floodplain, so that when floodplain inundation events do occur, the expected invertebrate “boom” is greatly diminished (Bond et al. 2008).

Impacts of water and landscape management

As for plankton, improved groundwater management, increasing the amount of floodplain, and projects increasing the frequency and duration of floodplain inundation would also benefit the benthic communities (Schemel et al. 2004; Benigno and Sommer 2008; Whipple et al. 2017).

Structural Vegetation: Reeds, Shrubs, and Trees

Status Quo

On natural floodplains, vegetation follows a succession trajectory starting with flood-tolerant species and slowly moving toward more upland species as features such as natural levees stabilize. Flooding can reset or instigate succession depending on the type of flood. Large woody debris transported through a flood and stranded on a floodplain can serve as a nucleus

for island formation. This leads to a diverse riparian community in various seral stages across the floodplain supporting a multitude of avian, amphibian and invertebrate species.

The Yolo Bypass and, to a lesser extent, the lower Cosumnes River floodplain are modified floodplains that do not greatly resemble the dynamic landscape of the historical river floodplains (Florsheim and Mount 2002; Suddeth 2014); however, the restoration of elements of the hydrologic regime to the Cosumnes River floodplain is enabling some of the dynamics to occur (Nichols and Viers 2017). After levee breaches occurred, sediment deposition created sandbars that were colonized by cottonwood and willow (Swenson et al. 2012).

Risks of Climate Change

Climate change is expected to reduce indigenous diversity, facilitate invasion of non-native species, increase fragmentation and result in simplified and less distinctive riparian floodplain ecosystems (Catford et al. 2013).

Increased temperatures will stress native vegetation and encourage growth of invasive vegetation because many non-native invasive species originate from tropical regions and are better adapted to hotter temperatures than native species (Penfound and Earle 1948; Nehring and Kolthoff 2011; Canavan et al. 2017). California's native flora is adapted to extreme swings in temperature but not to temperatures as high as climate change models are predicting or have already been observed in the past two decades (He and Gautam 2016). Higher water temperatures and shorter duration of below-freezing temperatures will allow existing invasive species to flourish and new non-natives to establish by eliminating conditions that can lead to extensive mortality in non-native species (Penfound and Earle 1948; Rahel and Olden 2008). Higher temperatures will also exacerbate the impacts of extreme droughts that are expected to increase in frequency due to climate change.

Longer, more severe droughts extend the duration of spells during which floodplains are not flooded, thus breaking lateral connectivity. Groundwater levels drop, causing many streams to lose surface water. Even robust riparian trees can become stressed and die as groundwater levels dip below their rooting depth for long periods of time (Bond et al. 2008; Kath et al. 2014). Recovery by biota varies hugely between seasonal and extreme multi-year droughts. Recovery from extreme droughts may be marked by dense populations of transient species, especially annuals replacing perennials, and the depletion of biota that normally occur in the streams (Lake 2003; Wassens et al. 2017). As a perturbation, droughts occur throughout large (landscape) spatial scales, so they potentially threaten the survival of individual aquatic organisms, regional populations, or species (Bond et al. 2008). The longer and more severe the drought, the longer recovery will take, with long lags and possibly local species extinctions (Lake 2003).

Increased frequency of high-magnitude floods or changed timing within the Yolo Bypass may not affect vegetation in the large, managed sections of the bypass. However, restoration projects in the Yolo Bypass such as Lookout Slough, Lower Yolo Ranch, Yolo Flyway Farms, and Prospect Island (Figure 10, water.ca.gov/Programs/All-Programs/EcoRestore) are likely to increase the area in the lower bypass that is open to floodplain action and that might respond to some extent like an active floodplain. In that case, it is likely that high magnitude floods may wipe out early successional communities such as tule-cattail marsh and even willow-dogwood communities. Longer dry periods between floods would normally favor these communities to reestablish in the floodplain; however, the planned action of installing a notch in the Fremont Weir is expected to increase the frequency and duration of moderate floods. This action should help maintain the patchwork of early successional communities in the bypass.

In the Cosumnes River floodplain, higher magnitude floods would likely cause changes that reset succession, lead to channel avulsion, or a change in the channel location, which would result in more early successional communities like reeds at the expense of older successional communities (Box 1). There will be shifts toward younger tree age, expansion of xeric pioneer shrubs, and replacement of herbaceous perennials by annuals. Woody stem density would increase, and basal area would decrease, indicating shifts toward younger forests. Increased flood intensity would also shift plant communities toward species with less ability to stabilize sediments (Stromberg et al. 2010). Early peaks in flood events would be universally detrimental to all floodplain species with phenological cycles, such as timing of flowering and seeding, adapted to the natural flood pulse regime (Junk et al. 1989). On the other hand, if timings are already disrupted (which is the case in the Delta) and management restored timing to historical regimes, then it will be universally beneficial to all native species (Catford et al. 2014).

As a result of the predicted changes, early and late successional communities might increase due to succession resetting and floodplain areas that are not disturbed very often in the Cosumnes River floodplain. However, middle successional communities may become rare, and overall, the heterogeneity of the floodplain may decrease, ultimately leading to a decrease in biodiversity. Plants that have evolved with the historical flood hydrograph and are already in decline because of impacts of flow regulation, will be further stressed by the change in timing and magnitude of flooding. Restoration projects may counter some of these impacts.

Other interacting factors

The increased probabilities of high-magnitude floods and long, extreme droughts lead to the increased probability of estuary whiplash – an extreme drought followed by an extreme flood (Swain et al. 2018). This combination can lead to impacts beyond that of just a flood or a drought. A prolonged drought can lead to stressed populations and higher mortality of native riparian trees and shrubs (Bond et al. 2008). If such a drought is followed by extreme floods, the already weakened species would be more likely to succumb to bank erosion, leading to huge

loss of longer-lived riparian trees and increased risk of levee failures that cause catastrophic change in the river floodplain topography.

Higher temperatures and longer duration of flooding could impact the biogeochemistry of the Yolo Bypass and Cosumnes River floodplain. Greater waterlogging would lead to anoxic microbial pathways and likely increase methane emissions compared to current conditions. While the microbial diversity is not likely to change with the floodplain supporting a range of conditions from aerobic to anaerobic water bodies the prevalence of low-oxygen environments would be higher. Anoxic conditions can also lead to mobilization of nutrients from the substrate and increase nutrient availability for primary production. On the other hand, long droughts can reduce nutrient availability except where groundwater comes to the surface – creating islands of biological activity and starving other areas of nutrients.

Impacts of water and landscape management

Restoration of natural flooding regimes will likely have a greater effect on structural vegetation in the Cosumnes River floodplain than climate change. Within the lower Cosumnes River floodplain, there are restoration projects in planning such as McCormack-Williamsons Tract and Grizzly Slough (DWR 2019; CNRA 2022). These will increase the floodplain area and allow for a dynamic floodplain. Larger, more catastrophic storms due to climate change could cause levee failures that could change the landscape, reworking the local topography and resetting succession.

Conclusion

Floodplains in the Sacramento-San Joaquin Delta are highly diminished and disturbed. Climate change is an additional stressor that will impact floodplain functioning. For natural floodplains like the Cosumnes River floodplain, the largest climate-change effect will come from changing patterns of river flows resulting in changing patterns of floodplain inundation. While inundation patterns of managed floodplains like the Yolo Bypass may also be affected by changing river flow patterns, management actions can have a stronger effect on inundation patterns.

The combination of higher temperatures, longer, more severe droughts, and increased frequency of high-magnitude floods is expected to reduce native species diversity, facilitate invasion of non-native species, and result in simplified, less distinctive, and fragmented riparian floodplain ecosystems. However, climate change is likely to not harm and may even benefit floodplain spawners including Sacramento Splittail, Sacramento Blackfish, and Carp and Goldfish. Similarly, Sacramento Pikeminnow and non-native floodplain foragers are less vulnerable to climate change and may even benefit from higher temperatures and changes in the inundation regime. For Chinook Salmon, there is a potential of increased mortality on floodplains caused by shifts in the timing, frequency, and duration of floodplain inundation.

Increasing temperatures may benefit phytoplankton and zooplankton abundance but cause changes in species composition.

Larger, more catastrophic storms could cause levee failures that could change the landscape, reworking the local topography and resetting succession. Restoring the natural flooding regimes will likely have a greater effect on the biota in the Cosumnes River floodplain than climate change. Improved floodplain connectivity to rivers will restore the ability of floodplains to absorb flood flows and recharge groundwater levels to increase resiliency of both wildlife and people to withstand droughts. Connecting floodplain and riparian habitats continuously through the Delta would provide more habitat to floodplain-dependent species.

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Chapter 5: Comparisons and Conclusions

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Comparisons and Conclusions

Climate change manifests as a global suite of parameters that change as the earth warms. In any particular region some of these globally covarying parameters are largely irrelevant, for example ocean acidification is not directly affecting conditions in the Delta. However, increased temperature, sea level rise, increased frequency of extreme events, and human alterations directly affect conditions in the Delta. We have not tried to anticipate human response to climate change. We do recognize relevant management actions that are underway.

Climate change is often described as trends through time, such as the gradual increase in mean annual air temperatures or sea level. However, climate change impacts on humans and other biota frequently occur as discrete events. Temperature may be trending upward, but it is the heatwaves that kill trees and fish, and such events contribute to long-term trends (Brown et al. 2013). We have attempted to view climate change impacts in the Delta as both a series of events and as a long-term shift in the baseline conditions.

Our synthesis of climate change effects on Delta ecology has highlighted a number of similarities and differences among the ecosystems we examined: open water, floodplains and tidal marsh. Prior to the year 2000, most studies in the Delta and Suisun Bay focused on the open water ecosystem because that is the habitat of Striped Bass, Chinook Salmon, and Delta Smelt, the main species of commercial or environmental concern at that time (Stevens 1977; Kjelson et al. 1982; Stevens and Miller 1983; Moyle et al. 1992). These open water studies were somewhat augmented by sampling in the littoral zone for juvenile fish, especially young salmon (Brandes and McLain 2001). As the new millennium started, studies showed that floodplains were important for both young salmon and Sacramento Splittail (that was listed under federal law from 1999-2003) (Sommer et al. 1997, 2001; Moyle et al. 2004). Tidal marshes were not as well studied because there were so few of them remaining in the Delta, but their importance to most species of concern in the Delta was recognized (Herbold et al. 2014). This, together with their already-known value to many species in the Bay has produced significant efforts to study and restore Delta marshes in the last 12 years. Leaning on knowledge gained from the long-term monitoring efforts, some of which started in the 1950s, and the growing diversity of ecological studies in the last 20 years, we have attempted to put these ecosystems into the context of a changing climate.

Open water habitats will be most affected by drought events and warmer temperatures. Decreased outflow in summer months, and especially during droughts, combines with sea level rise to produce conditions that favor many invasive fish, invertebrates, and aquatic weeds. Harmful algal blooms also thrive under conditions of warm water and high residence times (Lehman et al. 2020). These same conditions are detrimental to most, but not all, native fishes. Intervening years of high outflow reset the salinity regime, but the increased frequency of

drought conditions may not allow adequate time for populations to recover (Mahardja et al. 2021). Within most years, a reduced snowpack will cause an overall decline in water supply, leading to less water available to repel salinity in the Delta. This may lead to reconfigurations of the Delta, as with the proposed Franks Tract redesign, which would reduce salinity intrusion permanently. More saline conditions may favor some native fishes and aquatic vegetation over their invasive counterparts.

Floodplains are buffered from some effects of climate change by their location at the more upstream end of the Delta, where sea level rise and salinity intrusion, even storm surge, do not have large impacts. Inundation of floodplains occurs in the cooler, winter periods, and warming is expected to have less of a negative effect on wetted floodplains than other ecosystems. The larger floods we expect (and have seen recently) will produce floodplain benefits more often. If accompanied by warmer temperatures, floodplains may be more productive with positive effects on floodplain spawners and foragers. However, changes in the timing of flooding may reduce some of the benefits to migratory species that may not arrive at the shifted time of flooding. Intervening drought years may be detrimental to groundwater levels, affecting aquatic and riparian vegetation in the floodplains (Kath et al. 2014; Mac Nally et al. 2014). The highly managed Yolo Bypass offers a number of ways to reduce the negative impacts of climate change and to augment its benefits: reconfiguring weirs to improve fish access to the floodplain, modifying agricultural return flows to assist movement of food into the river, and facilitating groundwater recharge.

In addition to the various monitoring tools discussed above, improved analytical tools are needed to support SFE climate change science and management. In particular, better temperature models are needed to address habitat-specific responses to climate change. The temperature models described in the current review provide a reasonable indication of some of the expected responses of pelagic habitat. Temperature models were also used extensively as part of the CASCADE evaluation of climate change effects (Wagner et al. 2012). Still, temperature models are generally lacking for off-channel habitat, which is the target of most of the habitat restoration projects. This gap in temperature modeling is not, however, a consequence of an absence of temperature monitoring data for off-channel habitat. To the contrary, there are numerous temperature sensors in Suisun Marsh, as well as many years of continuous temperature data for the Yolo Bypass floodplain. An important next step for SFE climate science will be to incorporate data from these off-channel habitats into local and regional modeling frameworks.

Tidal marshes are a very small fraction of the Delta's area but will become more abundant through active restoration and passive transformation by levee failure in places of suitable elevation. Although marsh ecology elsewhere has been intensively studied, we are only beginning to understand marshes in the Delta. Shading and evapotranspiration by vegetation,

nighttime flooding of the marsh plain, and Delta breezes may provide thermal refugia for cold-water migrants (Enright et al. 2013). The high productivity of marshes can offset some of the lost productivity due to clams feeding in open water habitats. For unclear reasons, marshes seem resistant to invasion by clams and some other invasive species (Baumsteiger et al. 2017). There are conflicting pictures of sediment dynamics under climate change; sediment loads into the estuary sharply declined at the start of the new millennium, but larger floods may mobilize large amounts of sediment in pulses (Schoellhamer et al. 2018; Stern et al. 2020). How much sediment arrives in marshes will determine whether they can maintain their elevations in the face of sea level rise. Average salinity in marshes will rise with sea level which will change the biota that occur there.

Although we were able to identify some general trajectories of Delta ecosystems, it became evident through our synthesis effort that there are also key uncertainties linked to a lack of data. In the open water ecosystem, there is a need to expand monitoring of aquatic vegetation and to increase our knowledge of the role of native and invasive aquatic vegetation in the food web and in fish ecology. Monitoring of groundwater pumping and quantification of groundwater depth thresholds may be critical for preserving future biodiversity in floodplains. Given that tidal marshes may act as thermal refugia for cold-water species, a more systematic temperature monitoring scheme in tidal marsh channels can provide a better understanding of their importance. Monitoring of sediment dynamics during varying flood levels would help identify sustainable marsh sites.

The three ecosystems are driven by different aspects of climate change (Figure 1) and will have very different time scales of response. Marshes will change gradually, largely with trends in increasing sea level and salinity, as well as with shifts in sediment dynamics. Open water habitats will change greatly in temperature, flow, and salinity on short time scales, especially droughts and heatwaves. While the mobility of pelagic species buffers them from the effects of short-term changes, sessile benthic species such as clams must endure them. Finally, floodplains are an episodic ecosystem isolated from some climate change impacts and affected mostly by extreme flood events. Management and restoration of these ecosystems and the species that live in them will require an awareness of their different sensitivities and a better understanding of ecosystem processes.

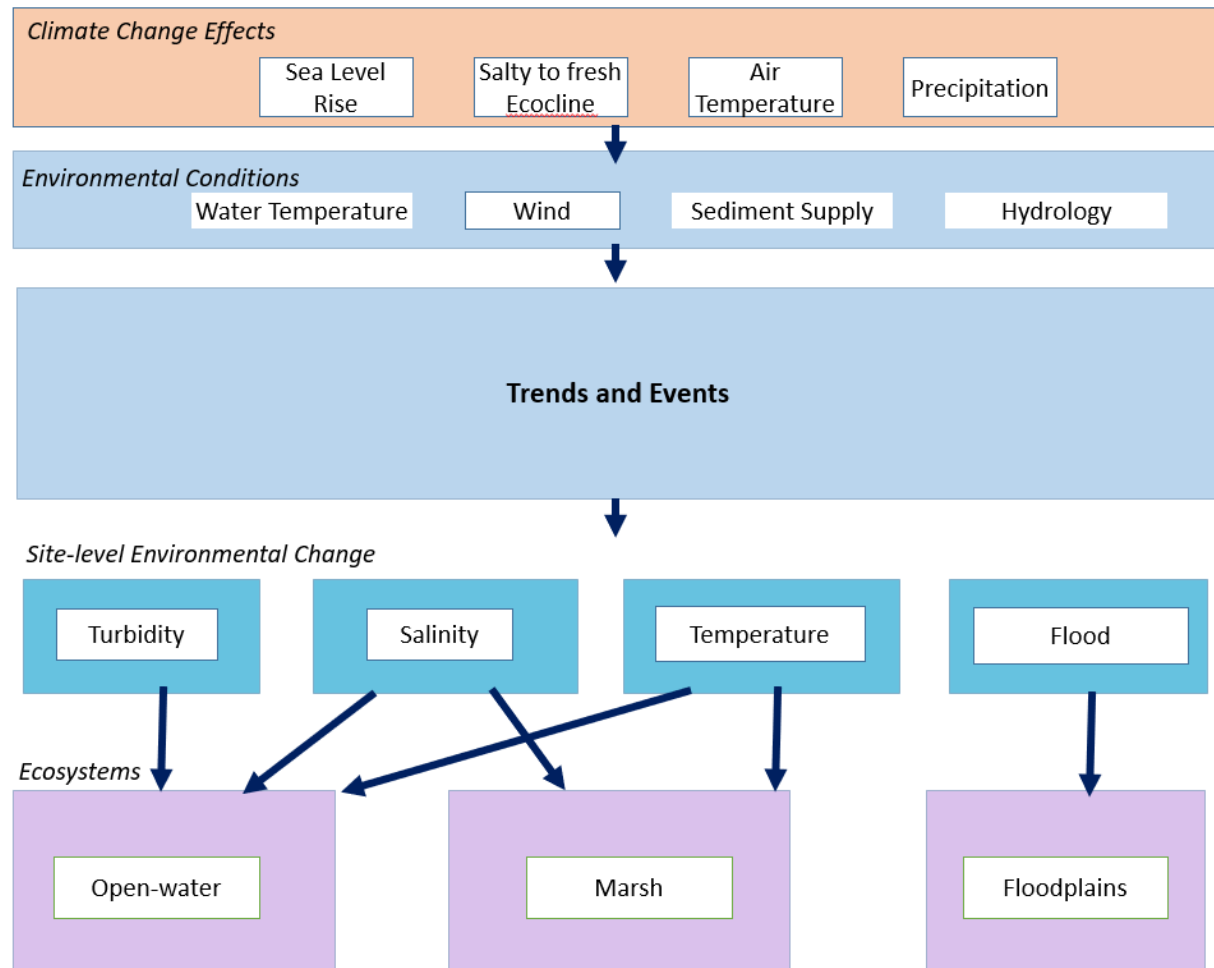


Figure 1. Schematic of the main climate change effects on regional conditions and their impact on specific conditions that affect the three ecosystems of interest.

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