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<https://escholarship.org/uc/item/5271t1bd>

Journal

San Francisco Estuary and Watershed Science, 19(2)

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Publication Date

2021

DOI

10.15447/sfews.2021v19iss2art3

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RESEARCH

Ecological Effects of Climate-Driven Salinity Variation in the San Francisco Estuary: Can We Anticipate and Manage the Coming Changes?

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SFEWS Volume 19 | Issue 2 | Article 3

<https://doi.org/10.15447/sfews.2021v19iss2art3>

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ABSTRACT

Climate change-driven sea level rise and altered precipitation regimes are predicted to alter patterns of salt intrusion within the San Francisco Estuary. A central question is: Can we use existing knowledge and future projections to predict and manage the anticipated ecological impacts? This was the subject of a 2018 symposium entitled “Ecological and Physiological Impacts of Salinization of Aquatic Systems from Human Activities.” The symposium brought together an inter-disciplinary group of scientists and researchers, resource managers, and policy-makers. Here, we summarize and review the presentations and discussions that arose during the symposium. From a historical perspective, salt intrusion has changed substantially over the past 10,000 years as a result of changing climate patterns, with additional shifts from recent anthropogenic effects. Current salinity patterns in the San Francisco Estuary are driven by a suite of hydrodynamic processes within the given contexts of water management and geography. Based on climate projections for the coming century, significant changes are expected in the processes that determine the spatial and temporal patterns of salinity. Given that native species—including fishes such as the Delta Smelt and Sacramento Splittail—track favorable habitats, exhibit physiological acclimation, and can adaptively evolve, we present a framework

for assessing their vulnerability to altered salinity in the San Francisco Estuary. We then present a range of regulatory and structural management tools that are available to control patterns of salinity within the San Francisco Estuary. Finally, we identify major research priorities that can help fill critical gaps in our knowledge about future salinity patterns and the consequences of climate change and sea level rise. These research projects will be most effective with strong linkages and communication between scientists and researchers, resource managers, and policy-makers.

KEY WORDS

Delta Smelt, Sacramento Splittail, sea level rise, salinity intrusion, freshwater inflow, hydrodynamics, habitat, paleosalinity

INTRODUCTION

Global sea levels continue to rise, and are doing so at increasing rates, in response to global warming through thermal expansion of the oceans, and the melting of glaciers (Church and White 2006; Nicholls and Cazenave 2010; IPCC 2014; Dangendorf et al. 2017). These trends in sea levels are predicted to continue, with projections of an additional increase of 60 cm to 2.7 m by the year 2100 (Nicholls and Cazenave 2010; Sweet et al. 2017; Fasullo and Nerem 2018). Increasing sea levels pose significant physical and biological risks for coastal environments, including submergence and increased flooding risk of coastal lands, salinization of estuarine habitats and freshwater resources, and increased extinction risk to biodiversity (Scavia et al. 2002; Basset et al. 2013). Yet, predicting how rising sea levels will affect coastal and connected inland ecosystems depends on diverse features of these natural systems and associated human effects and activities. This is particularly evident when attempting to predict and manage the effects of sea level rise and shifting climates on the salinization of freshwater resources.

The salinity gradients that form in the estuarine zone between freshwater rivers and the coastal

ocean are naturally dynamic, and change in response to tidal and other ocean influences, freshwater inputs, and changes in the physical structure of these environments (Herbert et al. 2015). Sea level rise will push high-salinity water further inland, resulting in salinization of low-salinity and freshwater areas (Chua and Xu 2014). However, the extent of this salinization depends on several other important natural and human-influenced factors. For example, the increased likelihood of extreme events such as prolonged droughts and heatwaves will decrease freshwater inputs from snow and rain, and increase evaporation rates, allowing saltwater to extend further inland (Nicholls and Cazenave 2010). At the same time, powerful storms may transiently increase river flows that push freshwater seaward and transiently raise sea level, enhancing salinity intrusion in the short term and altering the morphology of estuary channels, resulting in long-term changes in saltwater intrusion (Scavia et al. 2002). Human activities can magnify these salinization effects (e.g., water extraction for irrigation or drinking water, or salinity contamination by urban and agricultural runoff), which has led to what is referred to as the “freshwater salinization syndrome” (Kaushal et al. 2018). Anticipating and managing these risks represents a global challenge for coastal ecosystems; however, proposed regulatory solutions will ultimately depend on local conditions. Here, our focus is the risk presented by future salinization of the San Francisco Estuary ecosystem (hereafter “the estuary”).

The estuary is an expansive system that extends from the coastal ocean through San Francisco Bay and landward to the inland Sacramento–San Joaquin River Delta. The estuary is among the largest of North America’s estuaries, and includes the densely populated urban Bay Area as well as the sparsely populated but highly modified rural agricultural lands of the Central Valley. The importance of freshwater resources for drinking water, irrigation, and biodiversity cannot be overstated. How will future sea level rise and altered precipitation patterns affect this estuarine ecosystem through salinization? What risks can be managed, and which risks cannot? Can we use

our existing knowledge and future projections of the drivers of salinization to predict biological effects, and develop appropriate management plans, interventions, and regulations?

These questions were the subject of a symposium held on September 26th, 2018, entitled “Ecological and Physiological Impacts of Salinization of Aquatic Systems from Human Activities,” hosted by the Coastal and Marine Sciences Institute at the University of California, Davis, and supported in part by the Delta Stewardship Council (Delta Science Program) and the UC Agriculture and Natural Resources Program. The symposium brought together a diverse group of scientists and researchers, resource managers, and policy-makers interested in the complexity of and the potential for predicting future salinization scenarios, with a particular focus on the estuary. This paper is based on the presentations and discussions that arose during the symposium. Below, we characterize some of the main features of the estuary that have shaped historic and current patterns of salinity. We then review some of the future risk factors envisioned to increase salinity within the estuary, and the associated consequences for biodiversity and human populations. Next, we provide a list of tools available to resource managers that may be implemented to mitigate and reduce salinization. We end with some suggestions for future research priorities to address gaps in our knowledge, and some conclusions that might provide guidance for future studies.

HISTORIC AND CONTEMPORARY SALINITY IN THE ESTUARY

The inland portion of the estuary includes the Sacramento–San Joaquin River Delta (hereafter the Delta), which forms an extensive delta system that covers approximately 3,000 km² (Figure 1). These rivers bring freshwater into the Delta from a vast watershed that drains 40% of California, with headwaters in the Klamath and Sierra Nevada mountain ranges. The confluence of the rivers is just east of Suisun Bay, which is the shallow inner estuary and the contemporary interface of freshwater and saltwater under

moderate flow conditions. Yet, the historic patterns of salinity within the estuary have varied greatly over geologic and contemporary time-scales (e.g., Drexler et al. 2014; Hutton et al. 2016; Andrews et al. 2017; Rath et al. 2017; Gross et al. 2018), such that managing salinity in the face of future risks requires not only an assessment of current patterns of salinity, but also of historic patterns and trends. Characterizing historic salinity levels within the estuary provides not only a baseline by which to judge management actions, but also provides the context within which native species have evolved and historically thrived. Below, we review salinity patterns during three broad time-periods: (1) the paleo-record during the Holocene, predating any substantial human modification of the system; (2) the late 19th and early 20th centuries, which marked the beginning of increased freshwater extraction; and (3) the contemporary period, which is associated with major water projects, increased freshwater storage, managed flow, and increased demands on freshwater.

1. The Paleo-History of Salinity in the Estuary

The patterns of salinity fluctuation within the estuary have varied over the Holocene (i.e., the past 10,000 years) as changes in climate, sea levels, precipitation, and related physical and biological processes shaped the major features that characterize the system as a whole. Paleoclimatic data suggest the early Holocene was a period of warming temperatures and reduced precipitation, which peaked about 5,000 to 7,000 years ago, and was followed by cooler and more variable precipitation regimes (Malamud–Roam et al. 2006). Many of the major geographic features currently associated with the estuary appear to have formed in response to rapidly rising sea levels that peaked about 6,000 years ago and then remained nearly steady, allowing the formation of tidal marshes (Malamud–Roam et al. 2006). These physical conditions set the stage for the interplay between saline ocean waters and seasonal freshwater flows into the estuary. Similar to contemporary conditions, historic climatic conditions were characterized by an annual cycle of dry summer and fall conditions, winter precipitation, and spring and summer

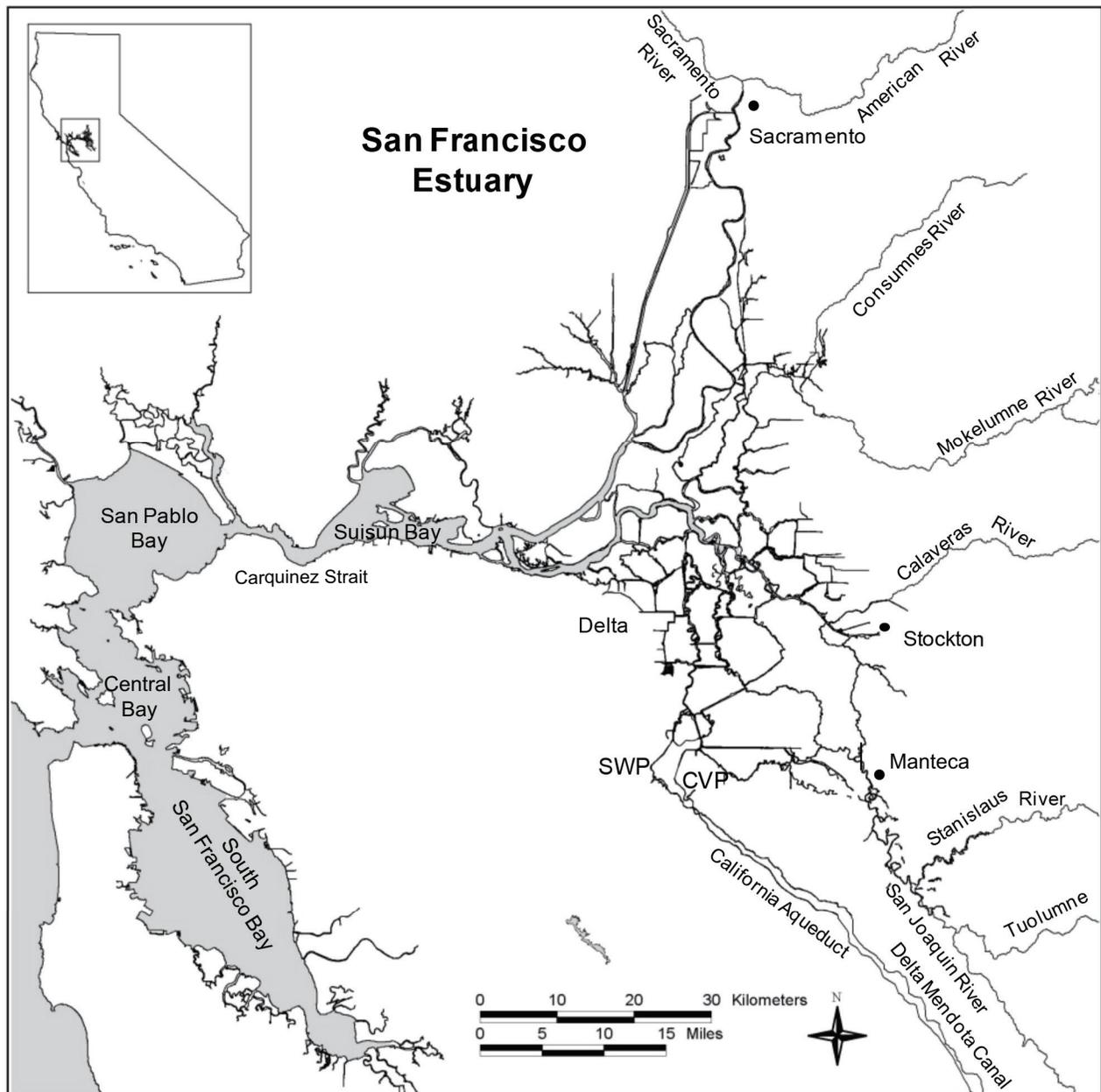


Figure 1 Map of the San Francisco estuary and river systems. SWP=State Water Project, CVP=Central Valley Project.

snowmelt that was comparable to contemporary freshwater flows into the system (Goman and Wells 2000). However, these historic conditions were characterized by more variable inflow from the upstream watershed, resulting in a more variable seasonal salinity regime (Gross et al. 2018). During winter rains and spring snowmelt, the rivers feeding the estuary would overflow their banks and inundate adjacent low-lying

floodplains with freshwater and sediment (Fox et al. 2015; Gross et al. 2018). As freshwater input declined over the summer, salinity levels within the estuary increased and peaked during the late fall, creating a predictable intra-annual shift in salt intrusion within the estuary (Gross et al. 2018). Variation in climatic conditions during the past 6,000 years suggest some spatial and temporal shifts in the distribution of

salinity within the estuary over this time-period (Ingram et al. 1996; May 1999; Stahle et al. 2001; Malamud–Roam and Ingram 2004; Malamud–Roam et al. 2006; Drexler et al. 2014). For example, paleoclimatic data suggest a prolonged reduction in salinity in the Suisun Bay that started approximately 3,800 years ago and lasted for 2,000 years, as well as a more recent freshening during the past 500 years (Malamud–Roam et al. 2006; Drexler et al. 2014). Nevertheless, Drexler et al. (2014) suggest the long-term paleosalinity patterns remained relatively stable during the past 6,000+ years; with high salinity in South Bay and Central Bay, and decreasing salinity with distance upstream toward Suisun Bay and the Delta (Figure 1). This work leads to the conclusion that the primary historical driver of salinity intrusion into the estuary is the amount of freshwater that flows into the estuary system. This conclusion is also confirmed by Andrews et al. (2017), who constructed three-dimensional (3-D) hydrodynamic models of the contemporary and pre-development (circa 1850) estuary, and found the amount of freshwater flow to be the best predictor of salt intrusion, with a smaller contribution from the altered geometry of the estuary.

2. Salinity in the Estuary Since the End of the 19th Century

The colonization of California by European settlers resulted in the transformation of the estuary from a pre-settlement to a post-settlement system (Fox et al. 2015). This transformation accelerated during and after the California Gold Rush (1848–1855), as an influx of people led to an increase in activities related to agriculture, mining, and the protection of human settlement and agricultural areas from flooding (Hutton et al. 2016; Gross et al. 2018; MacVean et al. 2018; Hutton and Roy 2019). Specifically, between the 1850s and 1920s there was a substantial increase in (1) agriculture, which led to the conversion of native vegetation and water diversion; (2) removal of riparian vegetation, (3) levee construction, stream channelization, and dredging to help in navigating rivers and controlling floods; (4) hydraulic mining; and (5) early development of in-stream storage facilities (e.g., dam building) (see Hutton and Roy 2019). This transformation

from a natural to an anthropogenic landscape in turn altered the historic patterns of salinity by reducing the amount—and shifting the timing—of freshwater that entered the estuary. Hutton and Roy (2019) use two important historic lines of evidence to document how the relationship between freshwater flow and salinity within the estuary was altered during the early part of the 20th century. First, they used records kept by the California and Hawaiian Sugar Refining Corporation (C&H), which relied on freshwater for its sugar refinery at Crockett (located on the Carquinez Strait just west of Suisun Bay, see Figure 1). Between 1908 and 1929, C&H collected freshwater using barges that traveled upstream on the Sacramento and San Joaquin rivers, and kept records of how far they had to travel and the salinity of the water at different locations. Second, Hutton and Roy (2019) used records of salinity at fixed locations across the salinity gradient beginning in 1911, collected by the California Department of Public Works (CDPW), to estimate freshwater flows. Hutton and Roy (2019) found a high correlation between these two data sets using models that relate freshwater flow and salinity in the estuary. A major conclusion from this effort is that there was a shift in salinity patterns within the estuary starting in 1918 that coincided with the increased irrigation that was associated with rice cultivation, reservoir construction, and summer water diversion (see also MacVean et al. 2018). As a result, there was typically greater salinity intrusion during the summer and fall months after 1918 than before 1918 (Hutton and Roy 2019). Increased salinity intrusion had observable consequences for users who depended on access to freshwater. For example, salinity intrusion had become such a problem that in 1920 the city of Antioch sued upstream irrigators for taking too much water, leading the state of California to implement a salinity monitoring program (Gross et al. 2018). Thus, while the amount of freshwater flow into the system remained a primary governing factor on the levels of salinity intrusion, the increased diversion of freshwater and land-use changes altered the predicted relationship between freshwater flow and the magnitude of salinity

intrusion (see MacVean et al. 2018; Hutton and Roy 2019 for more details).

3. The Contemporary Pattern of Salinity in the Estuary

The estuary has undergone substantial changes since the early 1900s, resulting in the complex, modified, and highly regulated system it is today. Several major water projects fundamentally transformed the estuary system. Beginning in the 1930s, the federal government and the state of California began the construction of large dams and irrigation distribution networks as part of the Central Valley Project (CVP) and the State Water Project (SWP). This led to the building of numerous dams, canals, and pipelines, which resulted in a significant redistribution of freshwater that would otherwise have flowed into the estuary. These modifications decoupled the historic relationship between intra-annual variation in precipitation and salinity intrusion (Enright and Culberson 2009). Indeed, the highly managed system allows for unprecedented control over the amount and timing of water released into the estuary. Nevertheless, the quantitative influence of the physical environment of the estuary and climate on salt intrusion remains an area of active research. The models developed by Gross et al. (2018) suggest that the major difference between the contemporary and pre-development estuary is in the seasonal variability of salt intrusion. In pre-development conditions, inland basins flooded under high-flow/flooding conditions, and much of this stored water flowed back to Delta channels through the wet season and into summer (Whipple et al. 2012). In contrast, contemporary conditions are marked by increased storage of water in reservoirs, which has reduced winter and spring runoff and allowed for more continuous release of freshwater later in the summer (Enright and Culberson 2009). Yet, the contemporary relationship between freshwater inflow and salt intrusion in the estuary shows greater salt intrusion for any given flow rate (Gross et al. 2018). Recent increases in sea level and erosion of Suisun Bay have likely contributed to these patterns (Enright and Culberson 2009).

UNDERSTANDING THE PROCESSES THAT CONTRIBUTE TO FUTURE RISK

Understanding how predicted climate change will alter the physical processes that control salinity intrusion provides insights into how future risk could be managed. Currently, salinity in the estuary typically ranges from fully marine [between 33 and 34 practical salinity units (psu)] during incoming tides at the Golden Gate (ocean entry to Central Bay; see Figure 1) to near-zero in the freshwater tributaries of the Delta. The interplay of tides and freshwater inflows is recognized to alter the distribution of salinity in the estuary on tidal, spring-neap, synoptic-event, and seasonal scales. The variation in the intrusion of saline waters can be understood by studying the balance of dispersion processes that transport salt landward, and net river flow that advects salt seaward. Key salt intrusion processes in estuaries include estuarine circulation (Geyer and MacCready 2014) and tidal dispersion processes such as tidal trapping (Fischer 1979). The strength of estuarine circulation processes increases with increased longitudinal salinity gradients and water column depth, and decreases with increased vertical mixing (Monismith et al. 2002). Tidal dispersion processes result from shear in tidal currents that are associated with the estuary's bathymetric and geometric complexities, including side embayments and channel junctions (Zimmerman 1986).

Climate change and regional human actions will continue to influence salt intrusion in the estuary on multiple time-scales and through multiple pathways. The major pathways include sea level rise and altered quantity and timing of freshwater inflow. Additional influences of climate change may include changes in ocean tidal range (Devlin et al. 2017), wind fields (Dettinger et al. 2016), and evapotranspiration from the estuary (Hemes et al. 2018). Inundation of Delta islands through levee failures or planned tidal restoration will alter the tidal prism and also influence salt intrusion (Lund et al. 2008).

While contemporary salinity conditions in the estuary vary on seasonal and interannual time-scales because of the large natural variability

in precipitation in the watershed, salinity is also strongly influenced by water management associated with water supply and water-quality standards at compliance points. To manage water quality in the face of this variability, a salt intrusion metric called X2 was developed; it is defined as the distance of the 2 psu near-bottom salinity isohaline from the Golden Gate (Monismith et al. 2002; see also below). Future salinity conditions in the estuary will arise from the combination of climate change, changes in estuarine geometry, changes in land use in the watershed, water-management practices in response to environmental change, water-quality regulations, and evolving water demand. Predicting these changes requires sophisticated tools and a range of assumptions/scenarios to characterize uncertainty from biophysical dynamics as well as uncertainty from human behavior. Below, we discuss these tools and assumptions in the context of how hydrology and water management will be influenced under predicted climate-change scenarios.

Estimated Hydrologic Changes under Climate Change

Freshwater inflow to the estuary is primarily influenced by the quantity and type of precipitation, temperature, land-use patterns, and reservoir operations. Climate change will directly or indirectly influence each of these factors, leading to shifts in the magnitude and seasonal timing of flows. To some extent, the natural variability of flows will be altered by management intended to meet water-quality standards and other management objectives. Models that predict future flows to the San Francisco estuary (e.g., Knowles et al. 2018; Vicuna et al. 2007; Anderson et al. 2008) require several components to represent physical processes and operational responses. Global climate models under a range of emission scenarios show that climate change will continue to warm northern California. These results are typically downscaled to provide more accurate and spatially resolved estimates of temperature and precipitation (e.g., Pierce et al. 2013). Predicted temperature increased for all 20 climate scenarios considered by Knowles et al. (2018),

with an average increase of 4.1° C during the 21st century, while predicted precipitation changes had a large degree of variability among scenarios, but a small increasing trend when averaged across scenarios. Much of the interannual variability in precipitation is attributed to the presence or absence of storms associated with atmospheric rivers (Dettinger et al. 2016), and the intensity of the largest storms is predicted to increase with climate change (Pierce et al. 2013). Partially as a result of increased retention of water vapor in the atmosphere with increased temperature, the future is likely to include more frequent “mega-storms” with widespread flooding and catastrophic damage (Dettinger and Ingram 2012; Yoon 2015), which have historically occurred at a 100- to 200-year return interval. A watershed model such as the Variable Infiltration Capacity model (VIC; Liang et al. 1994) is used to estimate unimpaired streamflow for given precipitation. Because the predicted form of precipitation shifts toward increasing rain and decreasing snow, and because snow melts faster in a warmer climate, peak flow events are predicted to occur earlier in the year (Anderson et al. 2008). With the exception of the Cosumnes River, all major tributaries of the Delta are regulated by reservoirs. The CALSIM 2 (Draper et al. 2004) model is a widely used operations model that estimates monthly reservoir inputs, exports, and other management decisions based on operational goals and constraints, including salinity-based water-quality standards. Using a modified version of this model, Knowles et al. (2018) estimated that the managed Delta inflow under climate-change scenarios would increase during winter and decrease during spring and summer, relative to contemporary conditions.

Estuarine Physics Under Climate Change

Salt intrusion in the contemporary estuary is determined largely by the balance between intrusion mechanisms and flushing by Delta outflow (Monismith et al. 2002). Tidally averaged salt intrusion for the contemporary estuary can be estimated from net Delta outflow alone, with a standard error of 3 to 4 km (Hutton et al. 2016), indicating that Delta outflow is the dominant determinant of tidally averaged salt intrusion for

a fixed estuary geometry and mean sea level. Secondary influences include varying tidal amplitude through the spring-neap cycle, wind, and barometric pressure (Walters and Gartner 1985). Specific events—including levee failures, tidal restoration actions, and dredging—also influence salinity distribution. The strength of salt intrusion mechanisms relates to estuarine geometry and salinity distribution itself. For the contemporary estuary, tidal dispersion processes primarily drive salt fluxes under low to moderate flow conditions, with a significant contribution from estuarine circulation processes in Central Bay and San Pablo Bay, which increase with the stronger salinity gradients typically present in these regions during and after high Delta outflows (Gross et al. 2009). Deepening of the estuary as sea levels rise or as a result of channel dredging and erosion can be expected to increase the strength of gravitational circulation (Monismith et al. 2002). In addition, modeling studies suggest that this deepening also increases the strength of tidal dispersion processes (DRMS 2006).

Observed sea level rise (sea level rise off California in the 20th century was about 20 cm (Dettinger et al. 2016). Future sea level-rise predictions span a large range, with typical sea level-rise scenarios for the 21st century ranging from 0.2 m to 2.7 m (Dettinger et al. 2016), and with more extreme predictions over 2.5 m associated with the melting of Antarctic ice (DeConto and Pollard 2016). Rath et al. (2017) analyzed historical salinity data to estimate that a sea level rise of 18.3 cm results in ~1 km landward shift in X2, for a fixed Delta outflow. Consistent with the estimate of Rath et al. (2017), a 3-D hydrodynamic simulation estimated that 20 cm of sea level rise would increase X2 by 0.9 km. This salt intrusion length increased to 7.9 km for 1.4 m sea level rise, assuming fixed Delta outflow of $260 \text{ m}^3\text{s}^{-1}$ for both scenarios (DRMS 2006). For a similar scenario of 1.39 m of sea level rise and fixed Delta outflow of $300 \text{ m}^3\text{s}^{-1}$, Chua and Xu (2014) estimated a larger X2 landward migration of 11.6 km. To comply with existing X2 standards, substantial additional reservoir releases would be required to offset the influence of sea level rise (Fleenor and Bombardelli 2013). However, because of the large computational expense of

3-D hydrodynamic models, existing attempts to simulate both physical processes and their associated management responses have largely relied on simplified and highly parameterized representations of salt-intrusion physics (Fleenor and Bombardelli 2013; DRMS 2006).

As sea levels rise, tidal dynamics in the oceans and the estuary will also change. Increases in tidal amplitude in the coastal ocean have been observed concurrently with sea level rise (Devlin et al. 2017) and, assuming current estuarine geometry, additional tidal amplification is likely inside the estuary (Holleman and Stacey 2014). Tidal amplification may increase salt intrusion, particularly during low to moderate flow conditions. For example, a tidal amplitude increase of 11% was estimated to lead to an additional 2-km increase in X2 for the 140-cm sea level-rise scenario with $260 \text{ m}^3\text{s}^{-1}$ outflow (DRMS 2006). MacWilliams and Gross (2010) estimated the time that varying salt intrusion influenced different sea level-rise scenarios, with a larger effect of sea level rise at low flow, and a roughly linear increase in salt intrusion length with the magnitude of sea level rise.

A primary difficulty in predicting salt intrusion under different climate-change scenarios is anticipating future management responses. While management responses to meet current objectives are reflected in CALSIM 2 and other models, under future scenarios, additional management responses are likely (Lund et al. 2008). For example, some levees will be fortified to accommodate sea level rise, and some will be allowed to overtop. Levees are at risk not just from overtopping but also from failure mechanisms that result from seepage or catastrophic failure during an earthquake (Mount and Twiss 2005). These risks increase with sea level rise, amplification of tides, increased frequency of large floods, and subsidence, which over the 21st century is expected to drop much of the levee system below design thresholds (Brooks et al. 2012). Levee failures from any cause lead to both rapid salt intrusion as a result of the net landward advection required to fill Delta islands (DRMS 2006) and, in some cases, longer-term

increases in salt intrusion from increased tidal dispersion. Since the 1890s, more than 100 levee failures have been observed (Brooks et al. 2012). Recovery of water quality after multiple-island flooding events could require approximately 2 years (CDWR 2018). Tidal inundation in Delta islands and other regions also results from planned restoration projects. Effects depend on the location and design details of restoration projects, and are more likely to increase salt intrusion if located along the salinity gradient (RMA 2009).

Water Management Under Climate Change

While both hydrology and estuarine physics will be altered by climate change, these effects may be largely mitigated by water-management practices to meet water-quality standards and other objectives. However, the shift in timing of runoff to earlier in the year—when reservoir operations for flood control requirements limit storage (Anderson et al. 2008)—will leave less impounded water volume available to offset summer and fall salt intrusion. This difficulty may be aggravated by the increased strength of salt intrusion mechanisms from sea level rise, tidal restoration, or unplanned levee failures. The tools currently available to mitigate climate-change effects may prove inadequate. The relaxation of salinity-based water-quality standards in 2015, and the management action of installing an emergency drought barrier in False River (lower San Joaquin Delta), may provide a preview of management responses to future climate and related summer drought conditions (Sommer 2020).

As time passes and climate changes, both water demand and water-management objectives are also likely to change (Anderson et al. 2008). The infrastructure available to manage water will also evolve. In particular, future infrastructure projects may dramatically alter the kinds of management options available (e.g., the building of large underground tunnels to move freshwater, such as envisioned by the California Water Fix project). The competing objectives of Delta management along with the complexity of physical and ecological processes make managing

the Delta a “wicked problem” with no single best solution (Luoma et al. 2015a).

ANTICIPATING FUTURE ECOLOGICAL CONSEQUENCES

The climate-change scenarios described above will impose challenges for how salt intrusion is managed in the future for the biological resources within the estuary. The conceptual model for understanding how environmental conditions affect species abundance and distributions is largely based on the ecological niche framework that considers physiological tolerance to abiotic environmental factors (i.e., the fundamental niche) and the interactions with the biotic environment (i.e., the realized niche; Chase and Leibold 2003). For aquatic organisms, the fundamental salinity niche can generally be defined as the range of salinities where physiological capabilities are sufficiently maintained to allow for survival and reproduction. Osmoregulation is the active regulation of internal salinity concentrations and is a key physiological response necessary under changing salinities. These osmoregulatory responses vary between species, such that species fall along a continuum where they either tolerate only freshwater or only saltwater (i.e., stenohaline species) or they can tolerate a range of salinities (i.e., euryhaline species). Among euryhaline fish species that occupy estuaries and coastal habitats, the range of tolerated salinities also varies (e.g., Schultz and McCormick 2013). Such variation likely reflects historic evolved responses to different salinity environments (Schultz and McCormick 2013). However, osmoregulatory responses are also plastic, meaning that organisms can acclimate to different salinity levels within their lifetimes (McEnroe and Cech 1985; McCormick 1995; Sangiao-Alvarellos et al. 2005) and potentially through heritable trans-generational epigenetic mechanisms (Shama et al. 2014; Heckwolf et al. 2018). Thus, coping with fluctuating salinity levels reflects both the short-term (within-generation) acclimation responses of organisms and the longer-term (i.e., across generations) evolutionary responses. Indeed, we know that short-term osmoregulatory

responses are under strong natural selection in species exposed to variable salinities (e.g., Shaw et al. 2014), and that populations can evolve and adapt to different salinity environments (e.g., Lee and Peterson 2002; Gomez–Mestre and Tejedo 2003; Whitehead et al. 2011, 2013; Ketola and Hiltunen 2014; Velotta et al. 2015). As salinity regimes change through the coming decades, a key question is whether evolution can keep pace. In some cases, fish and other aquatic species can evolve quickly (e.g., decadal time-scales) in human-altered environments (e.g., Strauss et al. 2006; Smith and Bernatchez 2008; Allendorf and Hard 2009; Hoffmann and Sgrò 2011; Reid et al. 2016; Oziolor et al. 2019). Whether salinity adaptation in resident species can keep pace will depend on the genetic variation and architecture that underlies relevant traits, population size, generation time, and interactions with other species (Barrett and Schluter 2008; Bell and Gonzalez 2009; Bell 2013; Bergland et al. 2014; Lawrence et al. 2014; Orr and Unckless 2014).

Knowing the patterns of variation in short- and long-term salinity tolerance within and across species allows us to better understand the predicted biological effect associated with increased salinization. For example, we know that salinity tolerance can vary between species, between populations of the same species, between age classes (e.g., adults, juveniles, and eggs), and between different stages of the life cycle (e.g., migratory vs. resident periods; Schultz and McCormick 2012). Thus, predicting the ecological consequences of salinization or any other unfavorable environmental change requires consideration of several responses that are non-mutually exclusive. First, for mobile species like fish, a typical response will be to move away from historically used areas that have become unsuitable and shift their distributions to habitats that remain within their preferred tolerance range (Åkesson 2002). Second, spatial or temporal shifts in salinity can alter trophic relationships between predators and prey (Neuenfeldt and Beyer 2003). For example, salinity may alter the distribution and or abundance of the food source used by a species of concern, and similarly increase or decrease

the abundance and distribution of a predator that preys on the species of concern (Hintz and Relyea 2017). Third, salinization can alter the competitive interactions between species, such that once-dominant species become subordinate to species they have historically interacted with or with new invasive species they come in contact with (Alcaraz et al. 2008). Finally, a diversity of other salinity-induced changes is possible, including the effect on relationships with (1) disease, parasites, and pathogens; (2) disruption of microbial communities (i.e., the microbiome); and (3) synergistic effects with other environmental stressors such as temperature and pollutants. Thus, predicting how shifting salinity patterns will negatively or positively affect any given species is challenging, but not impossible.

Nonetheless, our ability to predict broader ecosystem changes is substantially more limited. For example, invasions are known to be a major driver of ecological regime change in the estuary, with prominent effects from benthic species (Kimmerer 2002; Sommer et al. 2007) as well as aquatic weeds (Ta et al. 2018). These invasions appear to have fundamentally changed many ecological processes such as food webs, and shifted biomass trends in entire communities (Mahardja et al. 2017). Therefore, we may be able to evaluate and anticipate some individual species' responses to changing salinity, but not the response of the entire community, which is sensitive to multiple interacting factors.

In this context, we discuss below the anticipated ecological effects of salt intrusion within the estuary for anadromous fish species (i.e., fish that hatch in freshwater, migrate to saltwater, and return to breed in freshwater), and two resident fish species of conservation concern (the Delta Smelt, *Hypomesus transpacificus*, and the Sacramento Splittail, *Pogonichthys macrolepidotus*).

Freshwater is often required for spawning and the early stages of development (eggs and larvae) of all species that are considered anadromous (Zydlewski and Wilkie 2013). Many of the high-profile native estuary species—e.g., Longfin

Smelt (*Spirinchus thaleichthys*), White Sturgeon (*Acipenser transmontanus*), Green Sturgeon (*Acipenser medirostris*), Chinook Salmon (*Oncorhynchus tshawytscha*)—are anadromous, but vary in their spawning sites and the capacity of adults and larvae to tolerate a wide range of salinities. For example, in some species or populations—such as Green Sturgeon—that move great distances upstream for spawning in freshwater streams far above any tidal influence, the future risk of increased salinization on early developmental stages may be minimal. However, increased salt intrusion may significantly affect species such as Striped Bass and American Shad that spawn just above the influence of tides, if the appropriate areas for spawning are pushed so far upstream (e.g., out of bays and into riverine areas) that there becomes less appropriate physical habitat for early survival and growth. Successful hatching and development of eggs and larvae for some anadromous species like the Longfin Smelt are strongly correlated to low-salinity events during the winter months (Rosenfeld and Baxter 2007). Further, rearing of larval Longfin Smelt is tightly linked to salinity. For example, reduced survival of larval Longfin Smelt has been suggested at >5psu (Hobbs et al. 2010), and peak abundance at 2 to 4psu (Grimaldo et al. 2017); however, larval Longfin Smelt have been found up to 12psu (Grimaldo et al. 2017). The effect of increased salinization is, therefore, likely to be species-specific and life-stage dependent. For example, juvenile White Sturgeon (0.4 to 50g) could tolerate salinity of ≤ 15 psu after an abrupt transfer from freshwater, whereas adult White Sturgeon (2.5 to 15kg) could tolerate and acclimate to 35psu (McEnroe and Cech 1985). In juvenile Green Sturgeon, 170 and 533 days post-hatch fish are able to better regulate ion levels than 100 days post-hatch fish because of differences in gill morphology and enzyme activities (Allen et al. 2009); however, all three age groups could survive 33 psu for 7 weeks, the length of the salinity exposures (Allen et al. 2009).

Salinization may also influence downstream migration and use of the estuary by anadromous species. Some salmonids with strong smolt development (such as Steelhead and Coho

Salmon) and the accompanying increase in salinity tolerance often move rapidly through estuaries. Therefore, these species are less likely to be affected by salinity itself. However, species such as Chinook Salmon that spend significant time in estuaries as part of their downstream migration may be strongly affected if salinization alters the abundance of preferred prey items. For example, the timing of downstream migration in anadromous fishes has been hypothesized to have been shaped by natural selection to take advantage of increased productivity in the estuarine and coastal ocean (McCormick et al. 1998), and alteration of the timing of increased productivity by salinization could negatively affect species that depend on these food resources. Similarly, higher salinity may induce broader community changes by allowing marine predators and competitors greater residence time within the estuary, which in turn would increase interactions with anadromous species.

In the context of sea level rise and salinization of the estuary, Delta Smelt and the Sacramento Splittail are two important resident fish species of conservation concern. They are both endemic to the estuary, and their distribution and preferred habitats are tightly linked to salinity patterns. Thus, both species have been extensively studied in the context of shifting spatial and temporal salinity patterns.

The Delta Smelt is generally associated with brackish water areas from San Pablo and Suisun Bays to upstream freshwater regions, including the Sacramento and San Joaquin rivers (Moyle et al. 1992; Sommer and Mejia 2013). Delta Smelt were historically abundant, but dramatic declines in the 1980s led to it being listed as threatened under the federal Endangered Species Act and endangered under the California Endangered Species Act (reviewed in Moyle et al. 2018). A couple of aspects of the Delta Smelt's biology are important to understand its responses to future changes in salinity regimes within the estuary. First, Delta Smelt are short-lived (usually living only a single year), semelparous (adults die after breeding), and in general produce relatively few eggs relative to their body size as 1-year-

olds (Moyle et al. 1992; Lindberg et al. 2013). Second, reproduction generally occurs via an annual upstream migration in the late fall–early winter to freshwater spawning sites, where the larvae develop until they reach post-larval stages and undergo a spring migration downstream to brackish water sites (ranging between 1 to 6 psu) in what is referred to as the “low-salinity zone” (Bennett 2005). However, there may be exceptions to this general migration pattern (Hobbs et al. 2019). When field survey data have been analyzed, these dynamic movements have been confirmed, and reveal that adults are most common in habitats with salinities less than 6 psu (Sommer and Mejia 2013). Experimental work has shown that Delta Smelt can survive at higher salinities (Komoroske et al. 2014; Kammerer et al. 2016) and can maintain their internal ion concentrations (i.e., osmolality) via changes in gill ionocytes (specialized cells involved in ion transport) and increased expression of stress-related genes at salinities outside of 1 to 6 psu (Hasenbein et al. 2013; Kammerer et al. 2016). Indeed, some Delta Smelt individuals have the physiological capacity to survive full-strength seawater (i.e., 34 psu); however, relative to individuals in the low-salinity zone, they have reduced overall body condition (i.e., an estimate of energy storage) and elevated osmolality (Komoroske et al. 2016). It is important to note there was ~19.5% mortality within 90 h of exposure to the 34-psu treatment (Komoroske et al. 2014). Komoroske et al. (2016) hypothesized that the energetic cost associated with osmoregulation at high salinities potentially interacts with other environmental factors to limit the distribution of Delta Smelt within the system. Such “sub-lethal” effects on condition and performance have been observed in other species in response to elevated salinities (e.g., Brauner et al. 1994). Therefore, it is likely there are other factors beyond simple salinity tolerance—such as food availability or interspecific interactions with competitors and predators—that will continue to interact with body condition and contribute to habitat constraints for Delta Smelt in the estuary system (e.g., Bever et al. 2016).

The Sacramento Splittail is currently considered a species of special concern in California, and the last surviving member of its genus (its close relative, the Clear Lake Splittail [*Pogonichthys ciscooides*]), went extinct in the 1970s (Moyle 2002; Mahardja et al. 2015). The Sacramento Splittail is a minnow (i.e., in the family Cyprinidae) that is endemic to sloughs, lakes, and rivers of the Central Valley and estuary (Moyle et al. 2004). Unlike the short-lived Delta Smelt, Sacramento Splittail live 7 to 9 years and produce a relatively large number of offspring for their body size (Moyle et al. 2004). Adults typically begin migrating upstream with the onset of winter rains (between November and January) and spawn between February and April during flow events that inundate floodplain and riparian areas (Moyle et al. 2004). However, there are two known genetically distinct populations of Sacramento Splittail—the Central Valley population and the San Pablo Bay population—that differ in their spawning grounds (Baerwald et al. 2007; Baerwald et al. 2008; Mahardja et al. 2015). The young from the Central Valley population use largely freshwater sections of the Sacramento and San Joaquin rivers (less than 1 psu) for early rearing and remain in these areas for 2 to 3 months, whereas the San Pablo Bay population uses the higher-salinity Napa and Petaluma rivers (8.5 to 14 psu), resulting in divergent selection for salinity tolerance between the populations (Feyrer et al. 2010; Verhille et al. 2016; Jeffries et al. 2019; Mundy et al. 2020). Indeed, several lines of evidence suggest that the Central Valley and San Pablo populations differ in their salinity tolerance. For example, mortality occurs at 18 psu for the San Pablo population, whereas the Central Valley population mortality occurs at 16 psu (Verhille et al. 2016). Gene expression changes in response to salinity challenge also differ between the San Pablo Bay and Central Valley populations, with the San Pablo Bay population’s response consistent with greater plasticity in its ability to acclimate to salinity (Jeffries et al. 2019; Mundy et al. 2020). High salinities in the estuary may prevent gene flow between Sacramento Splittail populations, and contribute to population divergence (Baerwald et al. 2007; Feyrer et al. 2015). These conditions are more likely to occur during periods of extreme

drought (Jeffries et al. 2019). Thus, extended periods of salinity beyond the tolerance limits for these populations (i.e., 16 to 18 psu; Verhille et al. 2016) have been suggested to contribute to habitat fragmentation and reproductive isolation that will facilitate further population divergence in the future (Jeffries et al. 2019).

The Delta Smelt and Sacramento Splittail pose similar and different management challenges when future changes in salinity regimes are considered. Delta Smelt and the Central Valley population of the Sacramento Splittail require access to freshwater spawning sites, whereas the San Pablo Bay population may not. However, in both species, there is evidence that the salinity of the habitats occupied is typically lower than the ranges they can experimentally tolerate (see above). Such results suggest that salinity interacts with other abiotic (e.g., temperature, turbidity, physical structure) and biotic (competitors, predators, disease) factors to shape the distribution and abundance of these fish. In this regard, Delta Smelt and Sacramento Splittail are unlikely to be different than other species within the estuary but have attracted more attention because of their conservation status. Therefore, a future challenge will be to better understand how salinity interacts with other factors, and how those factors can be managed in the future (see below).

The ecological consequences for salt intrusion and altered precipitation patterns are of course not limited to fish species, and effects on other species in the estuary will likely be widespread but variable (Parker et al. 2011). For example, increasing salinity may negatively affect aquatic plants, including seagrasses and other submerged plants (Short and Neckles 1999). Studies of salt marsh halophytes have also shown that increasing salinity can negatively affect plant performance, particularly under drought-stressed conditions (Crain et al. 2004; Wigginton et al. 2020). Many of these plants are important foundation species, so their loss could have substantial cascading effects on the invertebrates, small fishes, and birds that depend on them for refugia and trophic support (see Parker et al. 2011). Thus, a future

challenge will be to move beyond predictions for how single species respond, and consider how communities, food webs, and ecosystems will change.

Finally, while our focus here is largely on salt intrusion from sea level rise and reduced inflows from drought, it is important to acknowledge that extreme freshwater runoff events are also likely to increase in the future. Climate models predict California will experience a 50% increase in droughts and flooding (Yoon et al. 2015; Swain et al. 2016). These flooding events are often associated with long and narrow corridors of enhanced water vapor called “atmospheric rivers,” and are responsible for a substantial amount of California’s total annual precipitation (Dettinger et al. 2011). Cheng et al. (2016) describe how an atmospheric river storm resulted in extreme freshwater runoff into the estuary and resulted in the near 100% mortality of native Olympia oysters. The increasing frequency of these freshwater events coupled with increasing salinization will set up much more dramatic salinity changes in the estuary. The difference between increased salinities at the end of the dry season driven by salinization and the near-zero salinity associated with wet-season storms will be more physiologically stressful and affect local diversity (Montague and Ley 1993; Attril 2002). Thus, a future where the “pendulum” is likely to swing between extreme drought and precipitation events will need to be incorporated into how biological resources are managed.

THE MANAGEMENT TOOLS AVAILABLE

The estuary is among the most intensively managed ecosystems on the planet (Sommer 2020). The intensive management is needed because 150 years of intensifying surface water development has resulted in a population and economy where the demand for freshwater often exceeds the available supply (Monsen et al. 2007; Luoma et al. 2015a, 2015b; Brown et al. 2016; Reis et al. 2019). Indeed, the watershed serves as the freshwater supply for millions of Californians and a multi-billion-dollar irrigation-dependent agricultural industry (Monsen et al. 2007). These

issues are compounded by an imbalance in the distribution of where most precipitation occurs (Northern California) versus where most of the population lives (Southern California), and because of the extreme variability in annual precipitation (Dettinger et al. 2011).

Here, we describe some of the major tools that are available to manage salinity in the estuary. These tools represent a subset of the broader management approaches summarized in a more expansive review by Sommer (2020). Many of these approaches are currently used to manage salinities, and could potentially be used to a greater extent in future responses to climate-change-induced seawater intrusion. Note that our focus here is on the management of salt intrusion from the ocean, not on tributary inputs of agricultural salts. While both oceanic and agricultural sources are very important water-quality issues in the region, in this paper we emphasize the management of oceanic sources in response to future climate-change scenarios.

Non-Structural Mechanisms—Regulations

Salinity in the estuary is managed by a complex array of state and local regulations. A more comprehensive treatment of these regulations can be found in Sommer (2020). For example, local agreements are in place with regional water diverters in the west Delta such as Contra Costa Water District, and with wetland managers in Suisun Marsh. Under the federal Clean Water Act and the state's Porter-Cologne Water Quality Control Act, the state and regional water boards have the primary regulatory responsibility for protecting the estuary's water quality. A key driver of estuarine management is the State Water Resources Control Board's Decision D-1641, which sets seasonal salinity targets at compliance points along the axis of the estuary (SWRCB 1995). A unique regulatory feature is the management of the salinity distribution using the X2 metric. Low values of X2 reflect wetter years when the salinity field is pushed back close to the ocean; high values of X2 reflect dry periods when salt intrudes upstream. This innovative metric was developed in the mid-1990s based on the recognition that outflow was the primary factor

that affected the salinity field along the axis of the estuary, and because average seasonal X2 is correlated with the abundance of a suite of estuarine species (Jassby et al. 1995; Kimmerer 2002). State decision D-1641—the State Water Board primarily assigns responsibility for meeting Delta water-quality objectives to the State Water Project (SWP) and the federal Central Valley Project (CVP)—includes seasonal targets for location of X2, based on the historical pattern of this variable, and by water year type during winter and spring.

The management of seasonal estuarine salinity is also a major component of the Delta Smelt Biological Opinion issued to the State Water Project and Central Valley Project (SWP and CVP) under the Federal Endangered Species Act (USFWS 2008). The permit includes X2 requirements in fall, a time-period outside of that required for X2 management by D-1641. Specifically, the permits require X2 to be located further downstream during fall of above-normal and wet water years. These criteria have since been modified to include more targeted management actions in summer and fall (USFWS 2019; CDFW 2020).

Structural Tools

Reservoirs

Upstream reservoirs and their associated tributaries are a primary tool to manage estuarine salinity including X2 (Sommer 2020). While some of this water may enter the Delta as relatively unmanaged flow during very high flow events in winter and spring, much of the inflow to the estuary is intensively managed by a series of large upstream reservoirs. The largest reservoirs occur on the Sacramento River and its tributaries, but the San Joaquin River also has a substantial network of reservoirs. These reservoirs allow water to be stored during wetter years and seasons, then released downstream during other periods. These releases are therefore a critical tool to prevent seawater intrusion into the upper estuary during summer and fall, and during droughts.

Water Diversions

The amount of inflow to the lower estuary is primarily moderated by water diversions associated with the SWP and the CVP (see Sommer 2020). This inflow is regulated to maintain water-quality standards for municipal uses, agriculture, and wildlife in the presence of water exports; more water exports require more inflow (Reis et al. 2019). In addition to the SWP and CVP, there are over 2,000 smaller agricultural water diversions in the Delta (Herren and Kawasaki 2001). Although D-1641 allows up to 35% of inflow to be diverted by the two water export facilities in winter–spring and up to 65% of inflow to be diverted during summer–fall, the actual amount varies substantially based on the degree of salt intrusion (e.g., spring versus neap tides) and because of endangered species management. Water diversions are substantially reduced during drought periods, when inflows are so low that they must be reduced dramatically to avoid saline water intrusion into the Delta, which would make these sources unsuitable for use by local water users or exporters (Sommer 2020). For example, during the latter part of the recent historical drought (2012–2016), inflows reached such low levels that water diversions had to decrease their exports to minimal health and safety levels to allow Delta outflow sufficient to avoid major seawater intrusion into the central Delta. During the worst of the drought, there was no Delta outflow to repel estuarine influx and elevated salinity (Monismith 2016). With sea level rise, more of the available freshwater flow will be needed to hold back salt intrusion, which will severely constrain water exports even in normal years.

Barriers

As noted above, the recent historic drought resulted in major challenges in preventing salt intrusion into the freshwater tidal portion of the upper estuary. As the drought progressed, hydrologic modeling indicated that already low reservoirs and water export operations alone would be unlikely to avoid major salt intrusion into the Delta. A key concern was that once salinity intruded into the region, water quality would be unsuitable for months. To address

this issue, in 2015 water managers took the remarkable step of installing an Emergency Drought Barrier along one of the key corridors through which salinity enters the central Delta. The barrier was installed in False River during spring–fall of 2015, which successfully prevented salinity from intruding into Franks Tract, a flooded island that has a major effect on Delta water quality and hydrodynamics (Kimmerer et al. 2019).

Gates

As described above, water inflow and exports from reservoirs strongly affects salt intrusion into the Delta. When water export pumping rates are high relative to river inflow, salinity can intrude into the western and central Delta regions. To help reduce these effects, the pathway of Sacramento River inflow may be altered, allowing a more direct route for freshwater to reach the export facilities. This is achieved by using the Delta Cross-Channel, a set of gates on the lower Sacramento River (Monsen et al. 2010). When the gates are opened, Sacramento River flows have a relatively direct path via the Mokelumne River and Georgiana Slough to the export pumps, thereby reducing the hydrodynamic “pull” from the West Delta, which tends to draw in more oceanic salinity. However, these gates are often closed for long periods during winter and spring to protect Chinook salmon that are migrating down the Sacramento River (NMFS 2009).

The most unusual salinity-management facility in the estuary is the Suisun Marsh Salinity Control Gates (SMSCG; see also Sommer 2020). Suisun Marsh is the largest contiguous marsh on the Pacific Coast, supporting both managed and unmanaged wetland habitat. Early in the planning of the SWP, new water diversions were recognized to result in increased salinity in the marsh. This was a major concern for wetlands managers, who depended on low-salinity water for their managed habitat (e.g., duck clubs). Although this issue was partially addressed by water-quality standards for the region, water managers constructed operable gates to tidally “pump” freshwater into the marsh during drier periods. In the 1980s, the California Department

of Water Resources constructed the SMSCG, a novel facility that is typically operated October to May to maintain low-salinity conditions in the marsh. The facility includes three gates on Montezuma Slough, a primary source of tidal flows through Suisun Marsh. The gates are operated tidally. During ebb tides, the gates are opened to allow freshwater from the Delta to enter Montezuma Slough and flush throughout the marsh. During flood tides, the gates are closed, preventing salt from intruding into the marsh from the western outlet of Montezuma Slough. Essentially, freshwater is tidally pumped into the marsh through the SMSCG, a remarkably effective way to reduce salinities in this region. To our knowledge, there is no facility like it in other estuaries. However, the operations come with a trade-off. Redirecting freshwater flow into Suisun Marsh causes some upstream salt intrusion along the main tidal axis of the estuary, so additional flow (via export reductions or reservoir releases) is needed to counteract the resulting movement of the salt field (X2) along that axis.

In August 2018, the SMSCG facility was used in a completely different way: to manage salinities for fish habitat (Sommer 2020). As noted above, Suisun Bay and Suisun Marsh are a key part of the habitat for Delta Smelt, a high-profile endangered species in the estuary. During drier periods, such as summer, Delta Smelt may be at least partially excluded from Suisun Marsh because of salt intrusion. To provide improved habitat conditions for Delta Smelt, the SMSCG were operated for a month to reduce salinities in Suisun Marsh, allowing greater occupancy of this region. Predicted benefits included improvements in several areas: habitat conditions, food availability, growth, survival, and distribution. These pilot operations reduced marsh salinities during a key rearing period for Delta Smelt. Based on this initial trial, the SMSCG have been included in recent regulatory permits as a tool to manage fish habitat during periods of salt intrusion (USFWS 2019).

Channel Geometry

As described above, physical geometry significantly affects the location of the

salinity field, lateral mixing, and gravitational circulation. It is also clear that future inundation of Delta islands could significantly affect salinity levels in the estuary (Mount and Twiss 2005; Lund et al. 2010). Moreover, thousands of acres of tidal wetland restoration projects are planned, which could also affect the tidal prism and thus landward dispersion of salt into the Delta. Depending on the location of these projects, salt intrusion could be either enhanced or reduced (Lund et al. 2010). It is therefore possible that specific restoration projects could be planned to improve salinity management in the system, or at least partially mitigate the salinizing effects of the future loss of Delta islands through floods, earthquakes, or sea level rise.

FUTURE RESEARCH PRIORITIES

What should future research priorities for the estuary be, given our understanding of historic salinity patterns, future sea level-rise scenarios, how physical processes govern patterns of salt intrusion, salinity tolerance of species of concern, and ecological linkages?

We argue that one future priority needs to be improving physical models, particularly those focused on predicting salt intrusion under different natural and managed scenarios. Existing salt intrusion studies often make strong assumptions and simplifications about how sea level rise will affect coastal environments, and these models often fail to account for the complex physical processes or management responses that can either mitigate or amplify salt intrusion. For example, 3-D modeling studies that account for the effects of sea level rise on physical processes generally use fixed boundary conditions that do not account for management adaptation to meet water-quality objectives (e.g., Chua and Xu 2014). In contrast, Knowles et al. (2018) used a suite of models to predict flows and salinity that accounts for management responses to climate-change scenarios but does not consider the effect of sea level rise on salt intrusion, thus integrating representations of physical processes and management responses in an integrated water operations and 3-D model. Another approach

is to integrate into a water-operations model a parameterization of the effect of sea level rise on salt intrusion. An example is the California Water Fix study in which the artificial neural network of a water operations model was trained using salinity predictions from a 1-D model that was parameterized to reproduce the predicted salt intrusion from a 3-D model simulation. (https://www.waterboards.ca.gov/waterrights/water_issues/programs/bay_delta/california_waterfix/exhibits/exhibit102/index.html). In that case, the flows estimated by the water operations model can then be applied in a 3-D model to validate the parameterization of salt intrusion used in the operations model.

A related priority is to incorporate how the physical geometry of the estuary will change in the future. A current simplification when modeling future climate change scenarios is the use of existing geometry, which does not represent the expected additional inundation of low-lying areas with sea level rise. Furthermore, geomorphic adjustment will continue as estuary geometry and sea level evolve—but is typically neglected in existing studies. Thus, to estimate salinity distribution for realistic future scenarios of the estuary, a more complete and integrated representation of physical processes and management responses is required.

In terms of future research priorities to better predict and manage biological/ecological responses, a better understanding is needed of (1) the movement of fish and their ability to find and track suitable habitat, (2) their acclimation responses to altered salinity and the consequences for other traits, (3) their capacity to evolve in response to altered salinity patterns, and (4) ecosystem rearrangement.

As sea levels rise and salinity regimes shift within the estuary system, the availability of habitats suitable for many aquatic species will also shift, expand, or contract. Persistence of resident species will depend on the extent and accessibility of these remaining suitable habitats. Thus, the development of models of sea level rise that predict the spatial and temporal distribution

of habitats should be a future research priority (see Kimmerer et al. 2013; Bever et al. 2016). If sufficient suitable habitat is available but located in different regions of the estuary, then persistence will depend on the migratory abilities of the species and of other species that constitute a sustainable biotic community, which may be re-arranged owing to differences in ability to migrate and suitability of alternative habitat. If sufficient suitable habitat is not available or accessible, then species will be challenged to physiologically adjust (i.e., acclimate) to changing salinities, or evolve adaptations to these new conditions through natural selection. Little is known about how the movement patterns of entire fish communities might permanently shift in response to altered salinity regimes, but emerging tracking technology may allow us to better understand the timing and patterns of movement within the estuary (Åkesson 2002; Hussey et al. 2015; Colombano et al. 2020).

In contrast to movement patterns, much more is known about the physiological mechanisms that underlie osmoregulation and the ability to acclimate to different levels of salinity (Baldisserotto et al. 2019). Indeed, how salinity induces changes in hormones, levels of gene expression, and morphological changes in gills to maintain osmotic homeostasis has been the subject of decades of study (reviewed in Baldisserotto et al. 2019). However, while many of the key genes involved in ion transport are known, salinity exposure also causes changes in expression of many genes unrelated to osmoregulation (e.g., Whitehead et al. 2011; Gibbons et al. 2017; Mauro and Ghalambor 2020), suggesting that physiological responses to different salinity regimes extend to traits beyond those that only regulate osmotic homeostasis (e.g., feeding behavior, parasite resistance, vulnerability to predation). Determining what these additional traits are is an important area for future study. For example, microbial communities differ dramatically with environmental salinity (Lozupone and Knight 2007), which suggests that adjusting to new host-microbiome interactions may be necessary when species confront new osmotic environments. Similarly, in freshwater

the Three-Spined Stickleback (*Gasterosteus aculeatus*) has by natural selection evolved to overcome dietary deficiency in docosahexaenoic acid (DHA) that is lower in prey items in freshwater compared to those in seawater habitats (Ishikawa et al. 2019). Though many traits may matter for fitness in changing salinity regimes, osmoregulatory abilities are extremely important, given the considerable metabolic resources spent to maintain appropriate control of osmotic balance in aquatic species (Kültz 2015). Since the estuary spans osmotic habitats from marine to freshwater, resident species include those that span the physiological continuum from euryhaline to stenohaline; these physiological traits contribute to species' abilities to quickly acclimate to changing salinity conditions. Indeed, fish populations in the estuary show variation in how fast individuals can physiologically respond to changes in salinity (Jeffries et al. 2016; Verhille et al. 2016).

Acclimation may also emerge across generations (trans-generational plasticity); however, in the context of osmoregulatory acclimation, little is known of the ubiquity of this phenomenon, the nature of the environmental cues that trigger it, and the mechanisms through which information about the environment is transferred across generations (e.g., maternal provisioning or epigenetic inheritance; Heckwolf et al. 2018). To predict likelihood of persistence, it is important to understand the physiological limits and timing of osmotic acclimation for key native species resident within the estuary system. Schultz and McCormick (2013) summarized salinity tolerances from a broad range of fish orders, families, and species, which provides a framework for predicting vulnerabilities of different groups; generating similar information for key species in the estuary should be a high priority for future research.

Salt intrusion is unlikely to occur in isolation from other environmental factors associated with changing climatic conditions, such as temperature, flow, turbidity, water quality, and pH (e.g., Kimmerer 2004; Cloern et al. 2011; Cloern and Jassby 2012); thus, other future priorities are

to understand how organisms cope with these multiple stressors. The capacity for organisms to simultaneously acclimate or adaptively evolve to multiple stressors that exhibit increasing variability and directional change will likely be a key determinant in predicting which species will survive and persist into the future (Todgham and Stillman 2013; Gunderson et al. 2016). However, predicting how organisms will respond to multiple stressors is inherently difficult to study and to predict (e.g., Todgham and Stillman 2013; Gunderson et al. 2016). Controlled laboratory studies can be especially useful for understanding how multiple stressors can interact to affect an animal's ability to osmoregulate. For example, White Sturgeon can osmoregulate (e.g., McEnroe and Cech 1985), but when food availability is reduced it takes longer to acclimate to 24psu compared with fish fed to satiation (Lee et al. 2015). These types of lab studies provide critical insights into the conditions that place physiological limits for salinity tolerance but have limitations for predicting acclimation abilities in future environments. In contrast, while field studies offer insight into the "realized" salinity niche by describing how species deal with complex environments, they lack the control to isolate which aspects of the environment drive the observed patterns. For example, some Delta Smelt can survive at full-strength seawater, but they are generally found within the low-salinity zone of the estuary, suggesting that interactions with predators and food availability shape their distributions in nature (Komoroske et al. 2016).

Similarly, interactions with competitors can also restrict distributions to a smaller subset of habitats than would be expected based on salinity tolerance alone (e.g., Torres-Dowdall et al. 2013; Mauro and Ghaleb 2020). How future environmental change may disrupt species interactions—such as those between predators and prey, competitors, or hosts and parasites (Broitman et al. 2009; Gilman et al. 2010; Angert et al. 2013)—will complicate future predictions that are based on the current realized niche or distribution (Urban et al. 2016). Though uncertainty will still remain, future research can combine lab and field studies to better understand

the limits of key species in acclimating to salinity, and how other stressors affect these physiological responses. Such studies will contribute key information to better predicting the response of interacting species, and to setting conservation and management priorities.

If physiological acclimation to salinity and other stressors is insufficient to maintain a species' fitness in the future estuary, then its capacity to quickly evolve by natural selection will determine its persistence. The ability of species to rapidly adapt through natural selection depends largely on their generation time and the availability of additive genetic variation for the traits that affect fitness (Barrett and Schluter 2008; Orr and Unckless 2014). Therefore, knowledge of the nature and availability of additive genetic variation for osmoregulatory traits will be important for predicting a species' ability to adjust through natural selection. This is where quantitative genetics studies that use captive breeding experiments or field pedigree information could offer insights and contribute to species-management strategies. For example, quantitative genetics studies could identify genotypes that affect inter-individual variation in osmoregulatory abilities (e.g., Brennan et al. 2018), and these genotypes could be tracked and prioritized for maintenance within captive breeding programs (e.g., for Delta Smelt; Fisch et al. 2013). Furthermore, if populations in different regions of the estuary system harbor different genetic variants that affect osmoregulatory abilities—such as is observed for the Sacramento Splittail (e.g., Verhille et al. 2016; Jeffries et al. 2019)—then those populations could be prioritized for conservation, which would serve the long-term resilience of the species as the environment changes. Similarly, some stenohaline freshwater species (e.g., minnows of the family Cyprinidae), may have hard upper-salinity-tolerance limits and limited evolutionary potential (Schultz and McCormick 2012), making it unlikely that they possess the genetic variation necessary to rapidly adapt to salt intrusion.

CONCLUSIONS

This paper represents a perspective that integrates the physical and biological sciences to examine climate change and the physical processes that will shape patterns of salt intrusion into the estuary—and the expected ecological consequences. We have highlighted some of the available management options that can be used to mitigate these future threats, and some potential research priorities. This integrated perspective is important because the physical and biological sciences often operate separately from each other. Yet, understanding and managing complex ecosystems such as the estuary ultimately requires applying such inter-disciplinary thinking to the challenging decisions that resource managers and policy-makers face. Indeed, the community of scientists and researchers who study the estuary are at the forefront of interdisciplinary research via their integration of the physical and biological sciences (Feyrer et al. 2011; Kimmerer et al. 2013; Hance et al. 2020). Our goal here is to highlight how we can start the process of anticipating and responding to the changes that are predicted to arise because of climate-induced sea-level rise and altered precipitation patterns. We recognize that salt intrusion from higher sea levels is only one of many expected future challenges, but we hope that the perspective presented here can stimulate meaningful discussions and actions on how best to plan for these challenges.

We hope readers will take several important points from this paper. First, the extent of salt intrusion within the estuary has varied over geologic time, and, before humans modified the landscape, was governed by the physical geometry of the estuary, seasonal patterns of precipitation, and freshwater inflow. While these factors remain an important determinant of salt intrusion, human control of water storage, the timing and amount of freshwater release, and modifications to the physical structure of the estuary provide considerable control over current patterns of salt intrusion. Looking to the future, the natural and human-controlled determinants of salt intrusion will occur against the backdrop of rising sea levels and changes in freshwater

inflow. Improved hydrodynamic models, which incorporate management actions and geomorphic evolution, are needed to better predict future salinity. Second, the biological communities of the estuary have evolved physiological mechanisms to cope with seasonal and spatial shifts in salinity patterns, but these mechanisms vary, and their capacity to cope with ecological effects that can re-arrange the ecosystem is limited. Physiological and genetic variation in salinity tolerance and correlated traits within and among species will determine the future vulnerability of these species. Quantifying this variation should be a priority because it could help managers anticipate which populations are at greatest risk. Lastly, numerous water-management tools exist to control salinity patterns within the estuary. Managers could be encouraged to experiment and apply these tools to test their effectiveness.

We end with a few ideas we think would stimulate progress toward the goals described in this paper. Ongoing regional efforts are needed to coordinate and communicate research about the challenges of salt intrusion within estuary. While we encourage resource managers to consider the priorities for future research presented here and to encourage the kinds of inter-disciplinary research presented in this paper, we also recognize that physical and biological conditions in the future will be very uncertain. Scientific research, water and resource management, and policy would benefit from being prepared to embrace this uncertainty and respond accordingly. For example, one way that scientists and researchers, resource managers, and policy-makers can work closely together to respond proactively to changing conditions is by considering water-management projects as scientific experiments. If we approach water-management projects as ecological or physical experiments, then, as with any experiment, clearly stated assumptions, alternative hypotheses, and predictions should be part of the planning process. When possible, to test their effectiveness, the building of barriers or gates to influence local salt intrusion (see above) could be replicated across different physical or hydrological settings. Such projects have been successful as a management tool in the past,

but the range of environmental conditions that limit their effectiveness under future scenarios needs to be understood. If future management projects adopt such thinking during the planning and permitting process, then funding for these projects can be structured in a way that permits monitoring before and after implementation, to allow factors that contributed to their successes or failures to be evaluated. In this way, we can provide the best science-based management to maintain the integrity and value of the estuary.

ACKNOWLEDGMENTS

The authors wish to thank the Coastal and Marine Sciences Institute at the University of California, Davis, the Delta Stewardship Council (Delta Science Program), and the UC Agriculture and Natural Resources Program for the generous funding that allowed the symposium on which this paper was based to occur. John Kelly and two anonymous reviewers provided comments that improved this manuscript. CKG was supported by National Science Foundation grant (IOS 1457383). KMJ was supported by a Natural Sciences and Engineering Research Council of Canada Discovery Grant (05479).

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