White papers providing a synthesis of knowledge relating to Delta Smelt biology in the San Francisco Estuary, emphasizing effects of flow

Interagency
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Interagency Ecological Program
for the
San Francisco Bay-Delta Estuary

A Cooperative Program of:

California Department of Fish and Wildlife
National Marine Fisheries Service
US Army Corps of Engineers
US Environmental Protection Agency
US Geological Survey
California Department of Water Resources
State Water Resources Control Board
US Bureau of Reclamation
US Fish and Wildlife Service

Suggested Citation

FLOAT-MAST (Flow Alteration - Management Analysis and Synthesis Team), 2022. *White papers providing a synthesis of knowledge relating to Delta Smelt biology in the San Francisco Estuary, emphasizing effects of flow.* Interagency Ecological Program, Sacramento, CA. IEP Technical Report #98. 191 pp.

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1. Introduction to the Delta Smelt Flow Alteration White Papers

Larry Brown, USGS (deceased)

The management of the quantity and timing of freshwater flow into and through the San Francisco Estuary (SFE) is a perennial source of controversy in California. It is well known that freshwater outflow is a major environmental driver in estuarine ecosystems, including the SFE. However, the estuary is also the hub of California's water distribution system, which supplies water to over 25 million Californians and a multibillion-dollar agricultural industry. This tension between water supply and maintaining flows to maintain environmental quality is at the core of the controversy.

One of the major environmental issues is providing habitat for Delta Smelt (*Hypomesus transpacificus*). Delta Smelt is endemic to the SFE and is listed as threatened under the Federal Endangered Species Act and as endangered under the California Endangered Species Act (Bennett 2005). Early studies of Delta Smelt distribution within the SFE suggested that Delta Smelt summer and fall habitat is closely associated with freshwater flow, which affects the location and extent of the low-salinity zone of the estuary (Moyle et al. 1992). Subsequent studies have provided further information on many aspects of Delta Smelt ecology (e.g., IEP-MAST 2015, Moyle et al. 2016; Hobbs et al. 2019); however, a direct connection between freshwater outflow and increased abundance of Delta Smelt has been difficult to establish (Kimmerer et al. 2002 a, b). The most recent increase in the Delta Smelt population was coincidental with the wet year of 2011 (Brown et al. 2014), but the wet year of 2017 was not coincidental with a population increase, likely because of high water temperatures (FLOAT-MAST 2021). Overall, recent reports have stressed the need to assess the importance of multiple environmental variables over the entire Delta Smelt life cycle to better understand the combination of factors affecting Delta Smelt distribution and abundance.

Because of the now substantial amount of information available concerning Delta Smelt ecology and the importance of multiple abiotic and biotic factors to the distribution and abundance of Delta Smelt, it can be difficult to evaluate the possible advantages of proposed management actions, interpretations of new research results, or assessments of the effects of management actions and natural events. Providing sufficient background for readers in integrative reports (e.g., IEP-MAST 2015, FLOAT-MAST 2021) can result in products that, while comprehensive, are difficult to read because of extensive presentation of previous work. The purpose of this set of white papers is to provide background information on various topics that are consistently considered important for understanding Delta Smelt ecology, including abiotic habitat, biotic habitat, and measures of response of individual Delta Smelt and the population to environmental conditions. The intent is to provide a summary of available information on a topic rather than presenting arguments for the relative importance of one factor compared to another in a particular year or situation.

These white papers have been prepared by the Flow Alteration (FLOAT) Management Analysis and Synthesis Team (MAST) as part of developing an annual summary and synthesis of factors affecting the Delta Smelt population. Although originally formed as a part of the FLOAT Project Work Team (PWT) to address flow related management actions, it soon became clear that a wider perspective including all seasons and both flow and non-flow conditions is necessary to understand the responses of the Delta Smelt population to a management action. These white papers are intended to provide the necessary background for understanding the annual summary and synthesis (in development) but will also be useful to anybody needing a basic background in Delta Smelt ecology. These white papers are intended to be living documents that are updated at intervals to remain current with recent advances in understanding of the Delta Smelt population.

Approach

There have been several conceptual models developed for Delta Smelt life history and Delta Smelt response to environmental conditions (e.g., Bennett 2005, Brown et al. 2014, IEP-MAST 2015). We adopt the conceptual model developed by IEP-MAST (2015). This model includes an overview model (Figure 1) and a more detailed model for each season (see IEP-MAST 2015). We do not intend to explain this conceptual model in detail here, but Figure 1 illustrates that the Delta Smelt population is affected by a wide range of factors, including many that interact, and the important variables change with season and Delta Smelt life stage.

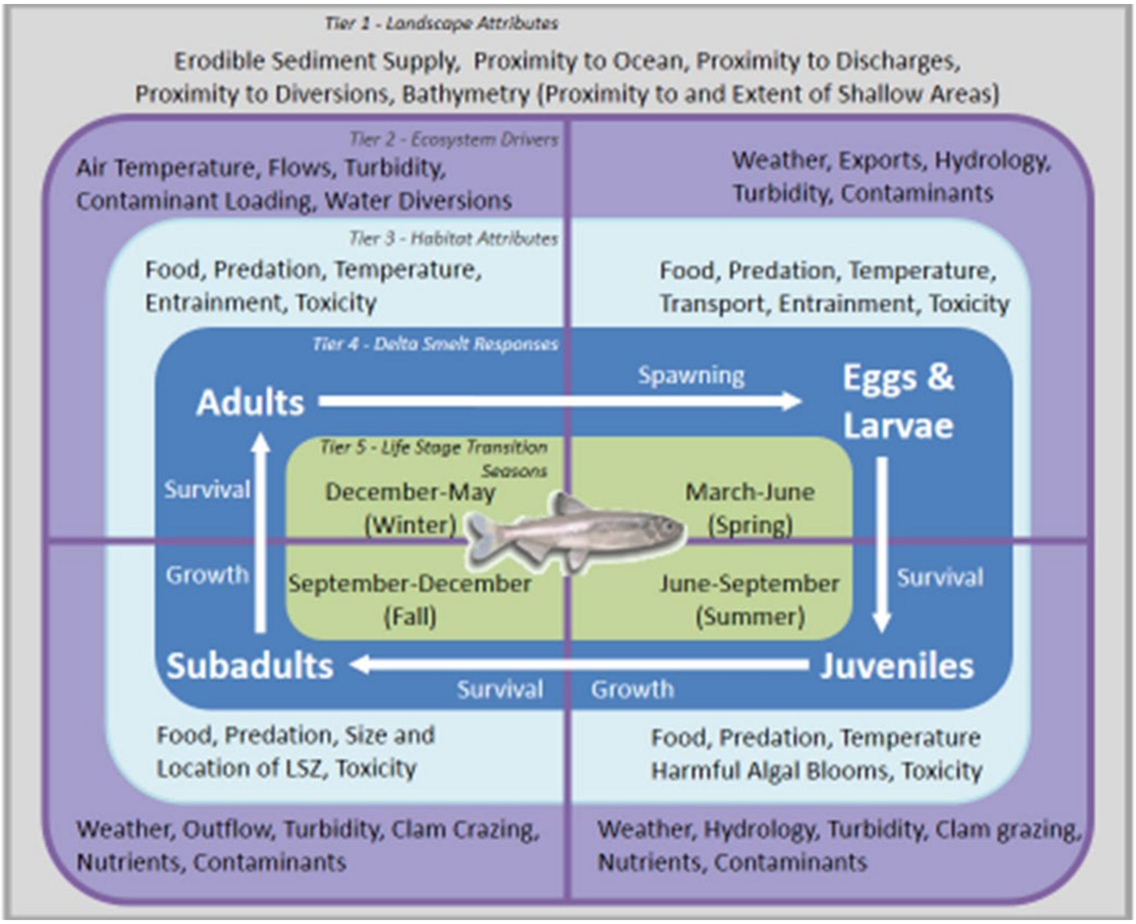

Figure 1. Delta Smelt general life cycle conceptual model (IEP-MAST 2015). LSZ = low salinity zone.

For the white papers, we selected factors important to at least one life stage. Also, the topic had to have sufficient background information available to support a written narrative. The topics selected include dynamic abiotic habitat (salinity, water temperature, and turbidity), phytoplankton, harmful algal blooms, zooplankton and Delta Smelt feeding success, invasive clams (biomass grazing rate and recruitment), aquatic vegetation, and species composition of the fish assemblage. We also provide background on several aspects of Delta smelt response to environmental conditions including growth rate, life history diversity, health metrics, Delta Smelt range and distribution, and Delta Smelt survival and population growth. Note that Delta Smelt feeding success is also a Delta Smelt response; however, feeding success is so closely linked to zooplankton abundance that they are discussed together.

A factor that may seem to be missing is flow. This is because the San Francisco Estuary, like all estuaries, is a tidal system. Except during extreme floods, the system is tidal, and there is much more water "sloshing" back and forth than there is net flow moving from the watershed to the ocean. Pelagic fish that live in the water column in open water areas such as channels and bays can choose to move with the tides or can utilize the tides for movement (Bennett and Burau, 2015). However, flow is important because it interacts with other factors and can influence the spatial and temporal distribution of constituents that can influence fish distribution and abundance. Therefore, we provide some basic background on flow in the white paper on Dynamic Abiotic Habitat. We recommend that all readers read Dynamic Abiotic Habitat first to provide the background needed to understand the subsequent white papers. Additional information on flow will be provided within other white papers as needed to understand the topic of interest.

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2. Dynamic Abiotic Habitat

Larry Brown (USGS), Steven Slater (CDFW), Michael MacWilliams (Anchor QEA)

Introduction

The factors affecting an organism can be divided into two general classes, abiotic and biotic. Abiotic factors include features of the physical and chemical environment, such as climate, water movement, and many aspects of water quality. Biotic factors refer to those involving living organisms and their interactions, such as the organisms and processes in a food web. We also distinguish between dynamic and stationary abiotic factors. Stationary abiotic factors are fixed in the environment and include things like landscape features (e.g., bays, channels, and surface elevations) that change relatively slowly over time. Dynamic abiotic factors vary over time and space at various scales ranging from sub-daily (e.g., tidal direction and velocity) to annually (e.g., total water inflow and outflow).

The objective of this white paper is to provide background on three types of dynamic habitat believed to be important as aspects of Delta Smelt (*Hypomesus transpacificus*) habitat: (1) salinity, (2) water temperature, and (3) water clarity. These three factors are thought to define the physical environment that define the region(s) potentially habitable by Delta Smelt. These regions must have tolerable values for all three factors for Delta Smelt to inhabit them. Within these regions of acceptable physical habitat, biotic factors then determine if conditions favor growth and survival of individual Delta Smelt and ultimately, the overall increase or decrease in the total population.

Because freshwater inflow to the estuary and its interactions with water diversions and tidal flows are important drivers of dynamic abiotic factors of interest, we first present information on hydrodynamics (flow) in the San Francisco Estuary (SFE). Flow related issues can also be important to some of the biotic factors of interest that are discussed in companion white papers(?). By presenting some of the basic background for flow in advance, we hope to reduce the repetition of such information in the other white papers(?).

Each section of this paper begins with a brief review of information about each topic – flow, salinity, water temperature, water clarity - including how they vary over time and space. This is followed by a brief review of the literature on the influence of each aspect of dynamic abiotic habitat on Delta Smelt. The general geographic scope for this white paper is the upper SFE, defined as the region extending from the eastern end of Carquinez Strait to the landward extent of tidal influence (Figure 1). Other regions, such as San Pablo Bay and Napa River (Figure 1) will be discussed as appropriate.

Flow

Freshwater inflow to the estuary is ultimately determined by the magnitude of precipitation in the watersheds of the Central Valley, primarily the Sacramento and San Joaquin Rivers (Figure 1), and patterns of water use as water travels downstream. California has a Mediterranean climate with a distinct winter-spring wet season and summer-fall dry season (Kimmerer 2004).

In the SFE watershed, precipitation can fall as either snow at higher elevations, where it is generally colder, or as rain at lower elevations, where it is generally warmer. Spring snowmelt results in a long period of elevated but slowly declining flows that is important to the lifecycle of many California fishes (Moyle 2002). Unfortunately, this seasonal cycle of wet and dry seasons is not conducive to the needs of our current human society, which requires a reliable year-around source of water to meet municipal, industrial, and agricultural needs.

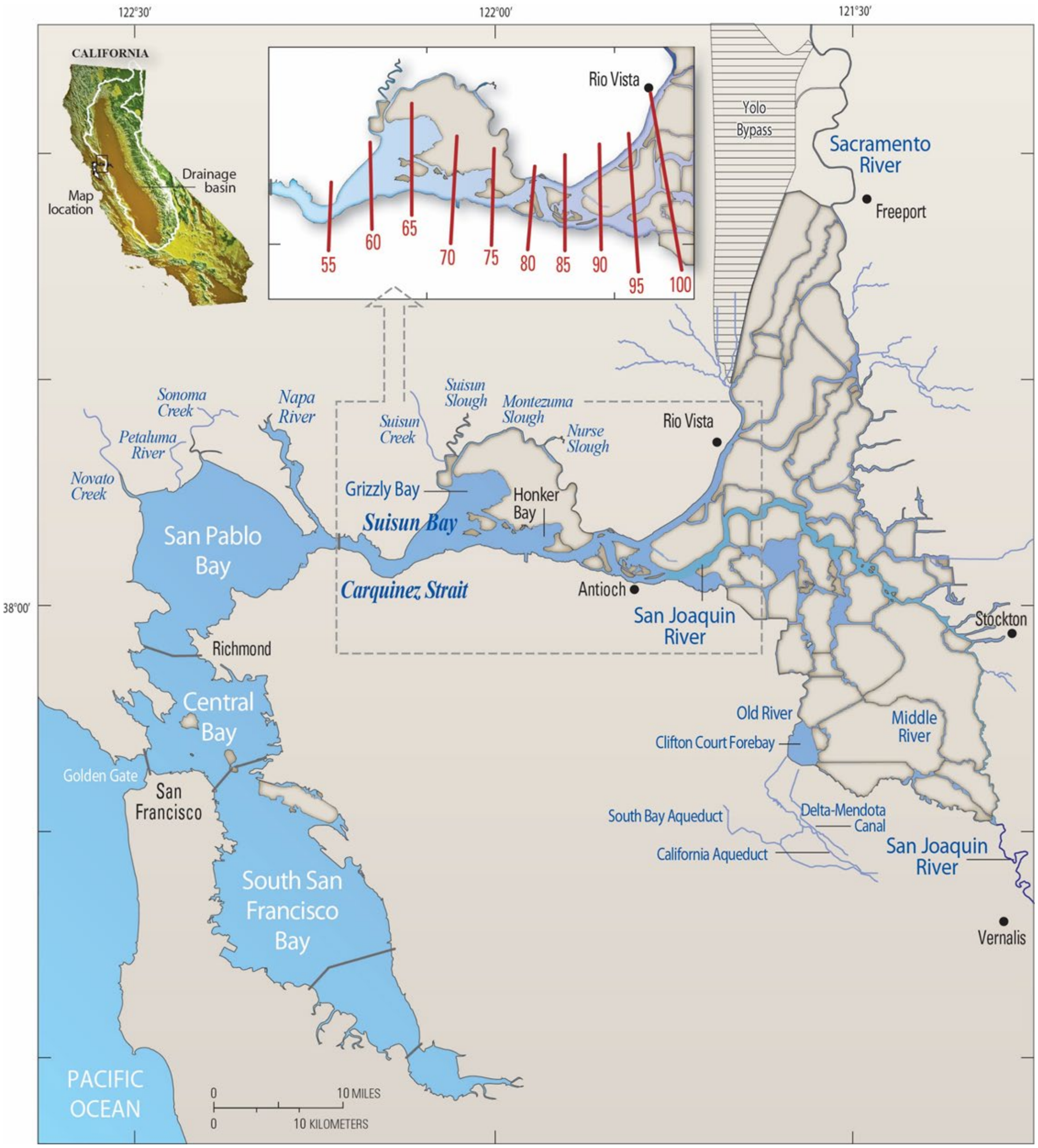

Figure 1. Map of the San Francisco Estuary. The smaller map shows the drainage basin of the Sacramento and San Joaquin Rivers. The inset shows various values of X2, the distance in kilometers from the Golden Gate to the near bottom salinity 2 isohaline (IEP-MAST 2015).

The need to make seasonal precipitation consistent with a reliable water supply and reduced flood risk resulted in the construction of some of the most complex water infrastructure in the world (Figure 2). All the major rivers in the SFE watershed have been dammed for multiple purposes but primarily for water storage and flood control. Water stored in reservoirs is diverted directly into water supply systems, released into the river channel for diversion at downstream facilities, or allowed to flow through the estuary into the Pacific Ocean. These water supply operations result in riverine flow regimes that are very different from the natural flow regime (Mount 1995, Brown and Bauer 2010, Zimmerman et al. 2018). The two largest water projects in this system are the federal Central Valley Project (CVP) and the State Water Project (SWP) (Figure 3). These projects have major water diversion facilities in the southern Delta (Figure 3). The export capabilities of these facilities (i.e., “the pumps”) are sufficient to affect the movement of water through Delta channels in ways that are thought to affect the aquatic ecosystem. Several other permanent and temporary facilities are also involved in water supply, water quality and flood operations in the estuary. The Delta Cross Channel facilitates movement of water from the Sacramento River through the central Delta to the pumps. The Suisun Marsh Salinity Control Gates (Figure 3) are operated to maintain desired salinities in Suisun Marsh. The Yolo Bypass is a large flood bypass (Figure 3) that protects the city of Sacramento and other nearby urban areas from flooding. In addition, there are several temporary rock barriers in the southern Delta intended to maintain water-surface elevations for instream diversions or to move water through selected channels. Together these facilities are operated according to regulations and operational rules intended to maintain both a reliable water supply and healthy ecosystem. Achieving these two goals simultaneously is challenging (Luoma et al. 2015).

Figure 2. Map of California water infrastructure (from the California Department of Water Resources).

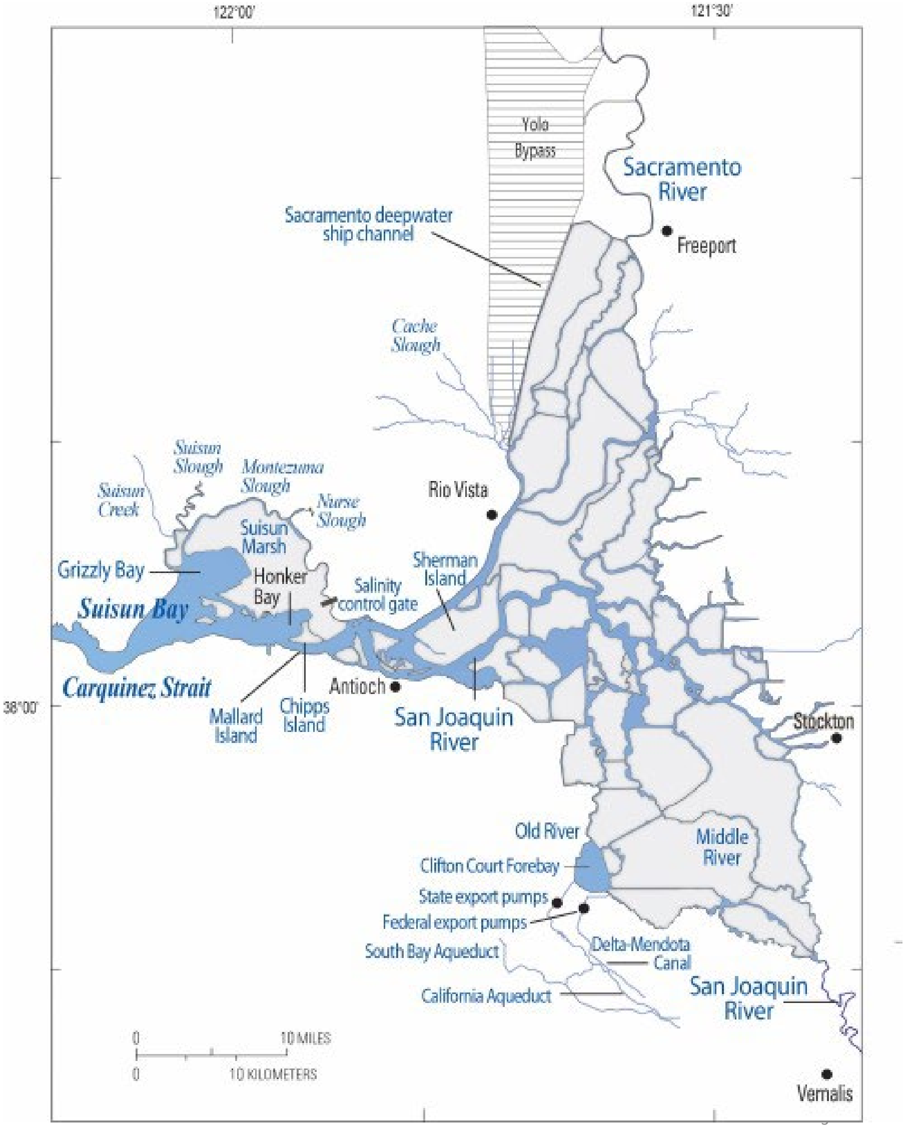

Figure 3.

Figure 3. Map of upper SFE with water infrastructure. The Sacramento River Deep Water Ship Channel is labeled as "Sacramento deepwater ship channel" on the map. The Governor Edmund G Brown California Aqueduct is labeled as "California Aqueduct" on the map.

Construction of the CVP and SWP raised many concerns about the possible effects of the projects on aquatic resources of concern, primarily anadromous Chinook Salmon (*Oncorhynchus tshawytscha*) and estuarine resident Striped Bass (*Morone saxatilis*). Adult Chinook Salmon migrate through the estuary on their way to upstream spawning grounds, and juveniles migrate through the estuary on their way to the ocean, spending variable amounts of time rearing in the Delta or Yolo Bypass. Chinook Salmon are native to California and support valuable sport and commercial fisheries. Striped Bass is an introduced species (Dill and Cordone 1997, Moyle 2002) and supports a valuable sport fishery. Striped Bass is largely an estuarine species in the SFE, although individuals are known to move upstream into the rivers and can migrate to the ocean when environmental conditions are favorable (Moyle 2002). Early work focused on the effects of Delta inflow, Delta outflow, and exports as causative factors and found statistical relationships between various measures of flow and species abundance indices (e.g., Stevens and Miller 1983, Kjelson et al. 1982). Entrainment of fish in exported water has also been a significant concern (e.g., Kimmerer 2008, Grimaldo et al. 2009, Miller 2011). However, regulating water supply to protect species of concern based on measures of Delta inflow, outflow, and exports alone is contentious in the absence of mechanistic understanding of how flow creates and supports environmental conditions supportive of species populations. Presumably, if the mechanisms are understood, conditions favorable for species of concern can be provided at reduced cost to water supply.

An important first step in developing an understanding of the relationships between flow and estuarine habitat was the development of the X2 concept; the metric of X2 was developed to describe the position of the salinity gradient within the estuary, with X2 defined as the distance in kilometers from the Golden Gate to the near bottom salinity 2 isohaline (Jassby et al. 1995). X2 is roughly at the center of the “low-salinity zone” (LSZ), with the low salinity zone variously defined as ranging from a minimum of 0.5-1.0 practical salinity units (PSU) to a maximum of 5-6 PSU (Jassby 2008, Kimmerer et al. 2013, IEP-Mast 2015). The LSZ is known to be an important region for the retention of organisms and particles and for nutrient cycling in the SFE and elsewhere. The salinity gradient, X2, and LSZ are discussed more fully in the **Salinity** section (below).

The important idea behind X2 is that it embodies a physical response of the estuary to Delta outflow; it decreases with increasing riverine outflow because outflow prevents seawater from moving landward. This physical response provides more or less favorable conditions for various aquatic species. Much subsequent research has focused on defining habitat requirements for species of interest and determining if flow management or other forms of management (e.g., habitat restoration) can be used to provide optimal conditions. In this sense, flow is not managed as a habitat variable in isolation but as a tool for manipulating one or more environmental variables that respond to flow. However, before moving onto using flow as a tool, it is necessary to understand how flow “works” in the SFE. This requires a basic understanding of hydrodynamics (the physics of water movement).

It is important to remember that estuaries are tidal systems. During most periods of the year tidal flows greatly exceed river flows in magnitude (Kimmerer 2004). This means that the back-and-forth movement of water with the tide is usually much more important than the smaller downstream movement associated with Delta inflow. Conceptually, a person in a raft at some location in a Delta channel at low tide would move a long distance upstream on the flood tide and then return to almost the same location at low tide but slightly seaward because of the small net movement from river inflow. This movement in response to net flow is known as advection. The repeated movement of water back and forth with the tides results in mixing of water because of turbulence caused by interactions of the water with the channel bottom and sides. This process is known as dispersion. The combination of advection and dispersion interacting within the interconnected channel network of the Delta (Figure 3) result in complex hydrodynamics processes that affect how water and dissolved (e.g., salts) and suspended constituents (e.g., sediment particles) move through the system.

These complexities make it difficult to accurately measure flows within and through the Delta, especially at low inflows. Most studies that include Delta inflow, outflow, and diversions at the pumps as variables utilize the model DayFlow (https://water.ca.gov/Programs/Environmental-Services/Compliance-Monitoring-And-Assessment/Dayflow-Data), which is basically a complex bookkeeping program that uses measured and estimated sources of Delta inflow, diversions at the pumps, and other within Delta sources and losses to estimate net Delta outflow and X2. DayFlow estimates do not always match measured values, especially at low flows (see documentation on Dayflow website). There are now several hydrodynamic models available that can be used to understand the hydrodynamics of the estuary in detail (MacWilliams et al. 2015), but these models are generally used to address specific questions rather than general flow conditions.

Discussions of flow on an annual basis are often in terms of water year and water year type. A water year begins on 1 October of the previous year and ends on 30 September of the current year. So, water year 2020 begins on 1 October 2019 and ends on 30 September 2020. This definition is used to ensure that the wet season is not divided between 2 different years. Water year type classifies years based on river inflows during the water year (https://cdec.water.ca.gov/reportapp/javareports?name=wsihist). Years are classified as wet, above normal, normal, below normal, dry, and critical. A separate water year index is calculated for the Sacramento and San Joaquin Rivers (https://cdec.water.ca.gov/reportapp/javareports?name=wsihist). The Sacramento River index is often given precedence because the Sacramento River generally supplies the bulk of Delta inflow (~80-90%, including flows through Yolo Bypass; Kimmerer 2004). Delta inflow, Delta outflow, and exports have been highly variable since 1960 (Figure 4). The CVP began diverting water in the early 1950s, and the SWP began diverting water in 1968. The first major fish monitoring program began in the estuary in 1959 (summer tow net, STN).

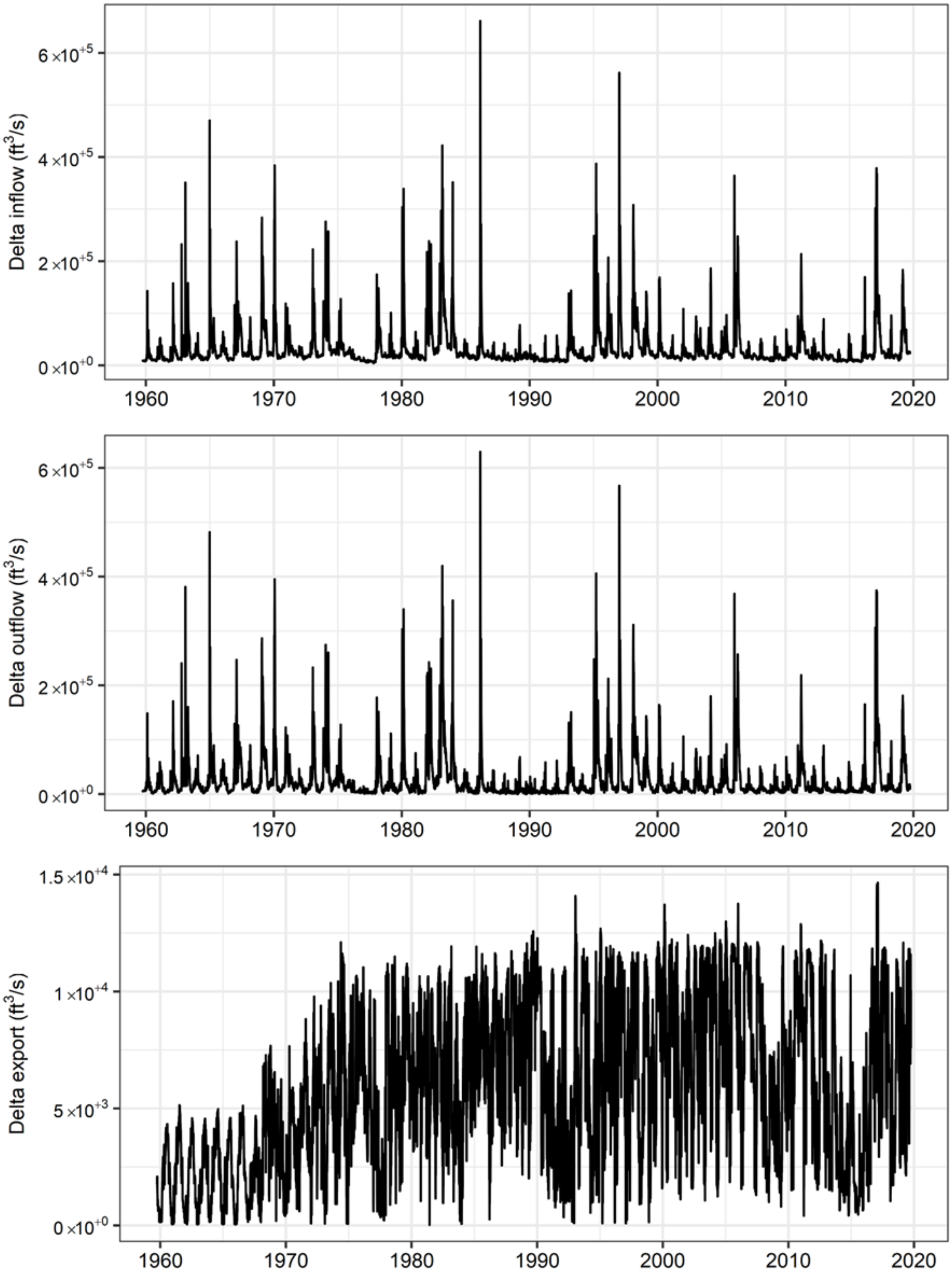

Figure 4. Daily total Delta inflow (A), outflow (B), and diversions (or "Delta exports") (C) for calendar years 1960 to 2020 (Data from DAYFLOW).

Flow management actions for the benefit of Delta Smelt are generally not focused on flow directly but rather on creating habitat conditions favorable for Delta Smelt. The work by Jassby et al. (1995) provided the basis for salinity/outflow standards for the Delta (State Water Resources Control Board 2018) established in 1995 that are intended to provide favorable habitat for several estuarine species, including Delta Smelt. These standards apply to the period from February through June. A similar action specifically intended to use flow to maintain the LSZ in a region believed to provide favorable habitat for Delta Smelt during the fall of wet and above normal years was proposed by the U.S. Fish and Wildlife Service in 2008 (U.S. Fish and Wildlife Service 2008). This action is often referred to as the “fall action” or “fall X2 action.” It has been difficult to link the fall action directly to increases in the abundance of Delta Smelt (FLOAT-MAST 2021), which has made this action more controversial than the State Water Resources Control Board objectives. The Yolo Bypass food web action is intended to supplement the food supply to Delta Smelt based on results from observational studies (Frantzich et al. 2018). Flow through the Toe Drain in Yolo Bypass (Figure 3) is intended to move phytoplankton and nutrients into the northern Delta to supplement the food web utilized by Delta Smelt. Finally, the Suisun Marsh Salinity Control Gate action is intended to provide suitable salinities in Suisun Marsh so that it is accessible to Delta Smelt. Suisun Marsh is believed to provide good habitat for Delta Smelt, and the action has been successfully implemented (Sommer et al. 2020).

Salinity

Estuaries are defined as regions where riverine sources of freshwater meet the ocean; thus, a major physical feature of estuaries is a salinity gradient ranging from freshwater (salinity < 0.5) to salt water (about salinity 35). A dynamic salinity gradient from freshwater to salt water is one of the most characteristic features of an estuary (Kimmerer 2004). A dynamic salinity gradient originates from the mixing of fresh inland water with salty ocean water through tidal dispersion and gravitational circulation (Monismith et al. 2002). Many estuarine-dependent organisms occur in distinct salinity ranges (e.g., Kimmerer 2002a, Feyrer et al. 2015), and the extent and location of water with suitable salinities is thus an important habitat attribute for estuarine organisms. Over the period of available monitoring data, there is no clear long-term trend in salinity levels and their spatial distributions in the estuary. Significant increases and decreases linked to changing flow patterns have been detected for various stations and months (e.g., Jassby et al. 1995, Enright and Culberson 2009, Shellenbarger and Schoellhamer 2011, Cloern and Jassby 2012). For example, summer salinities in the upper SFE tend to be higher during drier water year types because of lower spring flows and earlier intrusion of saline water from San Francisco Bay (Figure 5). The differences between water year types are less obvious in the fall because low summer and fall flows are typical of all water year types, allowing similar levels of saltwater intrusion (Figure 5).

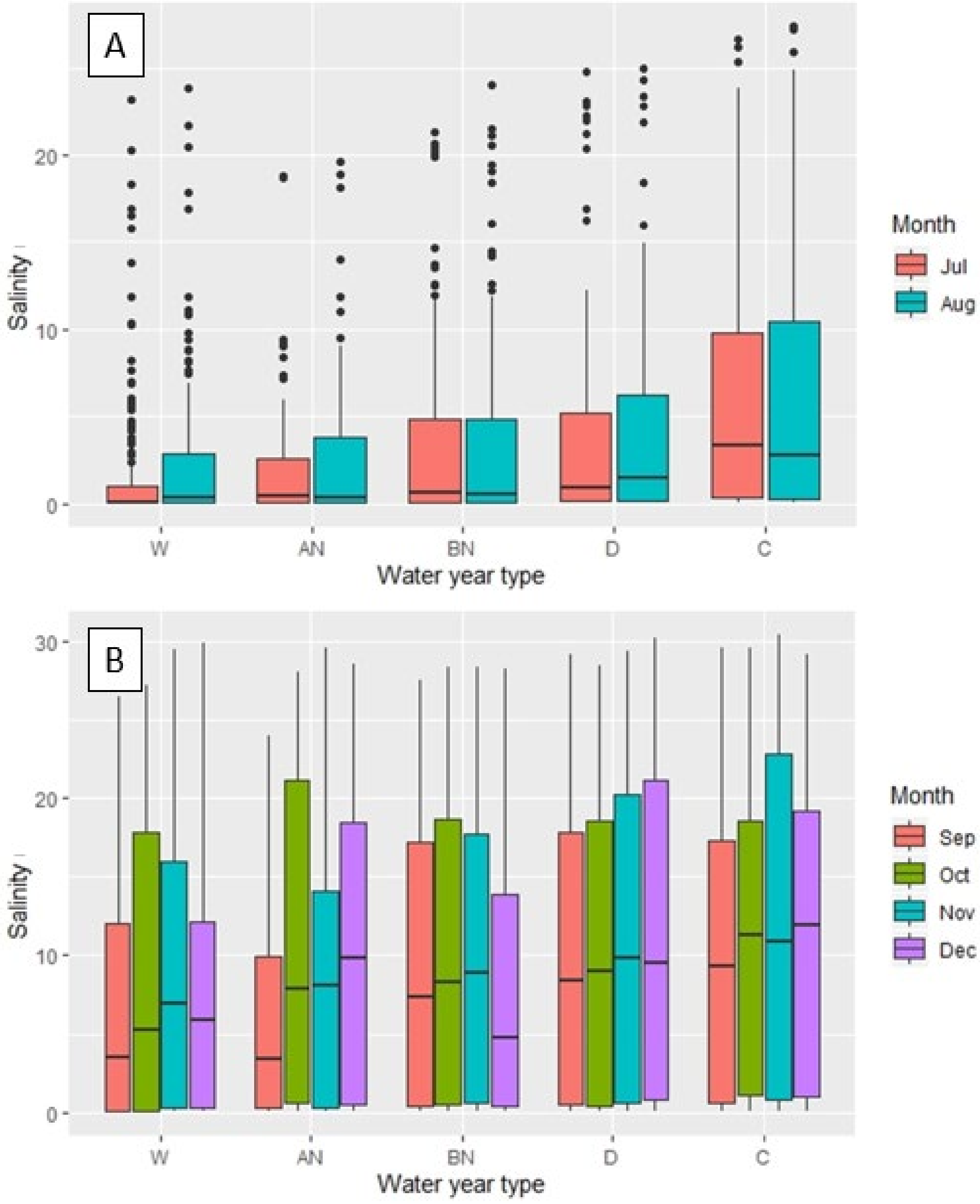

Figure 5. Salinity (in PSU) by water type for A) July and August collected by California Department of Fish and Wildlife Summer Townet Survey and B) in September-December collected by California Department of Fish and Wildlife FMWT at index stations during calendar years 2003-2017. Water Year Type per Sacramento Valley Index (Figure 15 from FLOAT-MAST 2021). Water year designations are as follows: W = wet, AN = above normal, BN = below normal, D = dry, C = critical.

The brackish LSZ is an important region for retention of organisms and particles and for nutrient cycling in many estuaries. In the SFE, the LSZ provides important habitat for numerous organisms including Delta Smelt (Kimmerer 2004, Bennett 2005). In this white paper, we define the LSZ as salinity 1-6 PSU; however, as noted previously, other salinity ranges have been used (Jassby 2008, Kimmerer et al. 2013, IEP-Mast 2015). Also, as noted above, in the SFE, the position of the LSZ is commonly expressed in terms of X2 (Jassby et al. 1995), which represents the approximate center of the LSZ (Kimmerer et al. 2013) (Figure 6).

The X2 index was developed as an easily measured, policy-relevant “habitat indicator.” Its ecological significance for multiple species and processes was established through statistical analyses of biological responses to seasonally or annually averaged X2 values (Jassby et al. 1995) and has since been reaffirmed in additional studies (e.g., Kimmerer 2002a, b, Kimmerer et al. 2009, 2013, Thomson et al. 2010, Mac Nally et al. 2010). There is, however, still much uncertainty regarding the causal mechanisms for the observed biological responses of biota to position of the LSZ. As with all statistically derived functional relationships, biological responses to X2 do not necessarily reflect direct causal relationships, and it is generally recognized that some of the causal mechanisms may not be directly linked to the size and location of the LSZ.

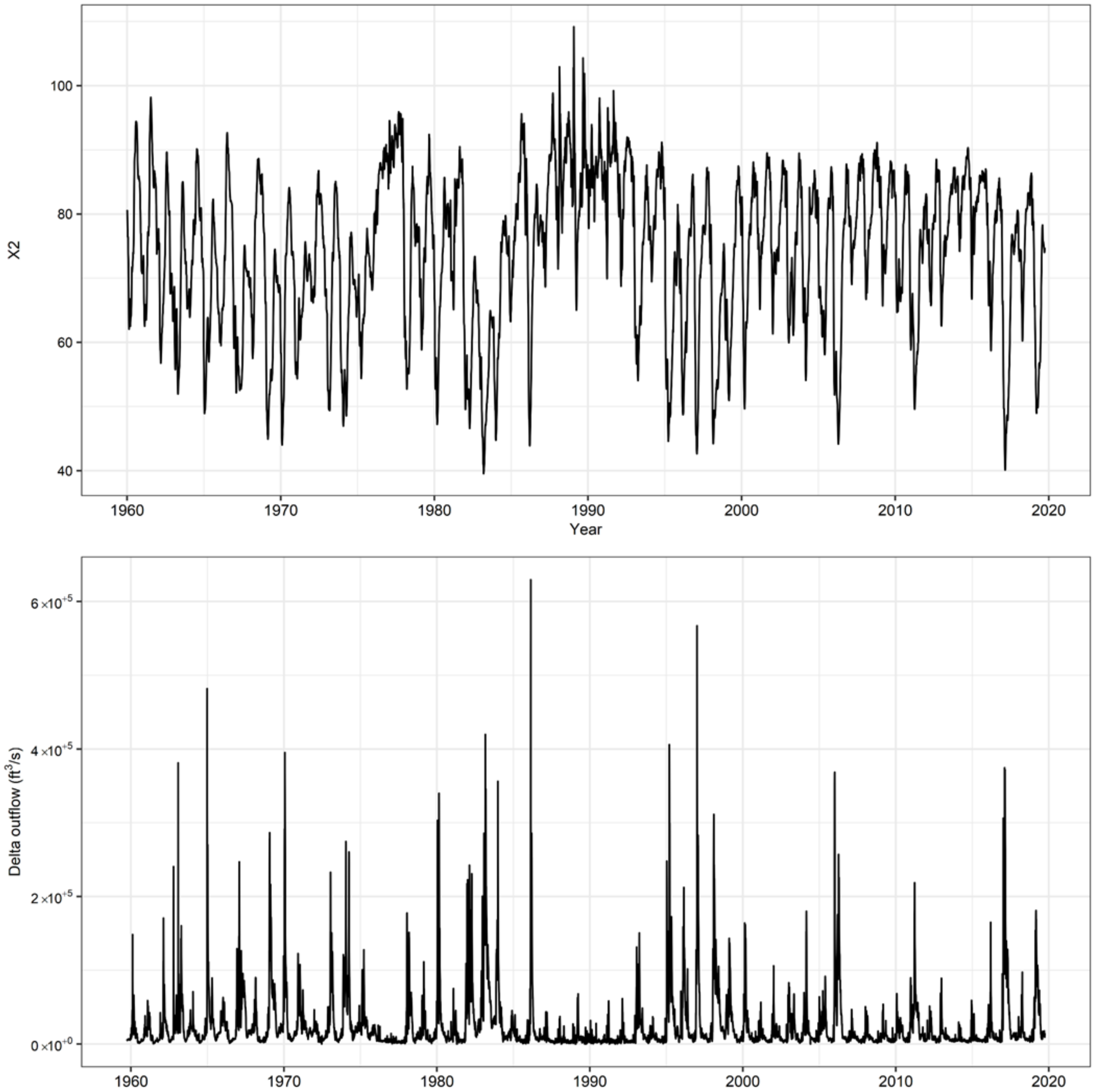

Figure 6. Daily X2 (km) (A), and total Delta outflow (B), from calendar years 1960 to 2020 (Data from DAYFLOW).

The size and location of the LSZ are considered key factors for determining the quantity and quality of low salinity rearing habitat available to Delta Smelt and other estuarine species. LSZ size and location are determined by the interaction of dynamic tidal and river flows with the stationary topography of the region (Kimmerer et al. 2013, IEP-MAST 2015). Three-dimensional hydrodynamic models can produce detailed maps of the distribution of salinity in the SFE under different outflow conditions (MacWilliams and Bever 2018). For example, under low outflow conditions typical of summer and fall months (outflow = 140 $m^3 s^{-1}$, X2 = 85 km), the LSZ is in the western Delta confluence region, including the Sacramento and San Joaquin Rivers upstream of Chipps Island (Figure 7), while under high outflow conditions typical of wet winter months (outflow = 1,440 $m^3 s^{-1}$, X2 = 51 km), the LSZ is much farther west in San Pablo Bay. At intermediate outflows (intermediate X2 = 74 km), it is located east of Carquinez Strait and covers Suisun Bay and parts of Suisun Marsh (Figure 8 and Figure 9).

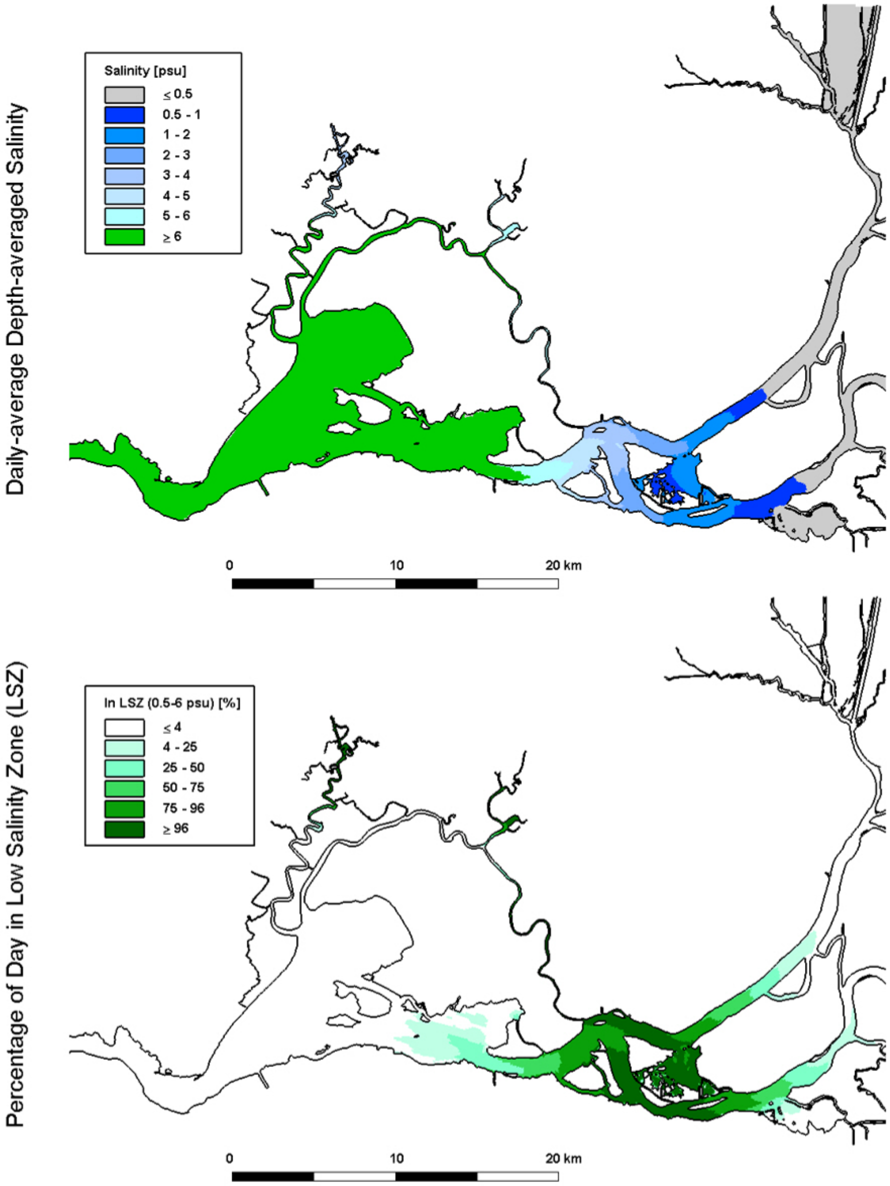

Figure 7. Salinity distribution at low outflow. The upper panel shows the area of the low-salinity zone (4,262 hectares) at X2 = 85 km, when positioned mostly between Antioch and Pittsburg. Connections to Suisun Bay and Suisun Marsh are minimal. The lower panel shows the percentage of day that the low-salinity zone occupies different areas (from IEP-MAST 2015).

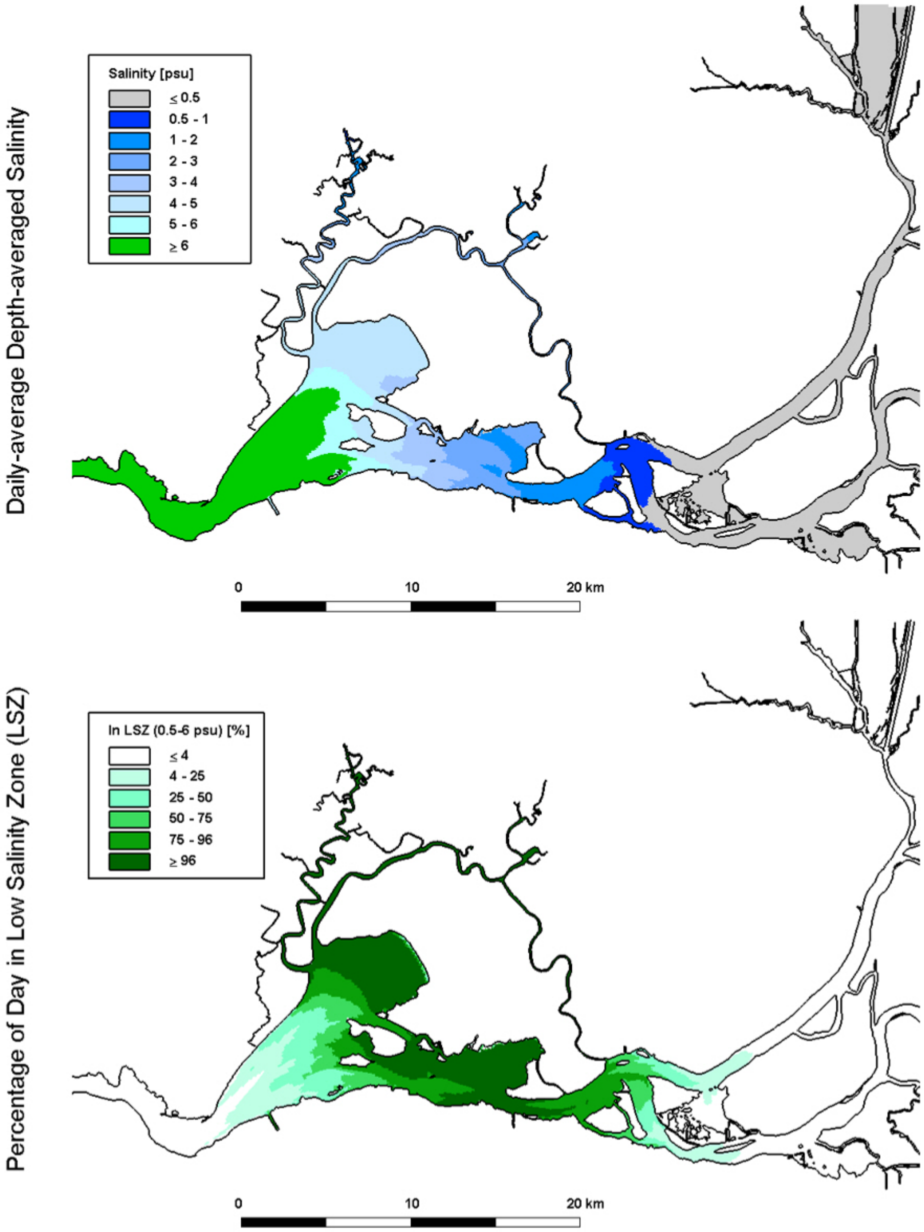

Figure 8. Salinity distribution at intermediate outflow. The upper panel shows the area of the low-salinity zone (9,140 hectares) at X2 = 74 km (at Chipps Island). The lower panel shows the percentage of day that the low-salinity zone occupies different areas (from IEP-MAST 2015).

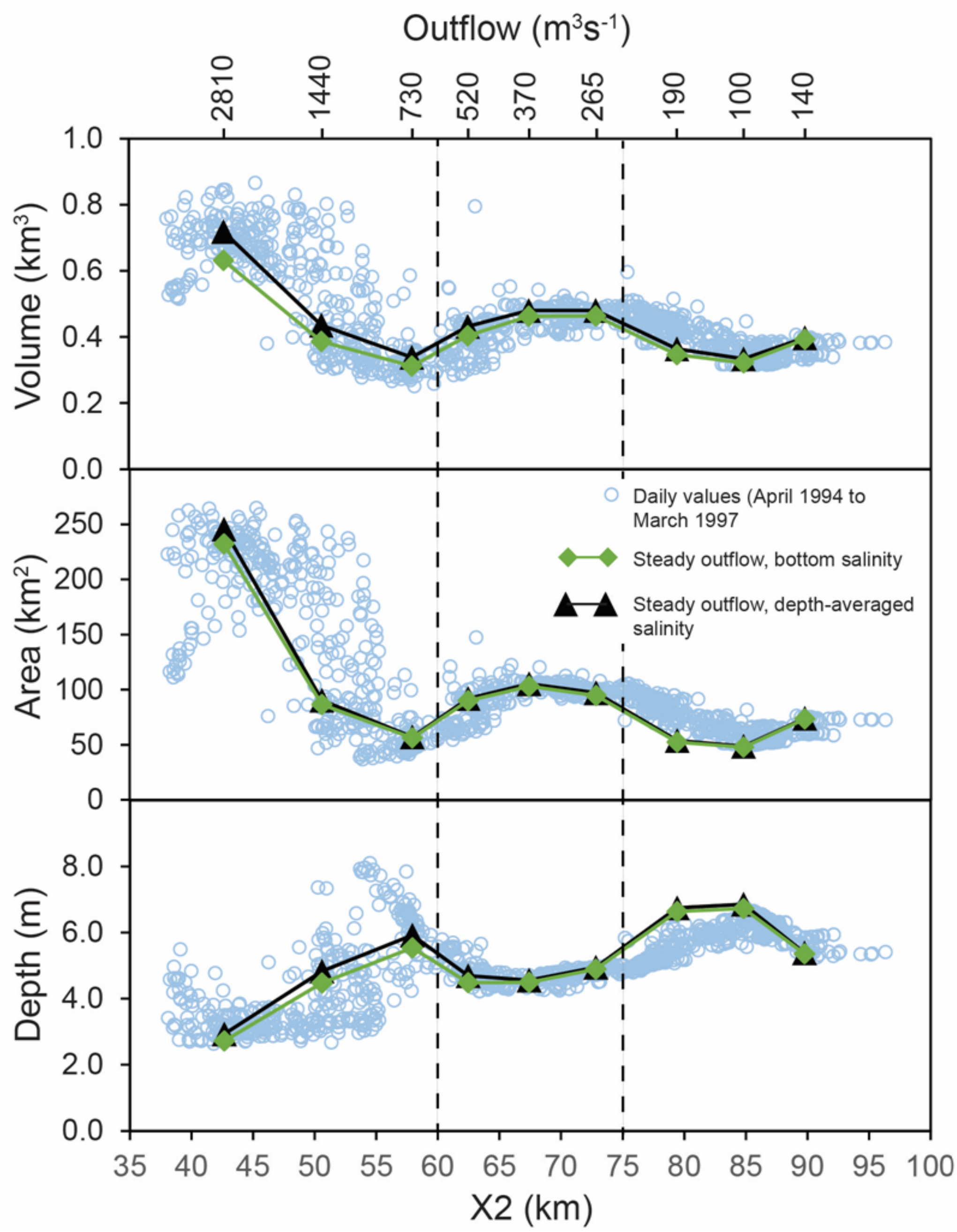

Figure 9. Modeled volume, area, and depth of the low salinity zone (salinity 0.5 to 6 PSU) at various values of X2 for nine steady state values of outflow using bottom salinity (green diamonds) and depth-averaged salinity (black diamonds) and for daily values based on variable values from April 1994 through March 1997 (blue circles) (modified from Kimmerer et al. 2013). The top axis gives the Delta outflow corresponding to the 9 steady state scenarios examined by Kimmerer et al. (2013).

Most of the scientific and management attention has focused on the LSZ and X2 from late winter to early summer (February-June) depending on the species of interest, but in recent years, the LSZ and X2 during the fall months (i.e., fall X2 action) has also received considerable scientific and policy attention. Annual abundance indices of several estuarine fish and invertebrate species have a negative relationship with February-June X2, meaning that abundance indices increase when X2 and the LSZ are more westward and Delta outflow is higher in the late winter and spring months (Jassby et al. 1995, Kimmerer 2002a, Kimmerer et al. 2009). Delta Smelt summer abundance indices have a significant relationship with prior fall X2 and fall abundance (U.S. Fish and Wildlife Service 2008, Mount et al. 2013). Changes in spring and fall position of the LSZ have been linked to long-term fish declines in the SFE (Thomson et al. 2010, Mac Nally et al. 2010).

Delta Smelt are found in the estuary at salinities up to 18 PSU (Bennett 2005) but are most common in the LSZ (Moyle et al. 1992, Sommer and Mejia 2013, Feyrer et al. 2007, Kimmerer et al. 2013, IEP-MAST 2015). Physiological experiments have shown Delta Smelt can survive in full strength sea water for a short period (Komoroske et al. 2014, 2016); however, salinities within the LSZ range seem to be optimum (Hasenbein et al. 2013, Komoroske et al. 2016). Delta Smelt is unusual compared to most other fishes in the estuary because it is a brackish water specialist, restricted largely to the low-salinity zone. Most other species are either freshwater or saltwater residents that can tolerate some level of brackishness, such as Largemouth Bass (*Micropterus salmoides*) and Starry Flounder (*Platichthys stellatus*), respectively, or generalists that can tolerate the full range of salinity, such as Rainbow Trout (*Oncorhynchus mykiss*) and Striped Bass (Moyle 2002).

Early descriptions of Delta Smelt life history describe them as a brackish water species that migrated to freshwater in the winter and spring to spawn (Moyle et al. 1992, Bennett 2005, Sommer et al. 2011). Subsequent work has shown Delta Smelt life history to be more complex. Based on otolith chemistry, it has been shown that Delta Smelt can complete their life cycle in freshwater and that spawning can take place in brackish water as well as freshwater (Hobbs et al. 2019a). However, the “traditional” life cycle of freshwater spawning followed by movement of juvenile fish into the LSZ (Dege and Brown 2004) appears to be the dominant strategy in the current population (Hobbs et al. 2019a). The majority of Delta Smelt appear to rear in the LSZ in the summer and fall; however, as already noted, some portion of the population rears in freshwater (Feyrer et al. 2007, Nobriga et al. 2008, Hobbs et al. 2019a).

How the Delta Smelt life cycle interacts with the recent salinity regime to determine population abundance remains a topic of debate. The recruitment success of Longfin Smelt (*Spirinchus thaleichthys*) and age-0 Striped Bass increases linearly with more westward positions of the LSZ during spring (Jassby et al. 1995, Kimmerer 2002a). In contrast, the relationships of annual Delta Smelt indices with spring LSZ position are more complex. We observe here that the current low abundance of Delta Smelt makes it difficult to reach conclusions about the importance of the size and location of the LSZ to the Delta Smelt population. The most recent year when the Delta Smelt population increased (2011, see Brown et al. 2014) was a wet year, but other recent wet years (2006, 2017, and 2019) when the LSZ should have been favorable for Delta Smelt did not result in a larger population (FLOAT-MAST 2021).

The upper SFE has undergone numerous changes that may have degraded the benefits once provided by the LSZ (Brown et al. 2016a, Moyle et al. 2016). The upper SFE has exhibited step declines in abundance of several pelagic species in the early 2000s, including Delta Smelt, which are likely related to changing conditions not necessarily directly linked to LSZ position (Sommer et al. 2007, Thomson et al. 2010, Mac Nally et al. 2010). Changes in the size, location, and dynamics of the LSZ likely interact in complex ways with other changes, such as changes in sediment and nutrient loadings and resulting turbidity and nutrient dynamics and their effects on Delta Smelt. For example, LSZ position affects recruitment of the invasive clam *Potamocorbula amurensis*, which may in turn affect phytoplankton and zooplankton biomass, size, and production (Thompson 2005, Winder and Jassby 2011, Brown et al. 2016a), and has likely affected fish-X2 relationships (Kimmerer et al. 2002a).

Despite the uncertainty regarding the mechanistic response of the Delta Smelt to position of the LSZ, there is still interest in management actions that are meant to affect the distribution of salinity. Using outflow to control the location of the LSZ in the fall is included in both the 2008 and 2019 Biological Opinions (U.S. Fish and Wildlife Service 2008, 2019). As previously noted, a positive response to LSZ position was noted in in the wet year of 2011 (Brown et al. 2014) but not in the wet year of 2017 with similar salinity conditions (FLOAT-MAST 2021). This difference in response was partially attributed to warm summertime water temperatures in 2017 that likely discouraged Delta Smelt from taking advantage of the freshwater and low-salinity habitat created by the action. A more focused action to change salinity to create favorable Delta Smelt habitat in Suisun Marsh was successful in creating the desired low-salinity habitat, and a few Delta Smelt were captured at nearby monitoring stations (Sommer et al. 2020). The close monitoring of these and similar actions, meant to manage the salinity field, would provide valuable insights of the benefits provided to Delta Smelt and other organisms.

Water temperature

Water temperature is fundamental to aquatic ecosystem health and function and directly influences biological, physical, and chemical processes. For aquatic organisms, water temperature influences metabolic rates and life histories, dissolved oxygen levels, primary productivity, and cycling of nutrients and other chemicals (Vannote and Sweeney 1980, Poole and Berman 2001, Null et al. 2013). Water temperature is an important variable for ectothermic (“cold-blooded”) animals, including all fishes and invertebrates in the SFE. In the most extreme case, when water temperature exceeds the thermal tolerance of an organism, the organism will die. Temperatures within the thermal tolerance of an organism control the rate and efficiency of many physiological processes, including activity, digestion, growth, reproductive development, and reproductive output.

Long-term temperature records from selected sites in the upper SFE show substantial seasonal and daily fluctuations in water temperature (Kimmerer 2004). While daily variations are evident and likely important to organisms, seasonal variations are much greater (Wagner et al. 2011). Median water-surface temperatures across all stations monitored by the Interagency Ecological Program (IEP) Environmental Monitoring Program (EMP; Figure 10) from 1975-2012 range from 9°C in January (minimum: 6°C) to 22°C in July (maximum: 28°C). There are also clear regional variations in water temperature (Figure 11). In July and August, the hottest summer months, water temperatures are usually highest at monitoring stations in the south Delta (average 23-26°C, maximum 28°C), lower at stations in the northern and western Delta (average 21-23°C, maximum 25°C), and lowest at stations in Suisun and San Pablo Bays (average 19-21°C, maximum 24°C). In January, the coldest winter month, average water temperatures are uniformly below 10°C in the upper SFE but above 10°C in San Pablo Bay.

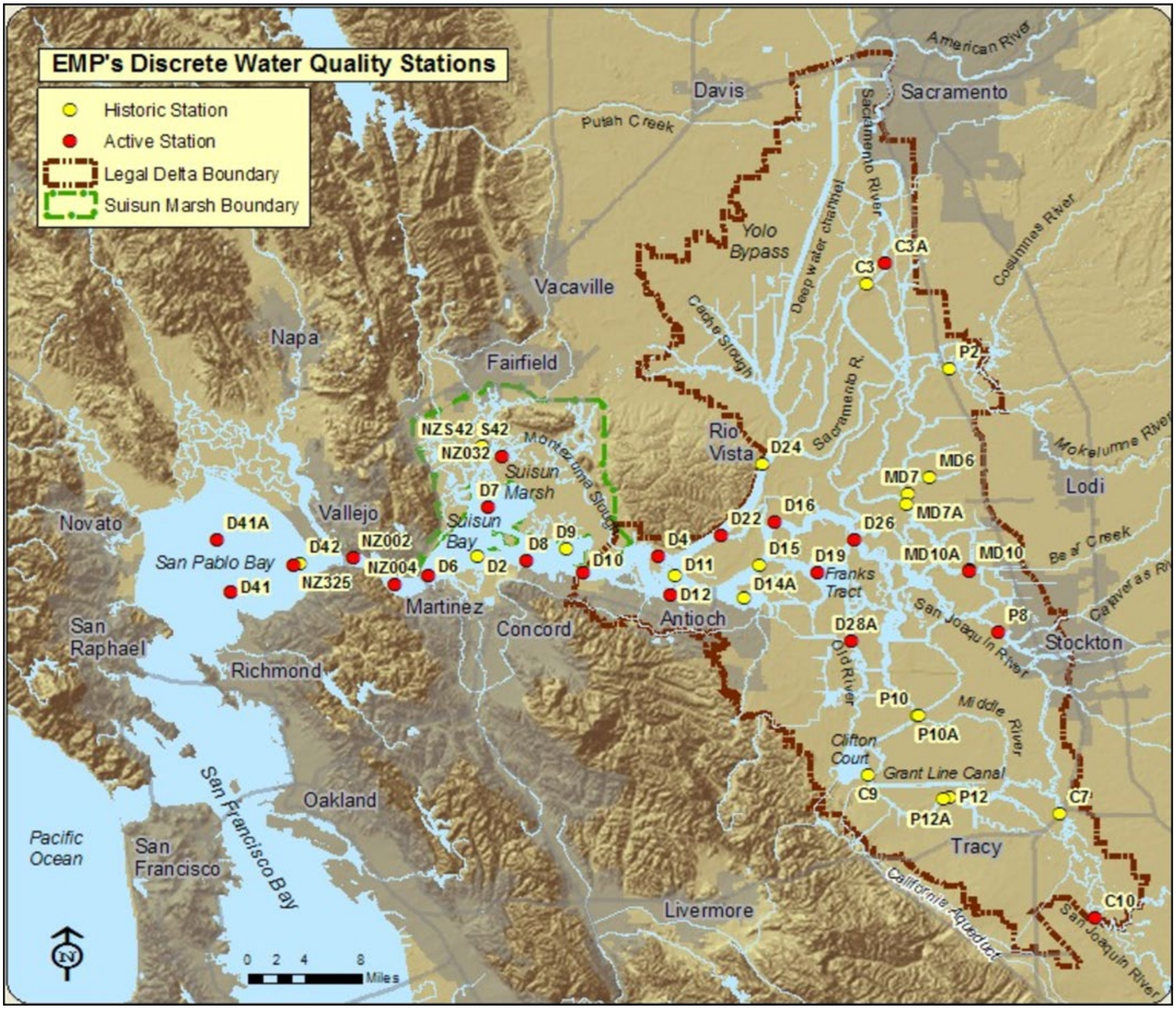

Figure 10. Locations of active and historical IEP Environmental Monitoring Program (EMP) sampling stations.

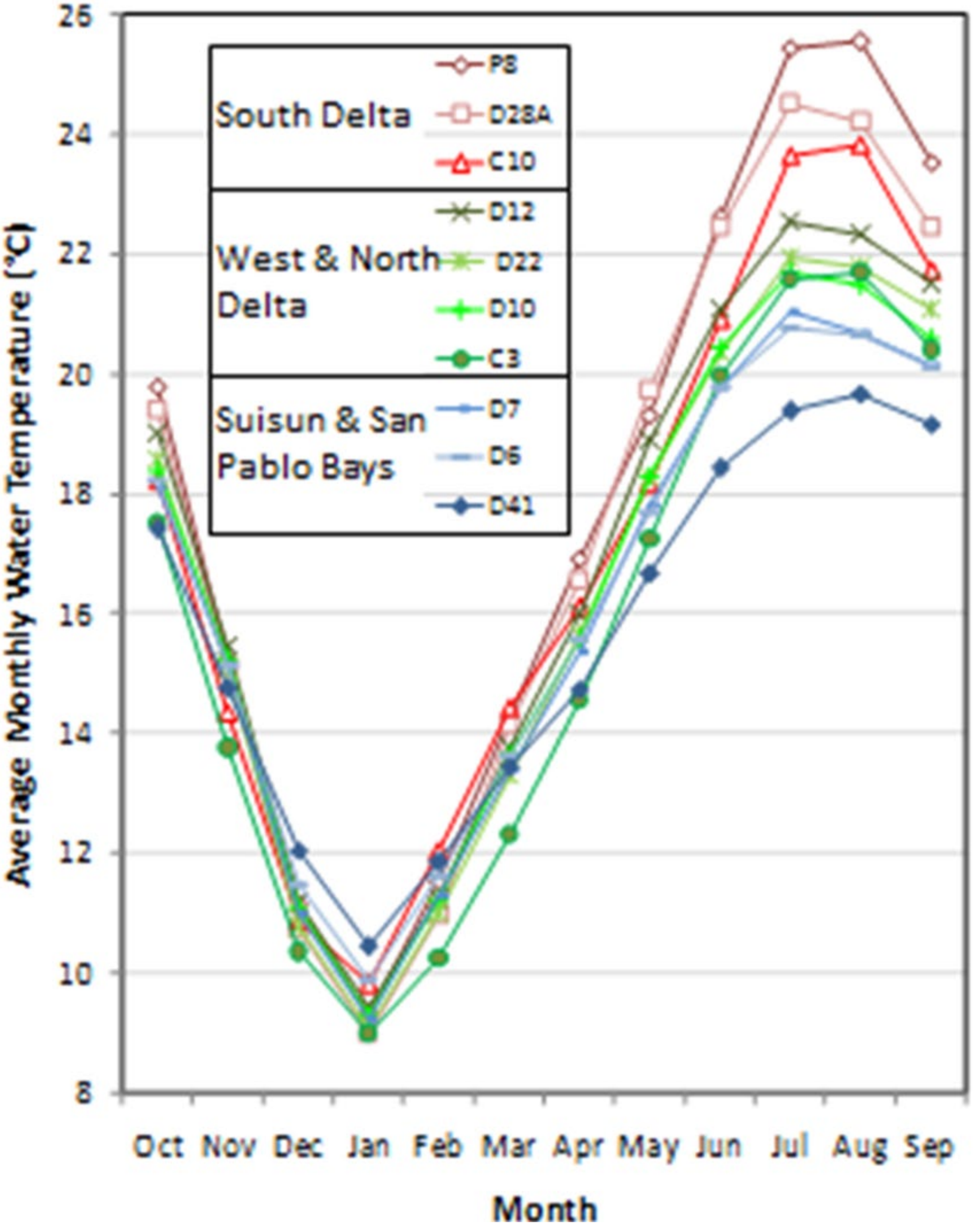

Figure 11. Average monthly temperature for stations monitored by the Environmental Monitoring Program from 1975-2012 (from IEP-MAST 2015). See Figure 9 for station locations.

There is currently little evidence for long-term trends in water temperatures in the upper SFE, although with climate change, increases are expected over the course of the current century (Cloern et al. 2011, Wagner et al. 2011, Brown et al. 2013, 2016b). Spring (March-June) water temperatures during 1996–2005 at IEP EMP water quality monitoring stations in the Delta increased by about 0.2°C per year, but a similar trend was not apparent for the longer-term data record from 1975-2005 or for stations in Suisun Bay (Jassby 2008). These findings are similar to the results of Nobriga et al. (2008) who found no long-term (1970-2004) trends in temperature data collected during summer fish monitoring surveys in the upper SFE. Nobriga et al. (2008) also noted that the long-term (1970-2004) mean July water temperature at STN fish monitoring stations in the southern region of the Delta is 24°C, with current mid-summer temperatures often exceeding 25°C. This temperature pattern agrees with average monthly EMP data from 1975-2012, which show July and August water temperatures at a monitoring station located in Old River (station D28A) and in the San Joaquin River near the Port of Stockton (station P8) of more than 24°C and 25°C, respectively (Figure 11).

In tidal systems, water temperature at a particular location is determined by the interaction between atmospheric forcing (e.g., air temperature and wind), tidal dispersion, and riverine flows (i.e., advection) across the estuarine landscape (Monismith et al. 2009). In particular, estuarine water temperature is driven by heat exchange at the air–water interface and mediated by tidal and riverine flow dynamics and estuarine geomorphology (Enright et al. 2013). Wagner et al. (2011) found that regional weather patterns, including air temperature and insolation (sunlight), are the primary drivers of water temperature variations in the upper SFE at fixed locations. Water flow and interaction with the stationary topography of the system also affects water temperature in the SFE, especially over shorter time scales and at smaller spatial scales. For example, Enright et al. (2013) showed that interaction of tides with tidal marsh topography can have a mediating effect on water temperature in tidal sloughs and on thermal variability at smaller spatial scales. Wagner et al. (2011) showed that high winter and spring inflows from snowmelt can temporarily lower water temperatures. Greenberg et al. (2012) found that the presence of riparian vegetation on Delta levees lowers insolation by about 9% compared to a hypothetical situation without vegetation and suggested that riparian vegetation thus contributes to locally cooler water temperatures. This finding suggests that, at least to some degree, water temperature can be managed locally and for short periods. Over larger scales, however, these types of locally mediated effects are overwhelmed by the effects of air temperature and insolation.

Air temperature and insolation in the upper SFE are correlated with each other (Wagner 2012) and vary strongly with proximity to the Pacific Ocean because of the contrasting climate regimes prevailing in inland central California and the central California coast. While inland central California has a large annual air temperature range with hot, dry, sunny summers and cool, wet, and often foggy winters, the central California coast has a smaller annual air temperature range with cooler and often foggy summers and milder winters (Conomos et al. 1985). The upper SFE has a transitional climate with greater spatial and temporal variability in air temperature than either the coastal or the inland regions (Whipple et al. 2012). This variability is due to the interplay of the dynamic air masses from these regions across the stationary estuarine topography. In the summer, this interplay often results in strong afternoon winds from the ocean locally known as the “Delta breeze.” These onshore winds usually advance into the western and central Delta and, depending on the depth of the marine layer, often also into its marginal areas. In the Delta, these southwest to northwest winds can persist throughout the night and into the next morning and produce a marked decline in water temperature. In the morning, this low is often followed by rapid warming once the winds subside and the high temperature inland air masses return to dominance (National Weather Service 2003). In the winter, ocean winds are weak and, during calm periods, cold air flows from the mountains into the estuary. This cold air results in the formation of dense, overnight, near-surface fog locally known as “tule fog.” These calm and foggy periods are interrupted by winter storms. Many of these storms arrive from the south and southeast as “atmospheric rivers” that can often produce gale force winds and heavy rains lasting several days (Conomos et al. 1985, Dettinger and Ingram 2013).

The large variability in air temperature in the Delta is reflected by the larger annual variability in water temperature measured from 1998-2002 at continuous monitoring stations in the interior Delta compared to stations farther upstream or downstream (Wagner et al. 2011). This high variability is also apparent in monthly water temperature data collected by the IEP Environmental Monitoring Program since 1975 (Figure 11). From 1975 to 2012, annual fluctuations in average monthly water temperature were greatest at stations in the south Delta (14-16°C), smaller at stations in the northern and western Delta (12-13°C), and lowest at stations in Suisun and San Pablo Bays (9-12°C). Jassby (2008) reported that maximum daily air temperature could explain almost half the variability in maximum daily water temperature at the continuous monitoring station at Antioch during the summer months. The relationship between air and water temperature was also strong in all other months except January.

There is also consistent temperature variability within the Delta, particularly during the summer. The combination of tidal dispersion of cooler more saline water from San Francisco Bay and the differences in air temperature described above result in cooler water in the western reaches of the upper SFE (FLOAT-MAST 2021). This interaction can be seen when water temperature is considered for different salinity zones (Figures 12 and 13). During July and August, freshwater regions are always warmer than the low salinity zone and the more saline zone (salinity >6). These high temperatures also exceed 22°C, which is likely stressful for Delta Smelt (see below). The LSZ and more saline zone are more similar in temperature with the LSZ sometimes slightly warmer, but temperatures were generally not considered stressful. This gradient begins to moderate in September and is largely gone by November (Figure 13). These temperature patterns appear to have little relation to water year type (Figures 12 and 13).

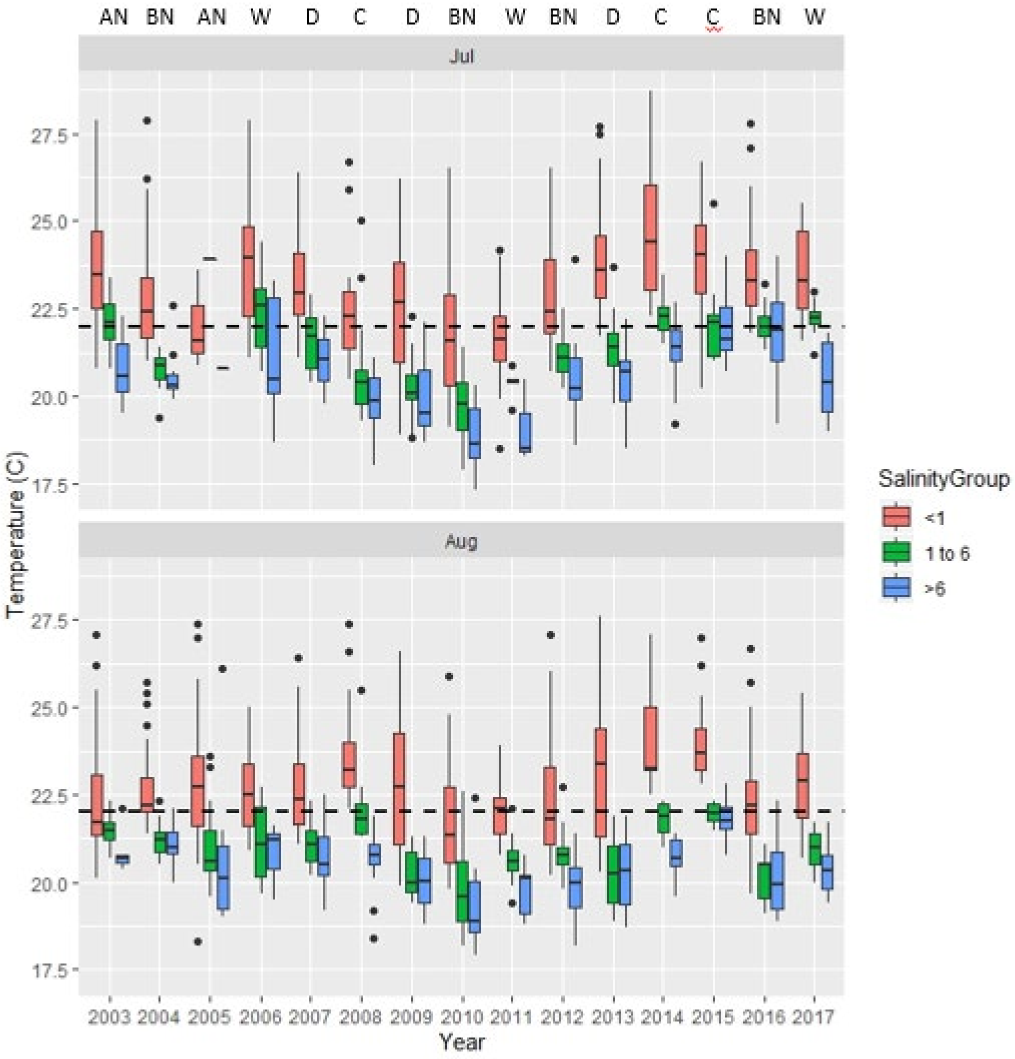

Figure 12. Water temperature at sites with salinity <1, 1-6 PSU , and ≤ 6 PSU for (A) July and (B) August collected by California Department of Fish and Wildlife Summer Townet Survey at index stations during 2003-2017. Water Year Type per Sacramento Valley Index across top of figure. The dashed line designates 22°C (Figure 17 from FLOAT-MAST 2021).

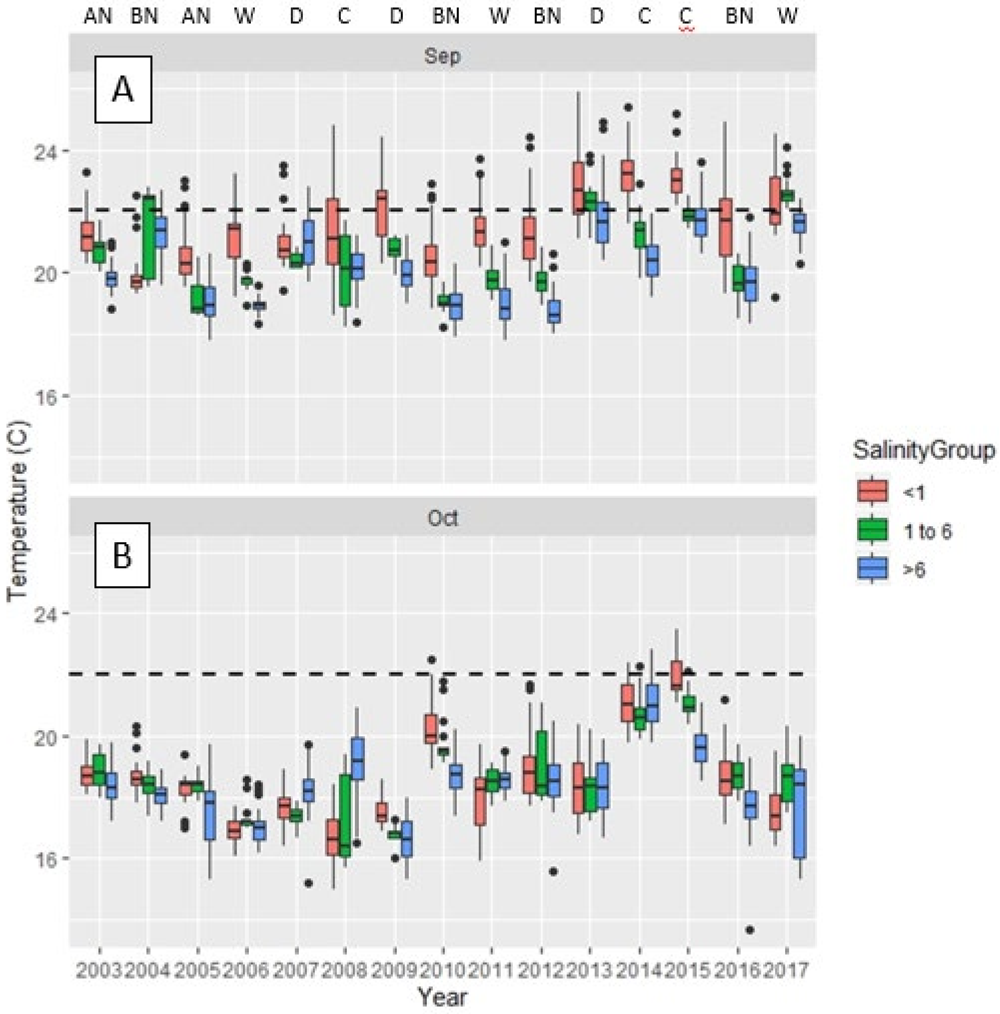

Figure 13. Water temperature at sites with salinity <1, 1-6 PSU, and ≤ 6 PSU for (A) September and (B) October collected by California Department of Fish and Wildlife Fall Midwater Trawl Survey at index stations during 2003-2017. Water Year Type per Sac Valley Index across top of figure. The dashed line designates 22°C (Figure 18 from FLOAT-MAST 2021).

Wagner et al. (2011) and Wagner (2012) developed simple regression models for predicting water temperature at fixed temperature monitoring stations in the SFE using only air temperature and insolation on the day of interest and the water temperature from the previous day. Water temperature from the previous day accounts for both previous air temperature and the sources of water to the site, including advective flow from rivers or dispersive flow from more downstream reaches of the SFE. Each model had a different set of coefficients because of the differing influences of incoming river water and tidal exchange with San Francisco Bay. For stations with greater than 1 year of calibration data, model R^2 for daily average temperature exceeded 0.93, indicating that water temperature was highly predictable within the limits of the calibration data sets. High winter and spring flows were responsible for the largest divergences of the model outputs from measured temperatures.

The simple statistical models for water temperature developed by Wagner et al. (2011) and Wagner (2012) should be used with caution because they only predict temperature at the site of the recording instrument and do not explicitly account for mechanistic heat exchange. The analyses therefore do not incorporate the possible effect of site-specific features such as shading by riparian vegetation (Greenberg et al. 2012) and cannot provide predictions for locations with insufficient monitoring data to develop a model. Similarly, there are lateral and vertical variations in temperature on daily time scales (Wagner 2012) that could be important to organisms; however, these differences appear to be small. For example, differences between observed surface and bottom temperatures rarely exceed 2°C and are usually less than 1°C (Brown et al. 2016b, FLOAT-MAST 2021).

In contrast to statistical modeling, which produces site-specific results, water temperature across regions can be modeled with computation-intensive deterministic simulation models. Such models use energy budgets to predict water temperature (Vroom et al. 2017, MacWilliams and Bever 2018). Simple stochastic models are also possible. Like the other types of models, these stochastic models generally rely on the relationship between air and water temperature (Caissie 2006, Null et al. 2013). We are not aware that these types of models have been developed – or tested – for the SFE.

Upper temperature limits for juvenile Delta Smelt survival are based on field observations and laboratory studies. Interpretation of the laboratory results is somewhat complicated as temperature tolerances can be affected by various factors including acclimation temperature, salinity, turbidity, and feeding status. Based on the critical thermal maximum, CTmax, juvenile wild Delta Smelt acclimated to 17°C could not tolerate temperatures higher than 25.4°C (Swanson et al. 2000). However, consistently higher CTmax were estimated for juvenile Delta Smelt acclimated to 11.9, 15.7 and 19.7 °C, (27.1, 28.2 and 28.9 °C, respectively; Komoroske et al. 2014), which corresponded closely to the maximum water temperatures at which Delta Smelt were captured in the Summer Townet and Fall Midwater Trawl surveys. Swanson et al. (2000) used wild-caught fish, while Komoroske et al. (2014) used hatchery-reared fish, which may have contributed to the differences in results. Komoroske et al. (2014) also found differences in temperature tolerances among life stages with younger fish more tolerant of high temperatures than adult fish. Based on the STN (Nobriga et al. 2008) and the 20-mm Survey (Sommer and Mejia 2013), most juvenile Delta Smelt were predicted to occur in field samples when water temperature was below 25°C.

Fishes prefer certain temperatures that are optimal for growth and survival (Jobling 1997) and can exhibit behaviors that enable them to find and utilize these preferred temperatures (Jobling 1997). Presumably, the low occurrence of Delta Smelt from field samples noted in the STN (Nobriga et al. 2008) and the 20-mm Surveys (Sommer and Mejia 2013) at warmer temperatures is due primarily to fish leaving the warmer regions rather than remaining and eventually dying. There are several pieces of information suggesting that Delta Smelt do disperse at warmer temperatures. Based on otolith data, Hobbs et al. (2019b) estimated that Delta Smelt begin dispersing out of warming areas when temperatures reach 20°C. In laboratory experiments, Davis et al. (2019) found that at 21°C, Delta Smelt increased swimming velocity, decreased turning angle, and exhibited larger inter-individual distances compared to fish tested at 17°C and at fluctuating temperature between 17 and 21°C. These behaviors are consistent with dispersal behavior away from unsuitable conditions.

Even assuming Delta Smelt will disperse to seek more appropriate water temperatures, it is unlikely that all individuals will be able to find an area with optimal water temperatures and, even if they do, other environmental conditions (e.g., food availability, salinity) may not be optimal at that location. Thus, it is important to understand what happens at suboptimal temperatures. In this context, it is important to consider bioenergetics, which is simply how an organism partitions energy from the food it eats to meet the energetic demands of survival. In general, the total metabolic rate of a fish will increase with temperature to an optimal temperature at which, given unlimited food, there is the maximum ability to grow and develop reproductive products (eggs or sperm) in addition to maintaining the basal metabolic rate required for survival, which also increases with temperature (Houde 1989, Hartman and Brandt 1995). As temperature increases beyond the optimum, metabolic rate continues to increase, but physiological processes become less and less efficient, and more energy is required just to meet the basal metabolic rate of the organism. Eventually, the metabolic rate begins to decline as temperatures approach the physiological limits of the organism, and the basal metabolic rate can no longer be maintained. Recent studies indicate that, in the wild, optimal Delta Smelt growth is at temperatures less than 20°C (Hobbs et al. 2019c). Growth then declines as water temperature continues to increase. FLOAT-MAST (2021) defined temperatures from 20-22°C as the beginning of bioenergetic stress and 22-24°C as moderate to severe bioenergetic stress. Beyond about 24°C, growth is minimized so the fish can compensate for increased stress on physiological systems (Komoroske et al. 2016).

Water temperature can also have important effects on the phenology of fishes. In this context, phenology is the study of the timing of life history events in relation to changes in season and climate. Brown et al. (2016b) studied phenology in the context of climate change, but the concepts apply equally well to the contrast of any warm and cold year. The basic idea is that the Delta Smelt life cycle can be affected by temperature at several points that can affect the reproductive success of the population (Figure 14). The size of female Delta Smelt has a strong effect on the number of eggs they produce (i.e., fecundity) in a clutch (Damon et al. 2016); therefore, the length of the maturation window, when growth potential is high, can have an important effect on the final size of spawning fish. The length of the spawning window is important for several reasons. First, both laboratory and wild populations of Delta Smelt can produce multiple clutches during the spawning season given sufficient time to develop additional mature eggs after the previous spawning event (Lindberg et al. 2013, Damon et al. 2016, Kurobe et al. 2016). The spawning window temperature range has been variously defined as: 15-20°C by Bennett (2005); 7-15°C by Wang (1986); 12-15°C by Baskerville-Bridges et al. (2004b); and 9-18°C by Damon et al. (2016). The second important function of a longer spawning window is to allow recruitment of multiple cohorts into the population rather than the population depending on a limited number of cohorts from just a few spawning events (Bennett 2005).

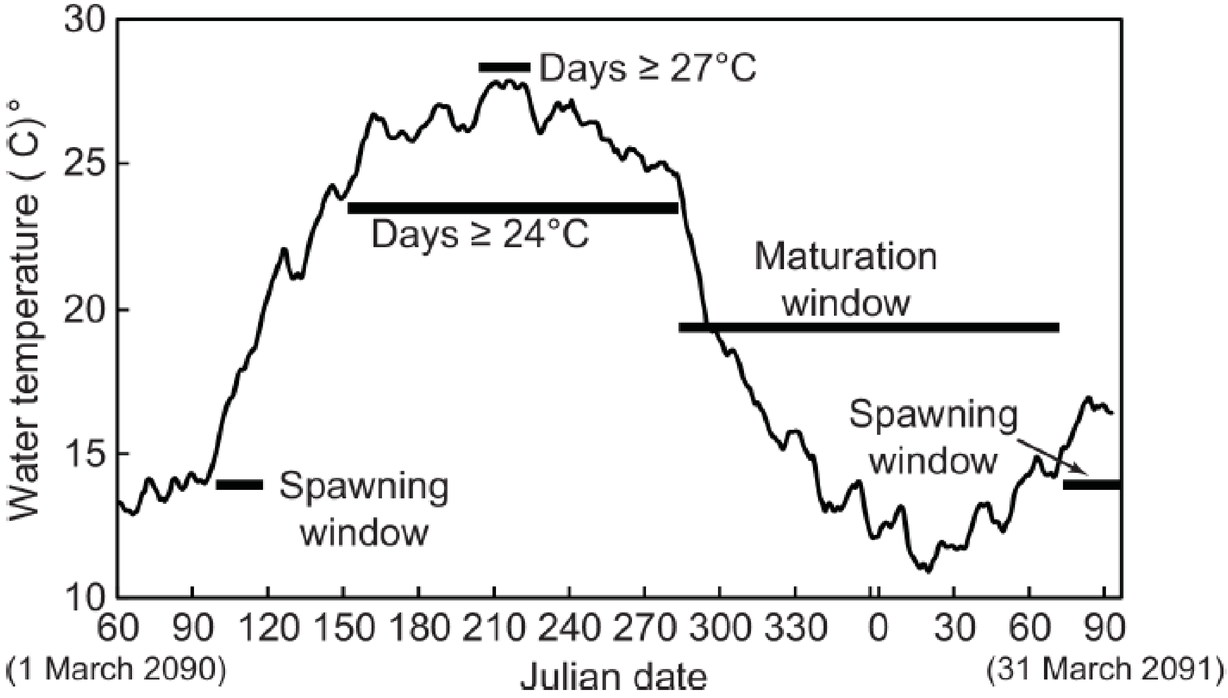

Figure 14. A conceptual view of Delta Smelt development in terms of seasonal water temperature. Growth can be limited by warm temperatures (Days ≥ 24°C) during the summer and early fall. Fish increase in size and become reproductively mature during the maturation window. Females then spawn one or more clutches of eggs depending on the length of the spawning window (modified from Brown et al. 2016b).

Water temperature can strongly influence hatching success of eggs. Bennett (2005) reported that optimal hatching success and larval survival were estimated to occur at 15–17°C based on studies conducted at 10, 15, and 20°C. The data indicated that as incubation and early rearing temperatures increased, size at hatching and size at first feeding linearly decreased, possibly because basal metabolism of the developing embryo used more energy, leaving less for growth. Fish that hatch relatively late in the season may experience high temperatures at a small size, which may reduce larval survival by several possible mechanisms. First, small size would limit the size of food items that the larvae could ingest because of smaller mouth size (see Nobriga 2002). Temperature may also affect food type and availability as discussed below. Second, small larvae are likely vulnerable to a larger range of predators for a longer period compared to larger larvae (e.g., 'stage duration hypothesis'; Anderson 1988). Third, these fish could be potentially more vulnerable to transport toward the CVP and SWP export facilities, when Old and Middle River (OMR) flow restrictions are lifted.

As explained above, higher water temperatures increase energetic requirements and thus the food requirements of fish. To meet the increased need for food, it is possible that Delta Smelt spend more time foraging during the day. Since greater foraging time during the day likely increases visibility to predators, and those predators would also increase their foraging rates at higher temperatures, the encounter rate of Delta Smelt and their predators would likely increase at higher water temperatures. The net effect could be an increase in Delta Smelt predation risk (e.g., Walters and Juanes 1993). High temperatures can also decrease antipredator behavior, as described for Sacramento River Chinook Salmon (Marine and Cech 2004). In other words, the fish may make a behavioral choice to feed, grow, and become less vulnerable to predators as rapidly as possible, even though the short-term predation risk might increase.

The same tradeoffs between feeding and predation risk may persist through the warmer months and into early fall but become less likely as the season progresses into late fall and winter. However, that predation risk is also influenced by a complex suite of other factors such as turbidity, life stage, and proximity to predator habitat, so the level of risk to Delta Smelt cannot be determined.

In addition to direct effects on Delta Smelt physiology and behavior, water temperature may affect their tolerance to other habitat attributes, such as resistance to disease and contaminants (Brooks et al. 2012). The responses to contaminants can vary depending on the type of contaminant. For example, low temperatures can decrease the toxicity of organophosphate insecticides, but increase the toxicity of pyrethroid and organochlorine insecticides (Harwood et al. 2009).

Another possible indirect effect of higher water temperatures is that they may promote harmful agal blooms (HABs) (Lehman et al. 2005), which may degrade Delta Smelt habitat quality in the summer and early fall (IEP-MAST 2015, FLOAT-MAST 2021). In the Delta, Lehman et al. (2013) found that blooms of the harmful cyanobacteria (blue-green algae) *Microcystis aeruginosa* required a water temperature of at least 19°C for initiation. Other drivers of HABs and the possible effects of HABs are discussed more fully in a separate white paper. The combination of large seasonal and regional water temperature variability in the SFE and substantial direct and indirect effects of water temperature for all life stages of Delta Smelt means that this variable should be considered one of the most important habitat attributes for Delta Smelt, especially in the context of climate change (Brown et al. 2013, 2016b). Differences in water temperature between regions or time periods may have important effects on the Delta Smelt population (Rose et al. 2013).

Turbidity

In addition to salinity gradients, estuaries often have turbidity gradients. Turbidity is the loss of transparency of water due to scattering of light by suspended particles. Typically, the upper reaches of estuaries have areas with high levels of suspended particles known as “estuarine turbidity maxima.” In many estuaries, these areas are in or near the low salinity zone and are associated with large numbers of fish and enhanced growth for larvae of some species (Sirois and Dodson 2000a, b, Shoji et al. 2005). In the SFE, turbidity is largely determined by the amount of suspended inorganic sediment in the water (Cloern 1987, Ganju et al. 2007, Schoellhamer et al. 2012), although organic components can also play a role (U.S. Geological Survey 2008). Sediment particles are constantly deposited, eroded, and resuspended, and are transported into, within, and out of the estuary. The amount of sediment that is suspended in the water column depends on the available hydrodynamic energy, which determines transport capacity, and on the supply of erodible bed sediment in the estuary and suspended sediments from the watershed.

Turbidity at any location is the result of several environmental drivers, including hydrology (transport from the watershed) and weather (wind and precipitation) interacting with the physical configuration of the region. In the SFE, suspended sediment is transported from the tributary watersheds into the system 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. This first storm driven turbidity event is often called “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. During the remainder of the year, turbidity is primarily caused by interactions of this stored 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 and water moving at high tidal 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 2000). Sediments may also be resuspended by turbulence related to wind waves. This process is mainly limited to areas with fine sediments on relatively shallow shoals where wind wave turbulence reaches the bottom. This process is most important in the shallows of Suisun, Grizzly, and Honker Bays and Liberty Island (Ruhl and Schoellhamer 2004, Warner et al. 2004, Morgan-King and Schoellhamer et al. 2013). Annual variation in these factors may have important effects. For example, during a drought there is little transport of suspended sediment by large storms, and the same wind patterns during the summer may result in less turbidity than would occur after a wet year because less sediment was stored as benthic sediment during the winter. There is also evidence of longer-term changes in turbidity (Schoellhamer 2011, Hestir et al. 2013), along with regional differences.

In addition to the inorganic component of turbidity, organic matter (e.g., phytoplankton, plant detrital material) also contributes to both suspended solids and the sediment load on the bed that is re-suspended with wind and wave action (McGann et al. 2013). In the SFE, phytoplankton concentration varies spatially, seasonally, and on an inter-annual scale (Cloern et al. 1985, Jassby 2008, Cloern and Jassby 2012) and is controlled by multiple factors, including benthic grazing, climate, river inflows (Jassby et al. 2002), nutrient dynamics (Glibert et al. 2011, Parker et al. 2012, Dugdale et al. 2013), and water residence time, which in turn are likely to affect the organic component of turbidity. Phytoplankton dynamics are discussed in detail in the Phytoplankton white paper, but it is important to note here that plankton concentration comprises part of the SFE turbidity.

Among the geographic regions of the upper SFE, the Suisun Bay region is one of the most turbid, when the system is not being influenced by storm flows. This results from strong turbulent hydrodynamics in the Suisun Bay region caused by strongly interacting tidal and riverine flows, bathymetric complexity, and high wind speeds, which create waves that resuspend erodible benthic sediment in the large and open shallow bays of the Suisun Bay region. The north Delta, especially the large open expanse of Liberty Island (flooded since 1998) and the adjacent Cache Slough region are also relatively turbid. Recent evidence suggests that Liberty Island acts as a sediment sink in the winter and a sediment source for the surrounding Cache Slough complex in the summer (Morgan-King and Schoellhamer 2013).

Turbidity is usually lower in the channels of the confluence of the Sacramento and San Joaquin Rivers compared to the Suisun Bay region and north Delta region. Turbidity dynamics in the deep channels of the river confluence are driven more by riverine and tidal processes while high wind and associated sediment resuspension has little if any effect (Ruhl and Schoellhamer 2004). Turbidity is generally lowest in the south Delta (Nobriga et al. 2008). This may in part be due to sediment trapping by large, dense beds of *Egeria densa*, an invasive species of submerged aquatic vegetation (Hestir et al. 2016, Work et al. 2020). In winter/spring during the comparison years the highest Secchi disc depths (lowest turbidity) were found in the freshwater regions of the estuary (<1 PSU), except for the Cache Slough region in the north Delta, which was as turbid as the saltier regions of the estuary (Figure 15).

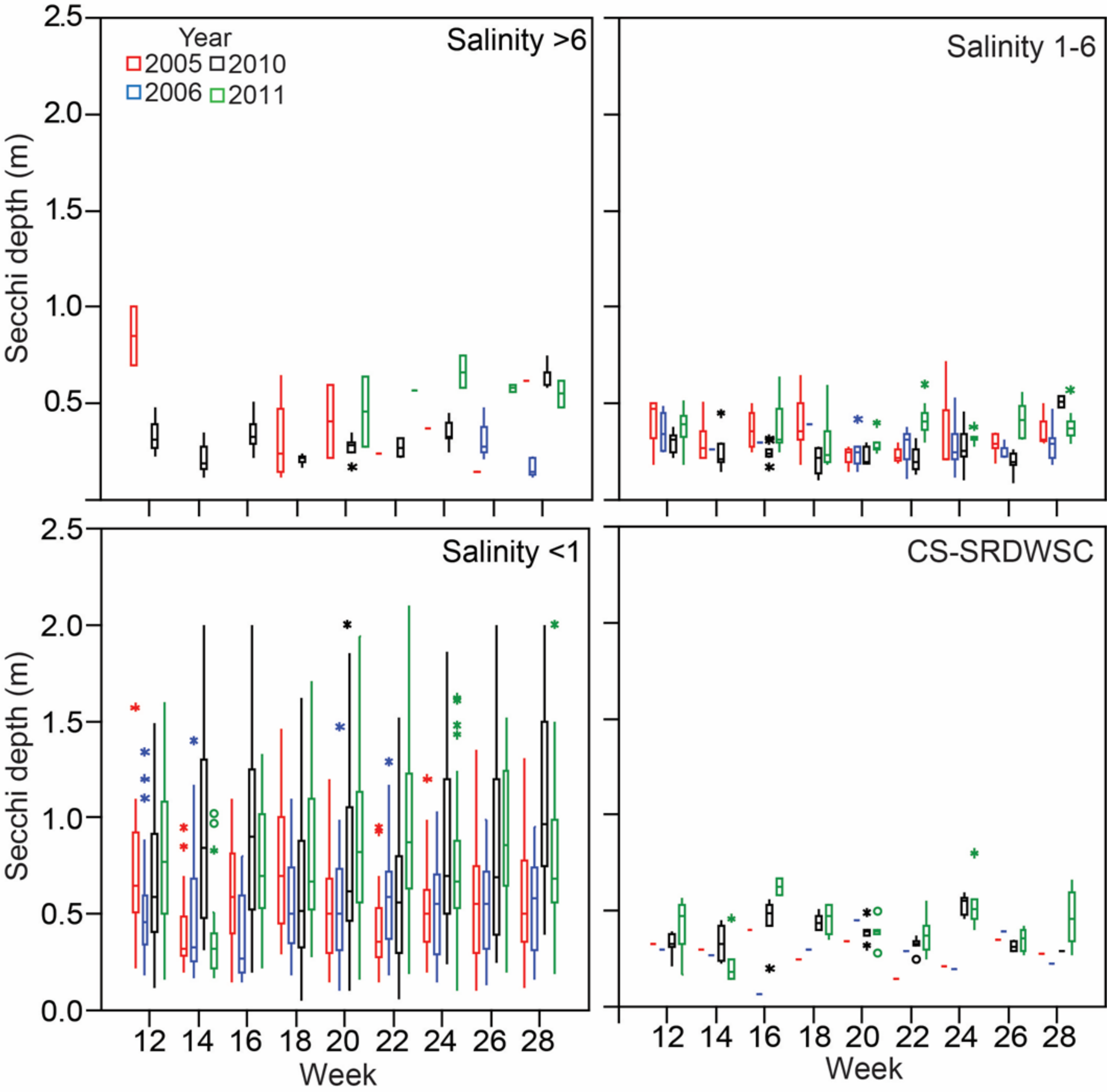

Figure 15. Secchi-depth data collected during the 20-mm survey. Surveys are conducted biweekly March-July (Figure 24 from IEP-MAST 2015). Boxplots: center horizontal line is the median of the data; the upper and lower ends of the box represent the upper and lower quartiles of the data; the lines extending above and below the box show the range of values falling within 1.5 times the inter-quartile distance; asterisks denote values within 1.5 to 3.0 times the inter-quartile distance; and circles denote values greater than 3.0 times the inter-quartile distance.

There is strong evidence for an initial increase of sediment transport followed by a more recent long-term decline in sediment transport into the upper estuary, likely due to anthropogenic activities during the last century and a half (Schoellhamer et al. 2013, Wright and Schoellhamer

2004). Schoellhamer et al. (2013) presented a conceptual model of the effects of human activities on the sediment supplies in the SFE with four successive regimes: 1) the natural state, 2) increasing sediment supplies due to mining, deforestation, agricultural expansion, etc., 3) decreasing sediment supply due to sediment flushing during high flow events and sediment trapping behind dams and dikes, and 4) a new altered state of low sediment supplies. The pulse of increased sediment inputs during and after the California gold rush and the more recent decline in these inputs is apparent in isotopic data from sediment cores taken in the estuary (Drexler et al. 2014).

The recent declines in sediment supplies have led to a long-term increase in water clarity in the upper estuary (Figure 16; Jassby et al. 2002, Feyrer et al. 2007, Jassby 2008). Jassby et al. (2002) documented a 50% decrease in total suspended-solids concentration (TSS, a laboratory measurement of total suspended solids), approximated by suspended sediment concentration (SSC, an optical measurement done in the field for these data) in the Delta from 1975-1995. Jassby (2008) found that the downward trend continued in the decade after 1995, although at a slower pace than over the entire 1975-2005. From 1975-2005, there were significant declines in SSC of up to 6% per year at 8 of 10 Delta stations (Jassby 2008). Jassby et al. (2005) showed that TSS concentrations in the north Delta dropped sharply toward the end of the 1982–1983 El Niño-Southern Oscillation (ENSO) event, which was associated with extremely high outflows, and did not recover afterward. This step decrease after 1983 has been corroborated by further trend analyses of TSS (Hestir et al. 2013). Following the El Niño event of 1997–1998, there was a 36% step decrease in SSC in San Francisco Bay as the threshold from transport to supply regulation was crossed as an anthropogenic erodible sediment pool was depleted (Schoellhamer 2011). As mentioned above, sediment trapping by dense beds of *Egeria densa* and other aquatic vegetation may be further reducing available sediment in the Delta (Hestir et al. 2016, Work et al. 2020). While other anthropogenic factors may have also contributed to long-term changes in turbidity (e.g., export operations), quantitative analyses of the effects of these factors have not been conducted.

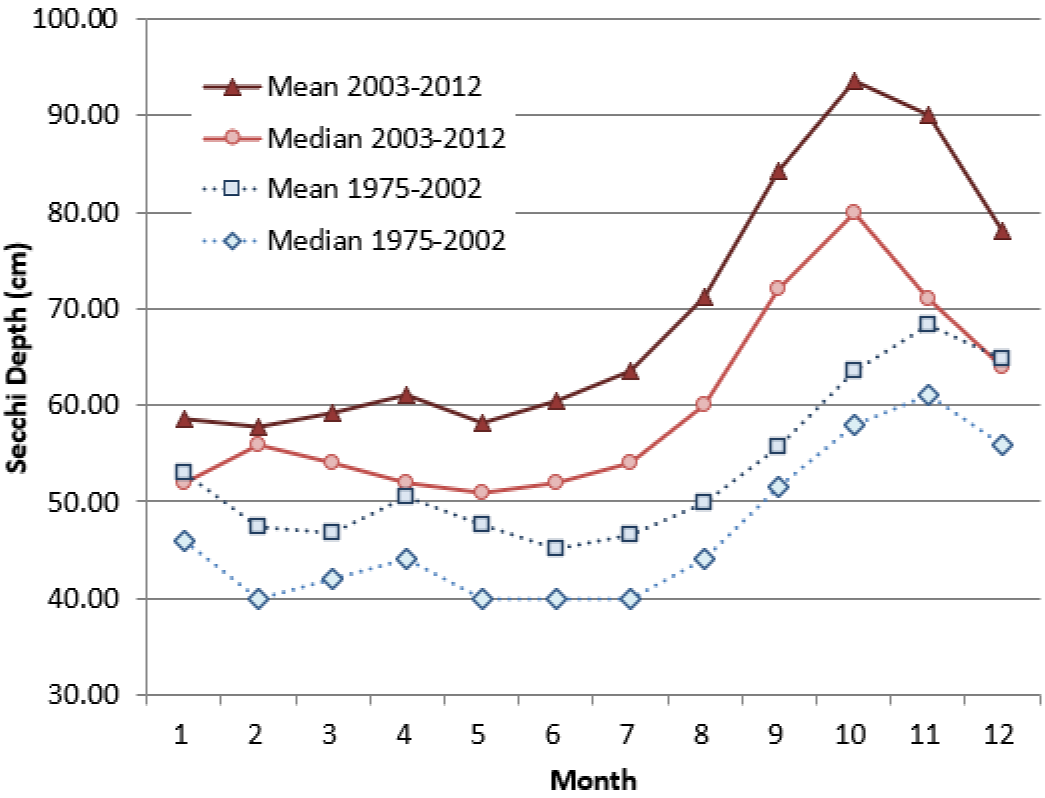

Figure 16. Average and median Secchi depth in cm from monthly sampling at IEP Environmental Monitoring Program stations. Data are shown for the period up to the pelagic organism decline (1975-2002) and after the decline (2003-2012) (Figure 25 from IEP-MAST 2015).

Multiple field and modeling studies have established the association between elevated turbidity and the occurrence and abundance of Delta Smelt. The abundance of larval/postlarval Delta Smelt larvae was well explained by salinity and Secchi depth (a proxy for turbidity) (Kimmerer et al. 2009). Sommer and Mejia (2013) and Nobriga et al. (2008) found that late-larval and juvenile Delta Smelt are strongly associated with turbid water, a pattern that continues through fall (Feyrer et al. 2007, Latour 2016). Long-term declines in turbidity may also be a key reason that juvenile Delta Smelt now rarely occur in the south Delta during summer (Nobriga et al. 2008). Thomson et al. (2010) found that water clarity was the only significant predictor variable that was shared by three of the four Pelagic Organism Decline (POD) species; all other significant predictor variables were unique to each species. Latour (2016) found water clarity to be important for all four species: Delta Smelt, Longfin Smelt, Threadfin Shad (*Dorosoma petenense*), and Striped Bass. Grimaldo et al. (2009) found that the occurrence of adult Delta Smelt at the SWP salvage facilities was linked, in part, with high turbidity associated with winter first flush events. Turbidity may also serve as a behavioral cue for small-scale (lateral and vertical movements in the water column) and larger-scale (migratory) Delta Smelt movements (Bennett and Burau 2015). Latour (2016) noted that these patterns in water clarity and fish abundance may be influenced to an unknown degree by changes in catchability if increased water clarity facilitates gear avoidance.

Delta Smelt are visual feeders that feed primarily on zooplankton between dawn and dusk (Hobbs et al. 2006, Slater and Baxter 2014). As for all visual feeders, visual range and prey density determine feeding success of Delta Smelt. Visual range depends on size, contrast and mobility of the prey, retinal sensitivity, and eye size of the visual feeder, and on the optical habitat attributes such as light scattering, absorption, and intensity (Aksnes and Giske 1993). Optical habitat attributes are affected by turbidity from suspended organic particles, such as algae and detritus, and inorganic particles, such as sand and silt. Somewhat counterintuitively, some level of turbidity appears important to the feeding success of larval Delta Smelt. Baskerville-Bridges et al. (2004a) conducted laboratory experiments in which algal densities (0, 0.5 x 106 cell/mL, and 2 x 10^6 cell/mL or 1, 3, and 11 NTU) and light levels (range tested: 0.01 µmoles/s x m^2, 0.3 µmoles/s x m^2, 1.9 µmoles/s x m^2) were manipulated and first-feeding success of larval Delta Smelt was quantified. They found that maximum feeding response occurred at the highest algal concentrations and light levels tested. In a subsequent experiment, when algae were removed entirely, the feeding response was very low. The addition of algae or some other form of suspended particle is now standard practice for successfully rearing Delta Smelt larvae in culture facilities (Baskerville-Bridges et al. 2005, Lindberg et al. 2013). Presumably the suspended particles provide a background of stationary particles that helps the larvae detect moving prey. Sufficient turbidity also appears to be important to reduce overall environmental stress and increase survival of larval Delta Smelt (Lindberg et al. 2013). Thus, it seems likely that turbidity is important to the feeding success and survival of larval Delta Smelt in the wild. Recent research on juvenile Delta Smelt, however, suggests that influence of turbidity on feeding success may vary across life stages and field conditions. Hasenbein et al. (2013) exposed juveniles to varying turbidities (5-250 NTU) and observed a negative relationship between turbidity and feeding rates, with a marked decline in feeding at 250 NTU. However, feeding rates were highest at 12 NTU and stable in the 12-120 NTU turbidity range, which is likely within the range experienced by juvenile Delta Smelt in typical summer conditions in the Delta. Turbidity values of 250 NTU are generally not observed during the summer; therefore, the typical summer turbidity range in the Delta likely does not limit juvenile feeding success. Hasenbein et al. (2016) evaluated survival, feeding, and physiological markers at the same set of turbidities and concluded the preferred turbidity range of late-larval Delta Smelt is 25-80 NTU.

In addition to its effects on feeding, turbidity may reduce predation risk. This is based on the general recognition that fish assemblages are often partitioned between turbid-water and clear-water assemblages (Rodríguez and Lewis 1997, Quist et al. 2004), and that turbidity can influence the predation rate on turbid-adapted fishes (Rodríguez and Lewis 1997, Gregory and Levings 1998, Quist et al. 2004). It has generally been assumed that juvenile and adult Delta Smelt are closely associated with turbidity to minimize their risk of predation in their generally open-water habitat. In mesocosm experiments Ferrari et al. (2014) showed that turbidity reduced predation success of Largemouth Bass feeding on Delta Smelt and that Delta Smelt did not utilize submerged aquatic vegetation as cover. There may also be complex interactions between feeding and predation risk that are mediated by turbidity. Thus, while laboratory studies have demonstrated that larvae have improved feeding success at higher (but not too high, see above) turbidities, in natural settings, turbidity and predation risk may interact (e.g., Miner and Stein 1996) to affect Delta Smelt habitat choice and feeding success.

Turbidity may also be a migration cue for Delta Smelt. Bennett and Burau (2015) investigated behavioral responses of Delta Smelt to winter “first flush” events in the Sacramento and San Joaquin Rivers near their confluence. This study found lateral turbidity gradients that changed with the tides and before and after first flush events and coincided with lateral Delta Smelt movements toward the channel during flood tides and toward the shoreline during ebb tides. The researchers concluded that this behavior likely facilitates maintaining channel position or moving upriver and cross-channel gradients in water turbidity may act as behavioral cue. Feyrer et al. (2013) also found small-scale lateral and vertical gradients in turbidity in the lower Sacramento River just prior to a wintertime first flush event. Feyrer et al. (2013) concluded that Delta Smelt may actively move in the water column by keying in on turbidity and salinity gradients or because of the physics underlying them.

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3. Phytoplankton

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Introduction

The spatial and temporal variation of photosynthetic plankton are critical to energy transfer across trophic levels. Photosynthetic plankton create sugars from raw materials (sunlight and inorganic material in the water) which provides food for organisms at the base of the aquatic food web. Individual photosynthetic plankton species are microscopic but may be visible as groups of cells or colonies (e.g., filaments, scums, flakes, films). There are two types of photosynthetic plankton, prokaryotes, also known as bacteria, in the phylum Cyanophyta (cyanobacteria) and eukaryotes, also known as phytoplankton. Phytoplankton are composed of many phyla and common ones in the upper San Francisco Estuary (USFE) are Bacillariophyta (diatoms), Chlorophyta (green algae), Chrysophyta (chrysophytes), Cryptophyta (cryptophytes) and Dinoflagellata (dinoflagellates).

Part I. Photosynthetic plankton biomass

Long-term pattern

Consistent monitoring of chlorophyll *a* concentration, an estimate of phytoplankton biomass, in the USFE began in the 1970s. At that time chlorophyll *a* concentration reached 250 µg L^{-1} in the upper San Joaquin River, 10 µg L^{-1} in the upper Sacramento River and 80 µg L^{-1} in Suisun Bay (Jassby 2008). Chlorophyll *a* concentration decreased beginning in the late 1970s to early 1980s following relatively high values during the 1976-1977 drought in the Sacramento and San Joaquin Rivers (Lehman 1992; 1996). This contrasted with Suisun Bay and nearby channels where chlorophyll *a* concentration decreased during the 1976-1977 drought, recovered during the late 1970s and then had two step decreases, one in the early 1980s and another in the mid-1980s (Cloern et al. 1983; Cloern et al. 1985; Alpine and Cloern 1992; Lehman 1992; 1996; Kimmerer 2004; Jassby 2008; Glibert et al. 2011; Cloern and Jassby 2012). Since the 2000s, chlorophyll *a* concentration in all regions has remained at 2-5 µg L^{-1}, with blooms only periodically reaching >20 µg L^{-1} (Glibert et al. 2014).

The decrease in chlorophyll *a* concentration in Suisun Bay and the low salinity zone was accompanied by a decrease in the size structure of the phytoplankton community. Elevated chlorophyll *a* concentration was associated with wide diameter (>5 µm) phytoplankton cells (primarily diatoms) in Suisun Bay and the nearby low salinity zone (Cloern et al. 1985; Kimmerer 1998; 2004; Lehman 2000; Kimmerer and Thompson 2014; Cloern 2018).

Causal factors

For phytoplankton biomass to increase, cells must be retained in an area long enough for growth rate to exceed the rate of loss due to all factors. Transects in the northern Delta indicated that chlorophyll *a* concentration was higher in areas with increased residence time (Stumpner et al. 2020). Efforts to develop a streamflow metric produced the X2 index, which is the distance in km from the ocean upstream in the Sacramento River to where bottom salinity is 2 (Jassby et al. 1995). This salinity index is often used as a proxy for residence time. High chlorophyll *a* concentration was measured in the low salinity zone (salinity 0.5 to 6) during the spring and summer when the X2 index was 70 to 85 km (Kimmerer 2002), in Suisun Bay when the X2 index was near 60 km (Jassby et al. 1995) and in the Delta during cyanobacteria blooms in the summer when the X2 index was ≥ 85 km (Lehman et al. in press). Attempts have also been made to quantify the amount of streamflow associated with elevated chlorophyll *a* concentration and include $< 1000\ m^3\ s^{-1}$ for the Delta (Jassby et al. 2002), $< 600\ m^3\ s^{-1}$ for Suisun Bay (Cloern et al. 1983), $>1000\ m^3\ s^{-1}$ for the low salinity zone (Kimmerer 2002; 2004), 200-600 $m^3\ s^{-1}$ for the upper Sacramento River (Lehman et al. 2013) and 9-35 $m^3\ s^{-1}$ in the San Joaquin River (Lehman et al. 2008; 2017; 2020).

Streamflow affects turbidity which is a key limiting factor for photosynthetic plankton growth in USFE; one of the most turbid estuaries in the world (Ball and Arthur 1979; Cloern and Cheng 1981; Cole and Cloern 1984; Cloern 1987; Jassby and Cloern 2002; Jassby 2008; Wilkerson et al. 2006; Cloern et al. 2012). In the deep river channels (13 m) of the Delta, light penetrates the water column only a few feet, creating a euphotic zone (lighted area) to total depth ratio less than 1, and results in net negative carbon production each day (Cole and Cloern 1984; Cloern 1987). In contrast, modeling studies suggest net photosynthetic plankton growth could be positive in shallow habitats where the euphotic zone to total depth ratio is positive, including flooded island habitats and Suisun Bay (Lopez et al. 2006; Alpine and Cloern 1988; Jassby and Cloern 2000). Given such light sensitive environments, small changes in the duration of daylight can significantly impact net primary productivity (Lucas et al. 2006). However, too much light can negatively impact net production due to energy lost to respiration (Rudek and Cloern 1996; Lehman et al. 2008).

Chlorophyll *a* concentration is transported with streamflow from the Sacramento River, Yolo Bypass, and upstream San Joaquin River into the Delta (Lehman 2007; 2004; Frantzich et al. 2018), and from the Delta to downstream locations including the low salinity zone and Suisun Bay (Ball 1987; Jassby et al. 1993; Jassby and Powell 1994; Lehman 1996; Jassby et al. 2002; Kimmerer 2004; Jassby 2008; Lehman et al. 2015). Horizontal transport from shoals into channel locations also leads to increased chlorophyll *a* in the channels of Suisun Bay (Arthur and Ball 1979; Cloern and Cheng 1981) and produces a turbidity maximum in Suisun Bay

(Peterson et al. 1975; Arthur and Ball 1979; Cloern et al. 1983; Jassby and Powell 1994; Kimmerer 2002). Further, USFE has large semi-diurnal tides and the net daily transport of phytoplankton biomass due to tide can be greater than that contributed by streamflow, as demonstrated for wetland habitats in Mildred Island, Franks Tract and Liberty Island (Lopez et al. 2006; Lucas and Cloern 2002; Lucas et al. 2006; Lehman et al. 2010).

The magnitude of chlorophyll a concentration usually depends on nutrient concentration, but nutrient concentrations for the major nutrients nitrate, soluble reactive phosphorus and silica are rarely limiting in the estuary. This is supported by the inverse or non-significant correlation between nutrient concentration and chlorophyll *a* concentration (Ball and Arthur 1979; Lehman 1992; Cloern 2001; Jassby 2008; Cloern et al. 2020). It was hypothesized that an increase in the ammonium concentration and change in the nitrogen to phosphorus ratio due to wastewater treatment discharge in the 1990s (Jassby 2008) might affect chlorophyll a concentration due to an impact on diatom nitrogen uptake and subsequent growth (Dugdale et al. 2007; Glibert et al. 2011; Parker et al. 2012a, b). However, Lagrangian studies of nutrient uptake and phytoplankton in the Sacramento River indicated ammonium concentration did not affect chlorophyll *a* concentration, phytoplankton growth or species composition (Kraus et al. 2020; Stumpner et al. 2020).

The net phytoplankton biomass produced each day also depends on loss due to removal. Many studies have demonstrated the ability of clam herbivory to control phytoplankton biomass in the shallows of Suisun Bay (Nichols 1985; 1990; Alpine and Cloern 1992; Lucas et al. 2002; 2016; Jassby et al. 2002; Jassby 2008; Hammock et al. 2019) and the adjacent low salinity zone by grazing (Kimmerer and Thompson 2014). During the 1976-1977 drought, the increase in salinity upstream enabled the clam, *Mya*, to establish in the shallows of Suisun Bay and graze the phytoplankton to record low levels during the summer (Nichols 1985; DiToro et al. 1971). Similarly, the establishment of the invasive clam *Potamocorbula amurensis* in the brackish regions of the estuary in 1986 reduced phytoplankton biomass in Suisun Bay and the low salinity zone by at least a factor of 5 (Nichols et al. 1990; Alpine and Cloern 1992; Canuel et al. 1995; Kimmerer et al. 2002; Kimmerer and Thompson 2014). Upstream in the freshwater reaches of the estuary, grazing by the freshwater clam, *Corbicula fluminea*, can control phytoplankton biomass in shallow habitats (Foe and Knight 1985; Lopez et al. 2006). However, many of the channels in the Delta are deep (13 m) and phytoplankton at the surface are not impacted by clams at the bottom of the channel, unless cell sinking rates are high (Dugdale et al. 2016; Lucas et al. 2016). Zooplankton at times may be more successful at removing large diameter (> 5 µm diameter) cells than clams (Kimmerer and Thompson 2014; Orsi and Mecum 1996). Water diversion is also a significant loss factor in the Delta (Arthur et al. 1996; Jassby et al. 1996; Hammock et al. 2019).

Ecosystem impacts

Photosynthetic plankton are an important in situ (autochthonous) source of carbon to the estuarine food web in the Delta and Suisun Bay (Jassby and Cloern 2000, Kimmerer 2004). In addition, photosynthetic plankton carbon is an important source of carbon exported from the Delta (allochthonous) into Suisun Bay (Lehman 1996; Kimmerer 2004). The contribution of photosynthetic plankton to the carbon in the estuary declined starting in the late 1970s. Modeling indicated the decline was also associated with a downward shift in phytoplankton growth rate in the Delta between 1975 and 1995 that resulted in an estimated carbon loss to the Dela of 43% (Jassby et al. 2002). The importance of carbon export from the Delta to Suisun Bay has likely increased over time, with the reduction of phytoplankton carbon due to grazing by the invasive clam *P. amurensis* (Jassby 2008).

The availability of photosynthetic plankton carbon affects the availability of zooplankton carbon at the base of the food web. The growth of cladocera and development indices for late copepodites of the copepod, *Pseudodiaptomus forbesi,* were correlated with chlorophyll *a* concentration (Kimmerer 2004; Kimmerer et al. 2018b). Long-term data also demonstrated a positive correlation between diatom carbon and both total zooplankton carbon and *Neomysis mercedis* carbon in the Delta (Lehman 2004). Regions with relatively high chlorophyll *a* concentration, such as the Cache Slough Complex, can have high growth rates of important zooplankton species like *P. forebesi* (Kimmerer et al. 2018a). In the Sacramento deep water shipping channel, a greater contribution of chlorophyll *a* to the zooplankton diet results in a higher abundance of herbivorous cladocerans compared to downstream areas (Young et al. 2020). The decline in chlorophyll *a* concentration since the 1970s was also associated with a shift from herbivorous to predatory zooplankton species that potentially affected the efficiency of trophic transfer to fish (Brown et al. 2016).

Total photosynthetic carbon contributes to the abundance of rotifers, cladocerans, and copepods such as *Acartia* spp. and *Sinocalanus doerrii* in the LSZ and the loss of total carbon may have contributed to the decline in zooplankton abundance since the mid-1980s (Jassby et al. 2002; Kimmerer 2004; Lehman 2004). The calanoid copepods *Eurytemora affinis* and *P. forbesi*, and the native mysid shrimp *Neomysis mercedis* also exhibit evidence of food limitation, making food resources a key controlling factor (Kimmerer and Peñalva 2000; Orsi and Mecum 1996). There may be a chlorophyll a threshold for zooplankton. A decrease in chlorophyll *a* concentration to less than 10 µg L^{-1} in the upper estuary was associated with a decrease in the growth rate and egg production of the zooplankton *E. affinis*, *P. forebsi*, and *L. tetraspina* (Kimmerer et al. 2014). Daphnia growth rate in laboratory bioassays also declined when chlorophyll *a* concentration was below about 10 µg L^{-1} (Müller-Solger et al. 2002; Kimmerer et al. 2005). Low food availability can lower salinity tolerance of *E. affinis*, an important prey species for *Hypomesus transpacificus* (Delta Smelt; Hammock et al. 2015). Low calanoid copepod abundance can impact Delta Smelt, which selectively prey upon them (Kimmerer 2004, Cloern and Jassby 2012).

Part II. Photosynthetic plankton community composition

Over the past 50 years, there has been a decrease in diatoms and an increase in cyanobacteria throughout the USFE (Lehman and Smith 1991, Lehman 2000, 2004’ Lehman et al, 2013, in press a; Cloern and Dufford 2005; Glibert et al. 2011; Cloern 2018). By 2018 cyanobacteria abundance comprised most of the photosynthetic plankton across the Delta and Suisun Bay (Perry and Brown 2020; Lehman et al. in press b). In addition, the ratio of small (5-20 µm) to wide (> 20 µm) diameter cells decreased between 1970 and 1993 in the low salinity zone, a key area of production in the estuary (Lehman 2000b). A similar decrease in cell diameter was measured in Suisun Bay (Cloern 2018). The loss of diatoms is important because these cells contain omega fatty acids needed for zooplankton growth (Galloway and Winder 2016). Diatoms are also wide diameter cells with high cell carbon content which facilitate efficient energy transfer in the food web (Cloern 2018).

Regional differences

Among regions, green algae are abundant in the upper reaches of the Sacramento River (Perry and Brown 2020; Stumpner et al. 2020). Diatoms and dinoflagellates occur seaward within the brackish waters of Suisun Bay (Cloern and Dufford 2005; Glibert et al 2014; 2018; Sutula et al. 2017; Peacock et al. 2018). The Yolo Bypass floodplain in the north Delta contains more diatoms and green algae than the nearby Sacramento River, which primarily contains cryptophytes (Lehman et al. 2008). In the San Joaquin River, upstream of the Delta, diatoms and green algae comprised a greater percentage of the plankton community compared with flagellates which were abundant in the tidal reaches of the southern and central Delta (Lehman 2007). Cyanobacteria harmful algal blooms have increased throughout the upper estuary, particularly in the southern Delta, since 1999 (Lehman et al. 2005; 2013, in press a). Initially the cyanobacteria blooms were dominated by *Microcystis* but are now comprised of a suite of toxic cyanobacteria (Lehman et al. in press a).

Seasonal variation

Diatoms are abundant in the winter and early spring (Glibert et al. 2014a; Kimmerer and Thompson 2014; Lehman and Smith 1991; Lehman 1996, 2000). Green algae are also abundant in the winter in upstream regions of the estuary (Perry and Brown 2020). Blooms in the fall are often composed of small flagellates, such as cryptophytes (Lehman and Smith 1991; Lehman 1996; Wilkerson et al. 2006; Lehman et al. 2013). Late fall diatom blooms can occur in October (Lehman et al. 2013, in press a). Total cyanobacteria abundance is high year-round (Perry and

Brown 2020) and toxic cyanobacteria blooms are common in the summer and fall (Lehman et al. 2008, 2013, in press a).

Causal factors

Diatom blooms are more common during wet and normal years when vertical mixing and turbidity are high and water temperature is low (Cloern et al. 1983; Lehman 1996, 2000, 2004). Dry and critically dry years before 1999 were characterized by cryptophytes, miscellaneous flagellates, and green flagellates which grow in stable water columns with little mixing, low turbidity, and elevated water temperature (Lehman 2000). Increased residence time within backwater sloughs of the North Delta also results in an increase in the presence of small cyanobacteria cells (Stumpner et al. 2020). Cyanobacteria blooms have increased in the Delta since 1999 during drought years (Lehman et al. 2013, in press a).

Physical transport and removal may also affect photosynthetic plankton composition. Total and centric diatom biovolume was negatively correlated with agricultural diversion (Lehman 2000). In addition, the abundance of diatoms in the Delta varied directly with the amount of streamflow from the upper San Joaquin River (Lehman 2007). Biological removal processes also contribute to the abundance of diatoms, which because of their relatively heavy frustules, sink more rapidly to the bottom than other phytoplankton or cyanobacteria and make them more susceptible to grazing by clams (Lucas et al. 2016; Dugdale et al. 2016). Zooplankton also prefer grazing on larger cells, which tends to remove diatoms from the water column (Kimmerer and Thompson 2014; Cloern 2018; Kayfetz and Kimmerer 2017).

Streamflow also affects turbidity which was associated with community composition along the salinity gradient of the estuary (Cloern and Dufford 2005). In the Delta, the influence of light on photosynthetic plankton was suggested by the inverse correlation of Secchi disk depth and diatom carbon (Lehman 2000; 2004). A recent experiment supported the hypothesis that hydrodynamics and light limitation were potentially important controlling factors due to the lack of variation of photosynthetic plankton with grazing and nitrogen species (Kraus et al. 2017).

Because nutrient concentration is usually not limiting in USFE, it is not considered to be an important controlling factor for phytoplankton community composition (Cloern and Dufford 2005; Jassby 2008; Cloern 2020). The negative correlation between diatom carbon and nutrient concentration supported nutrient uptake but not limitation for nitrate, soluble reactive phosphorus, or silica (Lehman 2000, 2004; Cloern and Dufford 2005; Kimmerer 2005; Cloern et al. 2020). A long-term increase in ammonium concentration was hypothesized to be the cause of the decline in diatoms in the estuary due to its negative impact on diatom growth rate compared with nitrate (Wilkerson et al. 2006; Dugdale et al. 2007; Parker et al. 2012ab; Glibert et al. 2014). However, measurements within the upper Sacramento River did not demonstrate a difference in phytoplankton composition, chlorophyll *a* concentration or plankton growth rate when the primary source of nitrogen was ammonium rather than nitrate (Kraus et al. 2017; Stumpner et al. 2020).

Ecosystem Impacts

Photosynthetic plankton composition can impact the composition of grazers and energy transfer across trophic levels due to their impact on nutrition. Phytoplankton (e.g., diatoms and green algae) provide higher-quality food for Daphnia than vascular plant detritus (Muller-Solger et al. 2002) and are traditionally thought to be the major source of energy for the food chain in the USFE (Sobczak et al. 2002, Jassby et al. 2003), but not all phytoplankton are equally nutritious. Laboratory studies indicated large calanoid copepods eat wide diameter plankton cells such as diatoms and ciliates while small cyclopoid copepods eat small flagellates (Kayfetz and Kimmerer 2017). The abundance of diatoms is also important because diatoms contain essential omega three fatty acids required for zooplankton growth, while other plankton, particularly, cyanobacteria do not (Galloway and Winder 2016). Further, both the cell diameter and quality of food within the plankton community will affect the efficiency of energy transfer among trophic levels, with larger cells and more nutritious food being more efficient (Cloern 2018).

Declines in the carbon or abundance of large-bodied zooplankton and pelagic fish coincided with a decline in the carbon or abundance of diatoms (Lehman 1996; Lehman 2004; Glibert 2011). Zooplankton often feed selectively on wide-diameter plankton cells, and decreases in diatom abundance reduce the diameter and carbon content of food particles (Lehman 1996). Diatoms are a primary source of food for *N. mercedis*, and food limitation is thought to be a primary contributor to the decline of this species (Kimmerer 2004; Orsi and Mecum 1996). Although cyanobacteria may be eaten by copepods, it is not nutritious food and is usually associated with poor growth rate (Ger et al. 2019). Only half of the spring-summer primary production in the LSZ is now composed of plankton large enough to be consumed by copepods, which are among the most important prey for Delta Smelt (Brown et al. 2016). Determining precisely which phytoplankton provide the best nutrition for zooplankton is not always straightforward. While detritus is not thought to be as nutritious as phytoplankton, recent studies found increased growth of zooplankton when fed a mix of detritus and phytoplankton (Harfmann et al. 2019).

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4. Zooplankton

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Introduction

Zooplankton are a vital trophic link between aquatic primary producers and higher-level consumers of the San Francisco Estuary (SFE). As primary consumers of phytoplankton, zooplankton facilitate the flow of carbon into a large and complex food web, and once supported abundant fisheries in the region (Schroeter et al. 2015; Kimmerer et al. 2018). Zooplankton in the SFE are also a key food source for several endangered and threatened species, notably the Delta Smelt (*Hypomesus transpacificus*), Longfin Smelt (*Spirinchus thaleichthys*) (Slater & Baxter 2014; Hobbs et al. 2006), and juvenile Chinook Salmon (Goertler et al. 2018). Substantial changes in the zooplankton community composition and abundance in the SFE have been linked to major declines in the pelagic fishes of the upper estuary known as the “Pelagic Organism Decline” (Sommer et al. 2007; Winder & Jassby 2011).

The concentration of available zooplankton can have a strong influence on the growth and survival of larval and juvenile fish that utilize estuary habitats as nursery grounds. These fluctuations in the growth and survival rates for larval fishes can then have disproportionate effects on population dynamics (Houde 1987). Young fish that have slower growth rates spend more time in vulnerable larval stages and are thus more susceptible to predation and other sources of mortality (Houde 1987). Increases in feeding success can then lead to further increases in growth rates, leading to even greater feeding success, growth, and survival (China and Holzman 2014, Levy et al. 2017). For Delta Smelt larvae, exposure to higher rotifer prey densities resulted in larvae with higher feeding incidence and gut fullness (Baskerville-Bridges 2004). Recent experiments on the growth of juvenile Coho Salmon (*Oncorhynchus kisutch*) showed that high prey abundance buffered the negative effects of increased temperatures, indicating that ecosystem productivity may provide some offset from the effects of climate change (Lusardi et al. 2019). Determining how to facilitate the production and sustainment of abundant zooplankton prey populations is necessary for the management and sustainment of endangered fishes in the estuary (Sommer 2020).

Existing zooplankton studies in the SFE

Starting in 1972 zooplankton sampling has been conducted throughout the upper SFE by the Interagency Ecological Program (IEP), initially starting with the long-term Environmental Monitoring Program (EMP) jointly run by California Department of Fish and Wildlife (CDFW) and the Department of Water Resources (DWR). Zooplankton sampling in the SFE was expanded in 1995 with the 20mm survey, which samples juvenile fish and zooplankton concurrently to investigate potential correlations between declining fish abundances and available food resources. Additional long-term monitoring fish surveys such as the Summer Townet survey

(STN), Fall Mid-water Trawl (FMWT), and the Fish Restoration Project (FRP) added concurrent zooplankton sampling to expand on the temporal and spatial coverage of existing zooplankton monitoring in the SFE (Figure 1). Only the EMP samples year-round, with other surveys having overlapping coverage with 20mm running from March through June, STN from June through August, FMWT from September through December, and recently changed for FRP from April – May and November - December (Kayfetz et al. 2020).

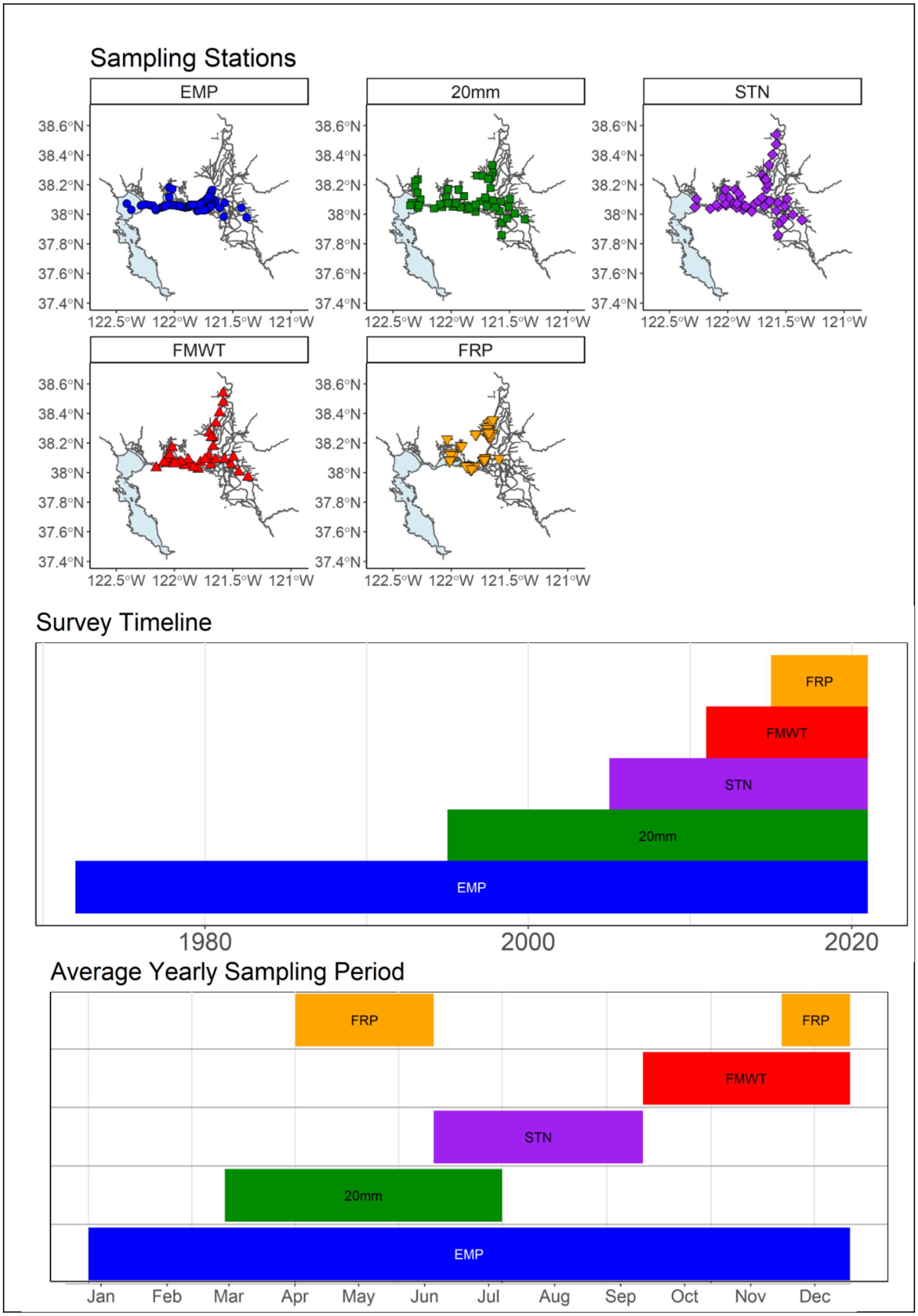

Figure 1. Spatial sampling coverage of SFE zooplankton monitoring surveys, Environmental Monitoring Program (EMP), 20mm Survey, Summer Townet (STN)Fall Mid-water Trawl (FMWT), and the Fish Restoration Project (FRP).

The EMP targets three size classes of zooplankton using three different gear types for each sampling event: a pump with a 43-micron mesh net for micro-zooplankton (rotifers, nauplii, and small cyclopoid copepods); a Clarke-Bumpus (CB) net with a 160-micron mesh for sampling meso-zooplankton (cladocera and most juvenile and adult calanoid copepods); and a mysid net with a 505-micron mesh for sampling mysid shrimp and other macro-zooplankton. Abundance indices are calculated for each organism based on the gear type most effective for its capture and reported as the mean catch-per-unit-effort (CPUE). FMWT and FRP both target meso-zooplankton and macro-zooplankton, while the STN and 20mm surveys only target meso-zooplankton.

While four of the surveys are run by IEP (FRP is funded separately through DWR as mitigation effort), they are each individually managed, which has presented challenges in analyzing abundance data across studies. For example: the list of taxa identified, and the level of taxonomic resolution can differ between each study. Recently the IEP Zooplankton Synthesis team reconciled the differences between these long-term monitoring datasets and integrated them to allow for a robust analysis of spatio/temporal trends in zooplankton abundance (Kayfetz et al. 2020 , Bashevkin et al. 2020). Utilizing this Zooplankton Integrated Dataset will facilitate greater depth in analysis of flow effects on zooplankton abundances and distributions in the SFE.

Other, supplemental studies have also been implemented to test the results of specific flow management actions. These include zooplankton samples and growth experiments collected concurrently with the North Delta Flow Action, additional zooplankton samples collected to evaluate the Suisun Marsh Salinity Control Gates action (Sommer et al. 2020), and the Directed Outflow Project, which collects zooplankton to evaluate biotic habitat for Delta Smelt concurrently with the Enhanced Delta Smelt Monitoring Program (Schultz et al. 2019).

Changes in zooplankton abundances and community composition

The SFE has shown a significant decrease in the overall abundance of zooplankton since implementation of zooplankton monitoring efforts in 1972 (Figure 2). The overall decrease in zooplankton abundance in the estuary coincided with a series of invasions into the estuary, most notably that of the Asian clam *Potamocorbula amurensis* in the mid-1980s (Kimmerer et al. 1994; Carlton et al. 1990). The spread of *P. amurensis* throughout the lower SFE has had significant impacts on planktonic abundance in the upper estuary due to its high filtration feeding rates on phytoplankton and copepod nauplii (Thompson 2005). Only the abundance of cyclopoid copepods has increased in the estuary during this period, driven by the invasion and spread of *Limnoithona tetraspina* in the lower SFE (Figure 2B). Not only has abundance decreased for most of the zooplankton groups, but important shifts in the composition of these communities have been detected over the course of monitoring periods. These changes have been driven by the introduction and spread of non-native zooplankton species throughout the estuary, compounded with changes to the abiotic and biotic environments.

When monitoring began in the early 1970s, the copepods *Eurytemora affinis* and *Acartia* spp. dominated the calanoid community abundances (Hennessey 2018). The non-native *E. affinis* was once the primary prey item of the endangered Delta Smelt, however its abundance has declined to a fraction of what it once was, forcing fish to switch to more recently introduced and more abundant calanoids like *Pseudodiaptomus forbesi* (Figure 2A) (Moyle et al. 1992; Slater & Baxter 2014). *P. forbesi* was first introduced and detected in the region in 1987, after the invasion of *P. amurensis*. This new copepod quickly outcompeted the other abundant calanoid copepod *E. affinis* (Orsi & Walter 1991). *P. forbesi* soon became the numerically dominant calanoid in the estuary and remains the most abundant to this day (Figure 2A), and even shifted the peak timing of *E. affinis* earlier towards March and April, as compared to its previous peak in July (Merz et al. 2016). The introduction of the predatory calanoid copepod *Acartiella sinensis* in 1993 is hypothesized to have narrowed the range of *P. forbesi* towards the freshwater zone of the upper estuary due to its predation on *P. forbesi* nauplii. (Slaughter et al. 2016; Kayfetz & Kimmerer 2017). Not only has the species composition of calanoid copepods available to Delta Smelt changed since monitoring began, the distribution and spatial availability of this altered community has been moved upriver away from the low salinity zone (LSZ) of the lower SFE (Figure 2A), which is important Delta Smelt habitat.

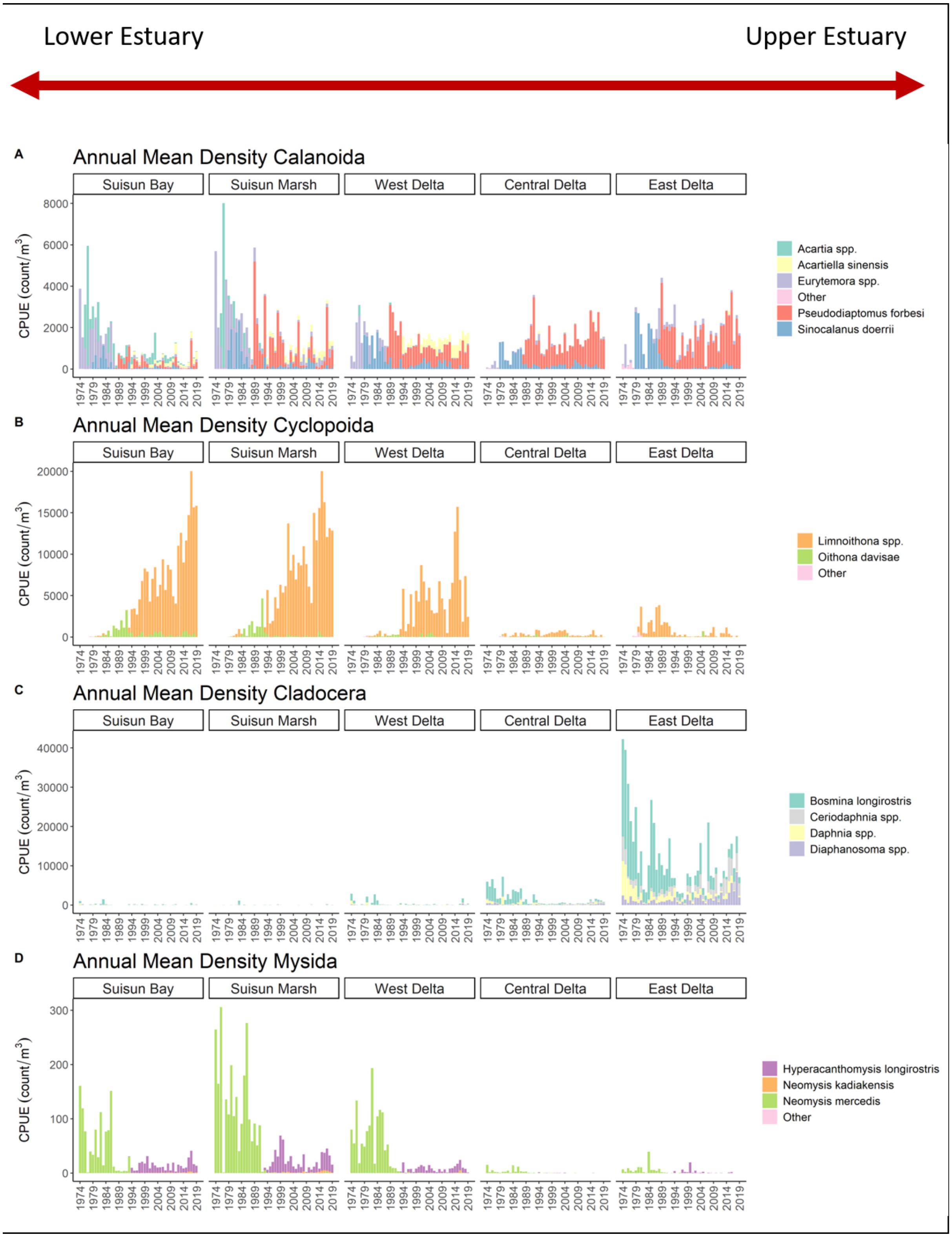

Figure 2. Annual (Mar-Nov) mean zooplankton CPUE by region for: A) Calanoida CPUE in the CB net; B) Cyclopoida CPUE in pump samples; C) Cladocera CPUE in the CB net; and, D) Mysid CPUE in the mysid net, from the EMP survey.

The mysid *Neomysis mercedis* was once a primary prey item of pelagic fishes in the estuary that has declined since the 1980's to almost undetectable numbers (Feyrer et al. 2003; Hennessy 2018). *N. mercedis* was an important source of food for juvenile and adult Delta Smelt when abundances were high (Moyle et al. 1992), but since then they have contributed little to diets (Slater & Baxter 2014, FLOAT MAST Diet Section). Along with the decline of the native *N. mercedis*, the estuary has also seen the invasion of the smaller mysid *Hypercanthomysis longirostris* (formerly *Acanthomysis bowmani*) (Modlin & Orsi 1997). The prevalence of *H. longirostris* at higher temperatures and its smaller size at maturity have been suggested as possible mechanisms for its successful invasion and spread into the estuary and may make it a less favorable food source for fishes (Avila & Hartman 2020).

In addition to the loss of calanoid copepods and mysids in the lower estuary, the cladocera community of the upper estuary, composed of *Bosmina*, *Daphnia*, *Ceriodaphnia*, and *Diaphanosoma* species, has seen substantial declines in abundance since the onset of monitoring (Figure 2C). These cladocera tend to be herbivorous, feeding primarily on phytoplankton, and may have been hard hit by the invasive clams (Baxter et al. 2008). Cladocera make up a significant portion of the diets of Delta Smelt, juvenile Chinook Salmon, and young-of-the-year Striped Bass throughout the upper estuary (Heubach et al. 1963; Slater and Baxter 2014; Goertler et al. 2018).

While overall zooplankton abundance has declined over the study period, the abundance of cyclopoid copepods has increased drastically (Figure 2). This is mostly due to the introduction of *Limnoithona sinensis* in the early 1980s, and the later identification of the invasive *Limnoithona tetraspina* in 1993 (Figure 2B)(Ferrari & Orsi 1984; Orsi & Ohtsuka 1999). Since the early 1990s, *Limnoithona* spp. abundance has outpaced total calanoid copepod abundance, and the small-bodied *L. tetraspina* has become the most common copepod in the upper estuary (note that *L. tetraspina* was not identified to species until 2007 by the EMP). This increase in *L. tetraspina* abundance could be due to a decline of Northern Anchovy in the upper SFE and subsequent decreased predation, as well as the cyclopoid's small size, high growth rate, and motionless behavior (Bouley & Kimmerer 2006; Greene et al. 2011). These characteristics may increase its ability to avoid predation in a region where visual predation is the most common feeding strategy among fish (Kimmerer 2006). The introduction of *L. tetraspina* is also linked to the range reduction of *P. forbesi* out of the low-salinity zone and towards the fresher regions of the estuary. This is likely due to high *L. tetraspina* densities feeding and sustaining larger populations of the predatory *A. sinensis*, which feed on *P. forbesi* nauplii (Kayfetz & Kimmerer 2017). *L. tetraspina* now accounts for 95% of total adult copepod abundance in the low-salinity zone, replacing the larger calanoid copepods that once dominated that region (Merz et al. 2016). However, due to its small size, the abundant cyclopoids utility as a food source is questioned, and it is not actively selected for by Age-0 Delta Smelt (Slater & Baxter 2014). The invasion and increase of suboptimal copepod prey such as *L. tetraspina* and the decline in cladocera has created a shift in the nutritional content of the plankton community available for fish, with yet to be determined consequences (Kratina and Winder 2015).

Correlation of abundance and distribution of zooplankton with outflow

The outflow of water through the estuary has been shown to influence the abundance of SFE zooplankton such as *N. mercedis* and *E. affinis* (Jassby et al. 1995; Kimmerer 2002a; Kimmerer 2002b). Understanding the possible effects outflow can have on zooplankton is important to understanding how water management decisions influence key Delta Smelt food resources in the estuary. Prior research in south San Francisco Bay suggested that increases in freshwater outflow increased stratification of the water column, in turn increasing overall productivity in the system (Cloern 1984). Outflow of lower density freshwater on the surface, and upstream tidal inflow from the high density more saline bottom current meet to create an “entrapment zone”. This is one possible mechanism for how outflow could influence zooplankton abundance in the rest of the estuary (Cloern 1984). However, this pattern does not hold up in the upper SFE (Schoellhamer and Burau 1998). Gravitational circulation can be locally important in specific times and places, especially in the fall in Suisun Bay, but stratification is usually small, and not spatially fixed in an “entrapment zone”, as was previously believed (Kimmerer 2004). However, high outflow may provide locally important increases in productivity that provide food for zooplankton. Lucas et al. (1999) suggested that phytoplankton blooms that begin in shallower, more productive areas could be horizontally dispersed via vertical stratification into nearby deeper channel regions. These areas are more prevalent during high outflow periods. The diel vertical migration of various zooplankton has been shown to allow organisms to maintain their horizontal position in the water column, enabling them to track these zones of high productivity (Orsi & Mecum 1986; Kimmerer et. al. 1998).

The river km distance from the Golden Gate to where the bottom salinity value is 2ppt, known as X2, is an important indicator of freshwater outflow and the location of the LSZ (Jassby et al. 1995). Some zooplankton taxa, such as *E. affinis*, show strong increases with low values of X2 (high outflow) during the spring, whereas other taxa, such as rotifers, show no relationship with X2 (Kimmerer 2002a). The location of the salinity field (X2) is thought to drive many of the flow-abundance relationships for key zooplankton taxa. Before the invasion of *P. amurensis*, positioning of the LSZ in the shallower areas of Suisun Bay during spring and summer led to higher levels of productivity due to higher water residence time and turbulent mixing (Cloern et al. 1983). This relationship changed after the clam invasion, due to the high grazing impact of *P. amurensis* on phytoplankton resulting in reduced zooplankton abundances (Kimmerer 2002b).

A more recently suggested mechanism of outflow influence on zooplankton abundances is through the spatial subsidy of organisms into the low-salinity zone from freshwater populations upriver (Kimmerer et al. 2018). Laboratory experiments on growth rates of *P. forbesi* coupled with field surveys examined the variation in abundances and development, reproductive, and growth rates to variations in freshwater outflow. Neither growth nor reproductive rates were found to vary with freshwater flows, even though field surveys showed higher abundances downstream when flows increased. This suggests that upstream populations may be transported downstream to subsidize populations in the LSZ. Predation on *P. forbesi* from the invasive *A. sinensis* and *P. amurensis* has also been shown to be remarkably high in the low-salinity zone, with mortality rates greater than local reproductive rates (Slaughter et al 2016; Kayfetz & Kimmerer 2017). The supplementation of downstream populations of *P. forbesi* from upstream freshwater populations during higher flows could maintain their availability as food for Delta Smelt in the LSZ.

Zooplankton goals of the FLOAT-MAST

One of the objectives of the FLOAT-MAST is to determine how the management of outflow through the upper SFE impacts the abundance and distribution of food resources available for Delta Smelt. Delta Smelt are becoming more and more rare, and thus harder to detect using traditional monitoring methods, so other variables besides abundance, such as food availability, could act as habitat indicators for endangered fish species. Furthermore, understanding the mechanistic drivers of zooplankton abundance is necessary to design management actions to improve food availibility and quality for Delta Smelt and other fishes. Modeling the interactions between outflow and prey abundance will allow managers to make more informed decisions on outflow in the SFE, and how those decisions will impact Delta Smelt habitat. Using the newly created Zooplankton Integrated Dataset, coupled with the Dayflow dataset produced by DWR, we aim to model the abundances and distribution of key Delta Smelt prey items based on the interactions of water temperature, salinity, average daily outflow, and the position of X2.

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5. Bivalves

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Bivalves are important as consumers of pelagic and demersal food resources. With sufficient biomass, they can compete with and, in some cases, outcompete other members of the pelagic food web for food resources such as phytoplankton and zooplankton. We include bivalves in the San Francisco Estuary (SFE) and Delta in the FLOAT MAST because they have been and continue to be an important member of the food web. Changes in the bivalves over the last 40 years have led us to hypothesize that bivalves may limit food resources for Delta Smelt and other pelagic fish species (Kimmerer and Thompson 2014, Sommer et al 2007).

We will discuss the two bivalves with the largest biomass, the estuarine bivalve *Potamocorbula amurensis* (hereafter *Potamocorbula*) and the freshwater bivalve *Corbicula fluminea* (hereafter *Corbicula*). The distribution of these two species together covers the full range of salinities between the Golden Gate and the upstream reaches of the SR and SJR. The species overlap in the region of X2. Both species' distributions expand or contract when the salinity distribution changes and do so in near synchrony with each other at a salinity of approximately 2. It is this interaction of both bivalves at their threshold levels of salinity within the ecologically sensitive low salinity zone (LSZ) in addition to their distribution in the rest of the system that determines each species effect on the food web.

History of *Potamocorbula* and *Corbicula* in SFE and Delta

Corbicula and *Potamocorbula* share some characteristics that result in similarities in the populations. Both *Potamocorbula* and *Corbicula* are exotic species that have survived and thrived in this system as opportunistic species. Native to estuaries of mainland East Asia, *Potamocorbula* thrives in brackish water, tolerates variable salinity (Paganini et al. 2010), and is well suited for the variable salinity of the SFE. In a similar manner, *Corbicula* thrives in all freshwater habitats (McMahon 1999), can tolerate salinity up to 12 (Evans et al 1979) as an adult and is therefore well suited for the dynamic changes in freshwater inflow in the SFE and Delta.

History of introductions

Potamocorbula amurensis (Carlton et al 1990, Nichols et al. 1990) invaded the SFE in 1987 and caused a severe change in the food web soon after (Brown et al. 2016); in Suisun Bay and the western Delta, phytoplankton biomass decreased about 5-fold (Alpine and Cloern 1992), the size distribution of phytoplankton shifted toward smaller cells (Kimmerer et al. 2014), and production by diatoms nearly ceased (Kimmerer 2005). The abundance of brackish-water rotifers, *Eurytemora affinis* and other copepods, and mysid shrimp (*Neomysis mercedis*, Orsi and Mecum 1996) also declined, apparently due to predation by and competition with bivalves (Kimmerer et al. 1994; Kimmerer and Lougee 2015). The changes in lower trophic levels associated with the *Potamocorbula* invasion were followed by shifts in diets, distributions, and abundance of many fish species including Delta Smelt (*Hypomesus transpacificus*) (Tempel et al. 2021).

The freshwater clam *Corbicula fluminea* was introduced in 1945 (Hanna 1966), before ecological monitoring began, so we do not have the record of changes resulting from its introduction as we do with *Potamocorbula*. *Corbicula* likely had effects on the food web in the freshwater Delta given its reported grazing impact on phytoplankton in the present-day Delta and elsewhere (Cohen et al. 1984; Lopez et al. 2006; Lucas and Thompson 2012). *Corbicula* appears to be food limited in the system (Prokopovich 1969, Foe and Knight 1985, Thompson and Parchaso 2013), further supporting the theory that they can and do thoroughly consume primary and some secondary producers in the water column. Like *Potamocorbula*, *Corbicula* can effectively filter both phytoplankton, zooplankton (Bolam et al. 2019), and bacteria (Reid et al. 1992) out of the water column.

General Distribution

Potamocorbula have been collected in the northern estuary in San Pablo, Suisun, Grizzly, and Honker Bays as well as in Suisun Marsh Sloughs, and the lower Sacramento, lower San Joaquin, Napa and Petaluma Rivers. Although they have been found in the large sloughs (Montezuma and Suisun Slough) they have not been seen in high densities in the smaller sloughs in Suisun Marsh (Baumsteiger et al 2017). *Corbicula* has been found throughout most of the Delta. Some habitats, such as the upper San Joaquin River, have very few *Corbicula* and it has been suggested that these locations are limited by toxins or food (Brown et al 2007). *Corbicula* occur in flooded islands including Franks Tract, Mildreds Island, Big Break, Liberty Island, and Sherman Island and in their surrounding sloughs (Zierdt Smith et al. 2021a). The *C. fluminea* populations in the watershed of the Delta and in the tributaries of the Sacramento and San Joaquin Rivers are important because these upstream populations may be a source of recruits for the Delta (Leland and Fend 1998, Brown et al. 2007).

Both *Potamocorbula* and *Corbicula* migrate with changes in salinity distribution. Although *Corbicula's* biomass is usually lowest in the downstream portion of the Delta today, *Corbicula* moved into Suisun Bay during the wet periods in the 1980's. They continued to be found in sufficient numbers to establish reasonable populations in Suisun Bay (Nichols et al 1990) until *Potamocorbula* appeared in1987. *Potamocorbula* frequently moves up the Sacramento River (Zierdt Smith et al. 2021a) during dry periods and moved up the San Joaquin in 2015 and persisted into the winter of 2016 when the False River drought barrier was built (Kimmerer et al. 2019).

Similarities in life history characteristics that allow *Potamocorbula* and *Corbicula* to tolerate both the SFE and Delta and to co-exist at some locations

Habitat: Both *Potamocorbula* and *Corbicula* have been observed in silt, clay, hard-pack clay, sand, gravel, peaty mud, and shell hash in the intertidal and the subtidal areas in the SFE and Delta. Both species live near the surface of the sediment and are therefore exposed to downstream transport in high flow periods. The only reported differences in their physical habitat are as follows: (1) *Potamocorbula* live in fluid mud, areas with high sedimentation and high erosion rates in the Yangtze River estuary (Chao et al. 2012). *Corbicula,* given the opportunity, may also be able to live in these areas. (2) *Corbicula* can attach to all substrates including concrete with byssal threads which has enabled them to invade and live in newly disturbed and anthropogenically altered habitats (McMahon 1991). *C. fluminea* is known as an opportunistic species that rapidly invades newly developed water conveyance canals (DWR 1967, Eng 1979) and dredged river channels (Kraemer 1979, Paunović 2007). (3) *Corbicula* can live within the *Egeria* and Tule beds.

Temperature: The Mediterranean climate of central California is temperate and thus not likely to be stressful to such cosmopolitan species. Although temperature can physiologically stress bivalves, it is its relationship to bivalve pumping rate that is less known but important here. Pumping rate is usually low at low temperatures, increases to some maximum (~30°C for *Corbicula*, Lauritsen 1986) and then declines sharply thereafter, so all pumping rates in this report have been adjusted using *in situ* temperature data.

The broadest adult temperature range reported for *Corbicula* is 0-38º C (Rodgers et al. 1979, Nascimento et al. 1996). Low temperatures may constrain reproduction when temperatures are <10 -15ºC (White and Burky 1984) but *Corbicula* can reproduce most months at present in the SFE and Delta. Given the probable temperature increase with climate change, it is as likely that *Corbicula* reproduction seasonality will be less constrained in the future. Koh and Shin (1988) report *Potamocorbula's in situ* temperature range to be 3.5-37.8 ºC in Korea, which brackets the range we would expect in the SFE and Delta.

Extending their range – the advantage in "Clamming Up": All bivalves can benefit from the ability to close their shells and wait for a stressor or lack of food to pass. Bivalves that are exposed and out of the water "clam-up" to survive. *C. fluminea* increase their survival rate and maintain aerobic metabolism by gaping their valves when they are exposed to the air (Byrne et al. 1988). In humid conditions, animals can survive about 27 days at 20ºC and 8 days at 30ºC, but only 14 and 7 days for dry conditions with the same temperatures (McMahon 1979).

Potamocorbula have been observed to survive extreme conditions in the laboratory by closing their shells but there have been no studies to accurately compare their ability to survive relative to *Corbicula*.

Important differences in life history characteristics of *Corbicula* and *Potamocorbula* that may determine distribution and success

Size and Maximum Age: *Corbicula's* larger size (~5cm) and maximum age of 4-5 years (Eng 1979, Mouthon 2001a, 2001b) is an advantage over *Potamocorbula's* maximum size (2.5 cm) and maximum age (2.5 years, Carlton et al 1990). In addition to size, morphology of the shell and shell thickness are also an advantage for *Corbicula* whose shell is relatively thick, robust, and spherical, making it less attractive to predators and more resistant to desiccation than

Potamocorbula's oblong shaped and relatively thin shell. The longer life span of *Corbicula* also allows populations to persist in marginal salinity as salinity tolerance increases with size and age. Due to *Potamocorbula's* maximum age of 2-2.5 years, their populations are not as persistent as *Corbicula's* populations in marginal habitats. The combination of size and age advantage for *Corbicula* can result in very high biomass values when compared to *Potamocorbula* as will be seen later.

Reproduction: *Corbicula* and *Potamocorbula* have different reproductive and recruitment strategies. *Potamocorbula* is dioecious with broadcast spawning and external fertilization. *Potamocorbula* spawns for 1–2 months in spring and fall (Parchaso and Thompson 2002); spawning may occur throughout the year during droughts (Parchaso 1993). Following larval development, mobile, suspension-feeding veliger larvae settle to the bottom. Juvenile clams mature and begin reproducing after two months, or at about 5 mm in length (Parchaso and Thompson 2002). *Potamocorbula's* rapid maturation to adulthood, high reproductive output, and pelagic larvae allow them to colonize and dominate new environments rapidly.

C. fluminea is a simultaneous hermaphrodite that broods its young and releases pediveligers into the water column for 48 hours before they settle. Adults can cross- and self-fertilize their eggs (Kraemer and Galloway 1986) thereby making it possible for one individual to establish a population. Once animals reach adult size (6-10mm, McMahon and Williams 1986) they become gravid and stay gravid for the rest of their life (Eng 1979, Kraemer and Galloway 1986). Therefore, it is the production and release of sperm that determines the reproductive period of *Corbicula*. Spermatogenesis begins on the rising temperature in spring when temperatures exceed 10°C (Kraemer and Galloway 1986) and continues until the temperature falls outside the acceptable range (13-30°C) or until they are food limited. The temperature range required for reproduction is met during most of the year in the SFE and Delta.

Recruitment

A larva's transition from pelagic to benthic organism is dependent on water quality being acceptable and the salinity being in the appropriate range. For this reason, the abundance of recruits of both species at a location can be related to the position of X2 in this estuary, as it is the bottom salinity that determines the success of the settling larvae. *Potamocorbula's* recruitment is usually greatest in spring, with fall recruitment being larger only in the wet years. Because the age limit is 2-2.5 years, the difference in population structure resulting from a dominant spring or a fall recruitment can result in some temporal differences in the magnitude of biomass in the following year.

Corbicula larvae are brooded and released into the plankton as pediveligers for 48 hours before they settle. Once the larvae settle to the bed they can be transported as bedload to other locations. Juveniles are commonly seen throughout the year in areas without co-occurring adults (Crauder et al 2016). Brown et al. (2007) suggest that recruits in the San Joaquin River and Sacramento River may originate with adults living in upstream tributaries and reservoirs in addition to local adults.

Food Resources and Storage

Adult *Potamocorbula* filter-feed phytoplankton and microzooplankton (Kimmerer and Thompson 2014, Greene et al. 2011) at a high pumping rate (400L/g AFDW/d at 20°C Cole et al. 1992, Werner and Hollibaugh 1993). *Potamocorbula* can filter and assimilate both phytoplankton and bacteria (<1.2 µm) from the water column (Werner and Hollibaugh 1993). *Potamocorbula* glycogen was reported as low by Werner et al. (2003), high by Miller and Stillman (2013), and as reflective of recent meals only by Canuel et al (1995). Lipid stores are generally lower in *Potamocorbula* than in other SFE bivalves (Richman and Lovvorn 2004). Thus, it seems *Potamocorbula* does not depend on energy stores during periods of stress.

One of the reasons why *C. fluminea* is successful in so many different environments is that it can effectively filter both phytoplankton and bacteria out of the water column and deposit feed when food becomes scarce in the water column. *Corbicula's* pumping rate is much lower than *Potamocorbula's* (~100 L/g AFDW/day at 20°C, Foe and Knight (1986)). Like *Potamocorbula*, *Corbicula* can consume larval copepods and other zooplankton (Bolam et al 2019, Rong et al. 2021). Unlike *Potamocorbula*, *Corbicula* does depend on stored energy in times of stress (Ortmann and Grieshaber 2003).

Salinity and X2

Most euryhaline bivalves are osmo-conformers with the ability to regulate their extracellular and intracellular haemolytic fluids with salinity changes up to some limit (Sokolov and Sokolova 2019). *Corbicula* closes its valves with salinities above 20 for up to 19 days before they die. *Corbicula's* salinity tolerance is limited by food availability (Ferreira-Rodriguez and Pardo 2015). The change in *Corbicula's* presence in Suisun Bay, which was common following wet years until the decline in phytoplankton in 1987 (Crauder et al. 2016, figure 39-40), may be a result of the reduction of phytoplankton. If so, *Corbicula's* persistent presence in the bay will be unlikely until the phytoplankton blooms return.

Potamocorbula can adapt to changes in salinity within 48 hours, can tolerate very low salinities (0.1) in the laboratory, but dies with 'prolonged' freshwater exposure (Werner et al. 2004).

Corbicula and *Potamocorbula* co-exist in the X2 zone because the salinity threshold for juvenile/larval settlement of both species is 2 (≥2 for *Potamocorbula* and ≤2 for *Corbicula*). Adults of both species are more tolerant of osmotic stress than the juveniles so adult *Potamocorbula* can frequently be found in freshwater and *Corbicula* is frequently seen in salinities around 5. Neither species reach their maximum biomass in the X2 zone where the salinity varies at tidal and longer time scales. Each bivalve's biomass peaks either upstream or downstream of X2 where the salinity is more appropriate for the species.

Predators

Adult *Potamocorbula* in the SFE are preyed on by Dungeness crab (*Cancer magister*, Carlton et al. 1990, Stewart et al. 2004), Sacramento Splittail (*Pogonichthys macrolepidotus*, Deng et al. 2007), White Sturgeon (*Acipenser transmontanus*, Adams et al. 2007, Urquhart and Regalado, 1991, Kogut 2008), and Green Sturgeon (*Acipenser medirostris*) (Adams et al. 2007) and diving ducks (Poulton et al. 2002, Hunt et al. 2003). Juvenile *Potamocorbula* are eaten by an exotic opisthobranch, *Philine auriformis,* in the more saline portion of the estuary (e.g. San Pablo Bay, Gosliner 1995).

Corbicula's shell is a good natural defense against most predators; once the shell exceeds ≈6mm in length the forces required to crack the shell greatly increase (Kennedy and Blundon 1983). There is little data on predation on *Corbicula* in SFE although we know they are consumed by demersal fish, large invertebrates, diving ducks, mammals, and sometimes by humans in other systems.

How do *Corbicula* and *Potamocorbula* affect the Delta Smelt food web?

Corbicula and *Potamocorbula* may have similar effects on the food web of Delta Smelt although the effects will be concentrated in different locations. Both bivalves can rapidly filter phytoplankton out of the water column, change the size distribution of phytoplankton, and filter small zooplankton and zooplankton larvae/juveniles (see summary in Kimmerer and Thompson 2014, Bolam et al 2019, and Ilarri and Sousa 2021). Although *Corbicula* has the potential for very high biomass relative to *Potamocorbula*, their low pumping rate (25% of *Potamocorbula's* rate) results in a balance of the grazing effects of the two species. When located in key areas for phytoplankton production (areas with good light availability, shallow water, abundant nutrients, and relatively long residence time) bivalve filter feeders can effectively "over-graze" the phytoplankton resulting in a low net growth rate of the phytoplankton (Lucas and Thompson 2012). This leaves pelagic secondary producers (zooplankton, mysid shrimp, Anchovies, etc) and their predators (eg. Delta Smelt) with little available food. When phytoplankton is produced in an amenable environment with little grazing, the phytoplankton can grow and be transported into the wider system where it can continue to grow and be consumed. These routes (conduits) from areas that produce phytoplankton to the wider system are commonly populated by filter feeding bivalves that take advantage of the food delivery and reduce the effectiveness of the transport. For example, *Corbicula* can build large populations in sloughs surrounding flooded islands that may be good areas to produce phytoplankton (Lopez et al 2006). Similarly, both *Corbicula* and *Potamocorbula*, occupy the larger sloughs of Suisun Marsh (Baumsteiger 2017), presumably benefitting from food produced in the shallow marsh. Although the grazing effect may be limited in many of these transport corridors due to the large water depth, the grazing can still reduce phytoplankton biomass (Lucas et al 2009, Thompson et al 2008).

Analysis Plan

To understand the effects of *Potamocorbula* and *Corbicula* on the Delta Smelt food web we need to know how successfully each bivalve species lives in environments that may or may not change as a result of varying freshwater flow. We will do this by exploring both species reactions to wet, dry, and year after wet years in the 10 years in which bivalve data is available (2007-2018).

Our goal is to end with a summary of how a range of hydrographic records (timing and magnitude of freshwater flow) affect (1) basic patterns of bivalve occurrence in the Delta and SFE, (2) the bivalves potential for reduction in phytoplankton growth based on these patterns, (3) areas of non-persistent bivalve populations, and (4) bivalves in conduits that transport produced phytoplankton to other less productive areas.

Data Sources

This summary includes a description of where each bivalve species resides with an emphasis on their biomass and grazing rate patterns in response to known limits on their distribution. We will use the spatial and temporal distribution of both bivalves during extreme freshwater events. These events help define controls on the distribution of these estuarine and freshwater bivalves that are critical in phytoplankton growth rate (phytoplankton bloom development) in the low salinity zone of the SFE.

The only agency consistently collecting benthic samples in the bay and delta is the California Department of Water Resources (DWR) as part of the Environmental Monitoring Program. They have collected samples since 1977 and today collect monthly samples at 10 stations in the northern estuary and delta. In addition to this time series collection, DWR also collected spatially intensive samples (175 stations, Figure 1) from 2008-2019 every May and October. The GRTS samples were subdivided into geographic areas that represent watersheds, relative tidal affects, and habitat type (Figure 1). These geographic areas were used in the analyses of the data. Both the monthly monitoring samples and the GRTS samples, in addition to samples collected by the USGS, were used by the USGS to estimate biomass of the bivalves and to calculate grazing rate and have been released in data reports and official data bases (Crauder et al 2016, Parchaso et al 2020, Shrader et al 2020a, Shrader et al 2020b, Shrader et al. 2020c, Zierdt et al, 2021). This report concentrates on the GRTS samples.

The bivalve grazing rate method is summarized in Kimmerer and Thompson 2014. Median is used in the summary calculations instead of the mean because the data are not normally distributed.

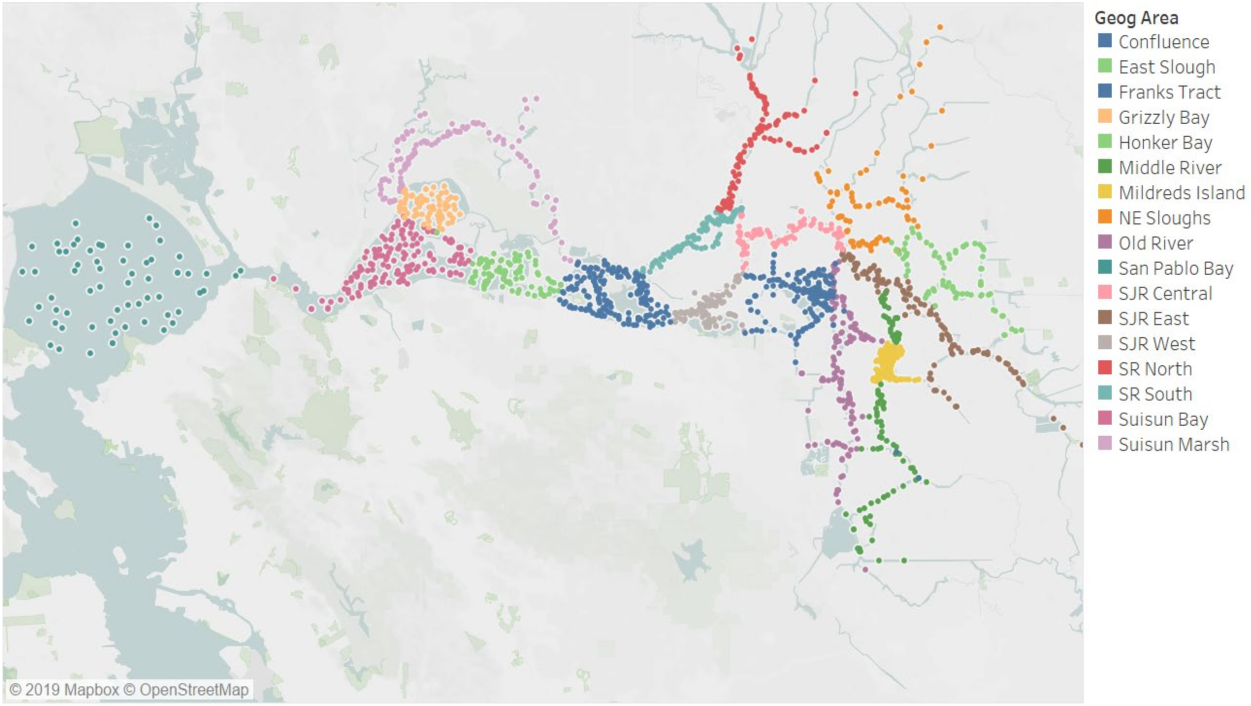

Figure 1. GRTS station locations with geographic areas used in the analyses denoted by color

Spatial Biomass and Grazing Distribution of *Corbicula* and *Potamocorbula* in May and October 2007-2018

How to make a bloom: When there is sufficient freshwater flow to reduce the bivalve presence, the residence time is usually short resulting in increased turbidity and low light availability which is not good for phytoplankton growth. Therefore, the scenario of reduced bivalve biomass during spring yielding an increase in spring phytoplankton growth is possible but dependent on non-bivalve factors. Spring *Potamocorbula* grazing in the LSZ is usually low and increases into fall when their grazing rate is sufficient to impair phytoplankton growth (Kimmerer and Thompson 2014). During years with a large enough freshwater outflow in spring to limit *Potamocorbula* recruitment and to stress adults, the fall grazing rate may also be reduced. Fall periods following wet springs may have favorable light and residence time, which could lead to increased phytoplankton growth. In general *Corbicula's* grazing rate is much lower than *Potamocorbula's* grazing rate. Although we have seen island-scale effects of *Corbicula* grazing on phytoplankton (Lopez et al 2006, Lucas et al 2002), there are no studies showing *Corbicula* grazing in the Delta to have similar phytoplankton effects as that observed with *Potamocorbula* in SFE.

First Impressions Corbicula's and Potamocorbula's distributions

At first glance (Figure 2) *Corbicula* biomass is mostly larger than *Potamocorbula* biomass. *Corbicula* biomass is greater in May than in October, whereas the opposite is true of *Potamocorbula* biomass which is larger in October than in May (Figure 2). *Potamocorbula* biomass is greatly reduced each spring and as summarized in Kimmerer and Thompson (2014), is most likely due to bird predation in the shallows each fall. The maximum median *Corbicula* biomass (50 g ash free dry weight (AFDW)/m^2) shown here is about 20 gC/m^2 using the bivalve ratio of 1 g AFDW ~0.41 gC (personal communication Robin Stewart, USGS). Similarly, the maximum *Potamocorbula* biomass in these data is 40 gAFDW/m^2 or about 16 gC/m^2.

The largest *Corbicula* biomass values were found in the northern Delta (SR North and South and the NE sloughs) and the second largest biomass values were in the central Delta in Mildreds Is. and Middle River (Figure 2).

The largest and most inter-annually consistent biomass pattern for *Potamocorbula* was found in Suisun and Grizzly Bays. San Pablo Bay *Potamocorbula* biomass has not been included in our geographic and annual medians because their biomass seems most related to a predator that is not annually predictable, but the data have been included in Figures 2 and 3 and will be discussed in general terms.

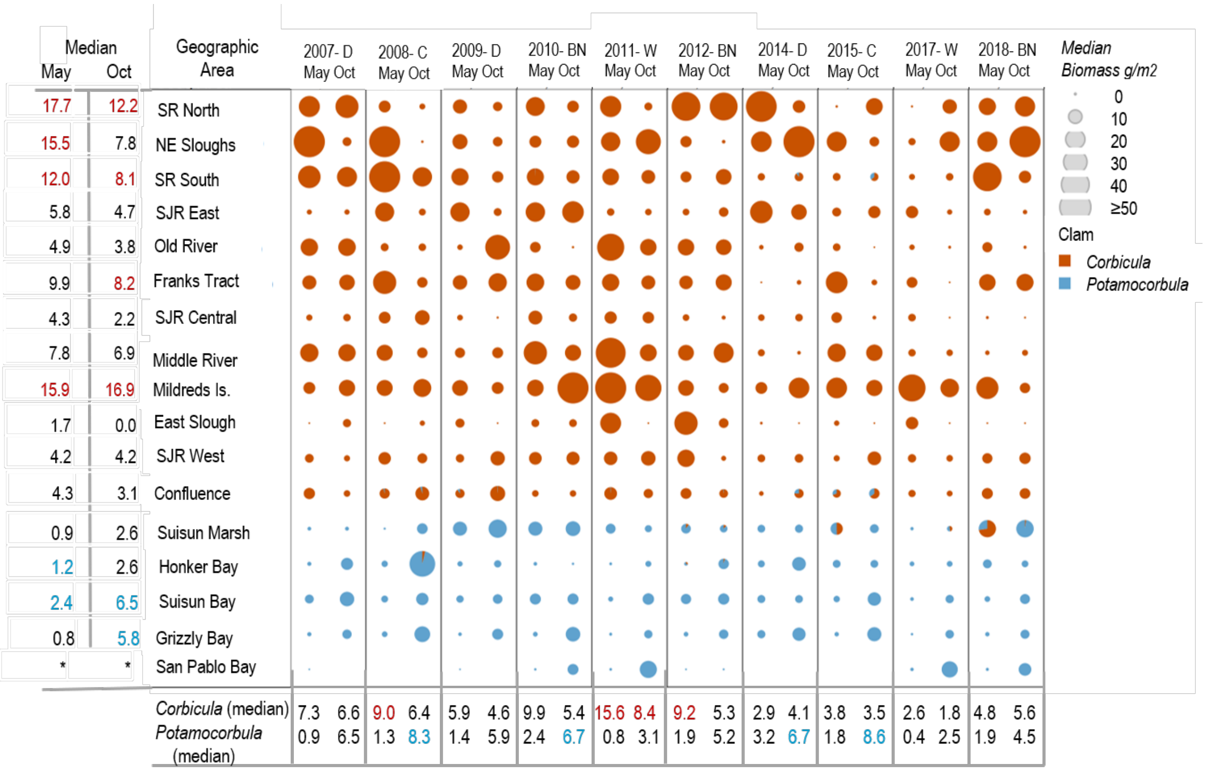

Figure 2. Median biomass in all geographic areas of the GRTS study 2007-2018 (excluding 2013 and 2016). *Corbicula* values are brown circles and *Potamocorbula* are blue circles. Areas where the bivalves overlap are shown as pie diagrams. Geographic median values are shown on the left and annual median values for each bivalve is shown on the bottom.

Figure 3 best represents the grazing effect the bivalves could have on the phytoplankton and small zooplankton at each month and location. Although grazing rate (GR) is related to biomass (GR=biomass x pumping rate), we see a different distribution of magnitudes in Figure 3 than seen in Figure 2. The grazing rate turnover (GRTO) shown here is grazing rate normalized by depth ((m^3/m^2/day)/(m)= /day) and it allows us to compare locations for grazing effects that incorporates depth differences. GRTO is an estimate of the number of times in a day a square meter of clams can filter through the water column above them, assuming the water column is well mixed and stationary. The higher pumping rates of *Potamocorbula* and shallower depths in much of SFE than in the Delta result in larger median GRTO values for *Potamocorbula* (~0.4/day) than for *Corbicula* (~0.1/day) (Figure 3). Many of the locations in the Sacramento River have a diminished presence in Figure 3 relative to Figure 2 because the water depth reduces the impact of the grazing in the deep water. The most apparent pattern seen is that *Potamocorbula* has a larger grazing effect than *Corbicula* and that fall is the dominant season of grazing. In general a GRTO >0.4/d is considered significant given normal conditions for phytoplankton; this GRTO means the bivalves filter through the water column every 2.5 days which can then be compared to the phytoplankton doubling rate to get an estimate of the importance of the grazing.

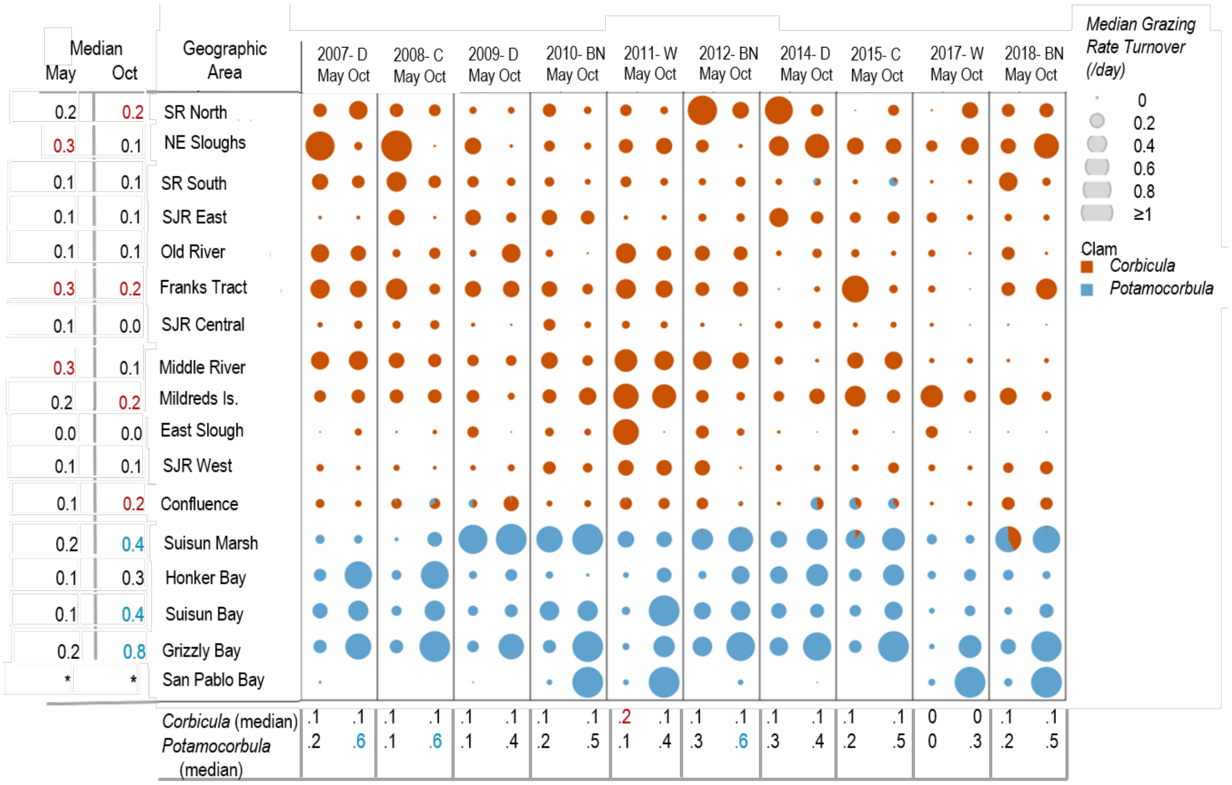

Figure 3. Median GRTO values in all geographic areas of the GRTS study 2007-2018 (excluding 2013 and 2016). *Corbicula* values are brown circles and *Potamocorbula* are blue circles. Areas where the bivalves overlap are shown as pie diagrams. Geographic median values are shown on the left and annual median values for each bivalve is shown on the bottom.

The distribution of both species in Figures 2 and 3 is largely due to recruitment success or failure, food availability (an unknown), and predation success or failure (also unknown). *Corbicula* distribution is a combination of the success of recruits that can occur throughout the year and the transport of all sizes of bivalves downriver with strong currents. This latter point is the explanation for the phenomenon of the sudden appearance of mature year classes or the disappearance of entire size ranges of bivalves from previously sampled locations despite the presence of freshwater.

If recruited in spring *Potamocorbula* biomass will peak in fall, followed by a large die-off of the population or predation event in the shallow water. Spring recruits become reproductive by the following fall and spring. Larvae unable to recruit in spring due to water quality issues (e.g., salinity is too low), can be recruited in fall but appear to be less successful than spring recruits, possibly a result of less food and more environmental stresses in winter.

Hydrographic Years

Wet Years (2011 and 2017)

We have data in two wet years, and conditions in neither of those years were catastrophic for either bivalve species. The biomass and GRTO of both species did however decline substantially in 2017 when the hydrograph increased in January and continued through April. The high freshwater flow was likely a challenge for juvenile and adult bivalves of both species in spring 2017. *Corbicula* biomass continued to be very low into October 2017 except in SR North, NE Sloughs and Mildred Island (Figure 2). Both the low biomass and low GRTO of both bivalves (median for both bivalves was <0.1/d) in May and October of 2017 may have resulted in increased phytoplankton growth. However, the reduced residence time and increased turbidity that was present in May 2017 likely compensated for any benefit of the reduced clam grazing. It is however possible that reduced grazing in October 2017 throughout most of the Delta (Figure 3) allowed for an increase in phytoplankton biomass at some locations. Similarly, Honker Bay and Suisun Marsh may have been amenable to increased phytoplankton growth. Suisun Marsh area, which is entirely focused on the large sloughs, is a conduit for food from the marsh out into the bay which might have been particularly successful in 2017 given the low GRTO (<0.1/d) in those sloughs.

In contrast, 2011 was a good year for *Corbicula* with biomass in May and October 2011 being the largest seen during the study. The hydrograph in 2011 was low until late March and this freshwater or some coincident environmental factor reduced the May 2011 *Potamocorbula* biomass to values lower relative to all other years except May 2017. May decreases in *Potamocorbula* biomass were likely a result of reduced recruitment in spring. *Potamocorbula* biomass was also lower in Oct 2011 and the continuing low biomass into October supports the assumption that the May 2011 recruitment was reduced.

However, *Potamocorbula* were not removed and were mostly thriving in the fall of the year following the wet years (2007, 2012, 2018). GRTO during these post wet year fall periods was also high enough (0.5-0.6/d) to limit phytoplankton growth with normal fall conditions. DWR/EMP benthic monitoring station data in Grizzly Bay (station D7) shows *Potamocorbula* biomass seasonally decreasing and not disappearing in the wet years 1995-1999 and returning to normal biomass levels in the 2000's (Crauder et al 2016). Thus, it seems doubtful that freshwater will eliminate *Potamocorbula* from SFE as that was an extraordinary period of freshwater flow.

The response of the bivalves to these two wet years is evidence that the timing and magnitude of the freshwater flow are important in understanding the effect of salinity and freshwater outflow on the bivalve dynamics, ie. not all wet years are alike. It seems that more freshwater, such as seen in 2017, was best at removing bivalves, even the freshwater tolerant *Corbicula*.

Dry and Below Normal Years after Wet Years (2007, 2012, 2018)

The length of the effect of freshwater flow events on *Potamocorbula* and *Corbicula* populations help us understand the limitations of assuming the biomass and GRTO will be low following a single freshwater event. Neither bivalve showed any major reduction in biomass during May following the wet years; although 2006 was not sampled as part of GRTS, it was a wet year that was similar in magnitude and timing of freshwater flow as 2017 and therefore we are able to include an analysis of the 2007 bivalve data. The large *Corbicula* biomass in May following all three wet years is associated with northern watersheds (Sacramento River, Mokelumne River/NE Sloughs) and could be a result of adults and juveniles being washed downstream during the wet years or recruitment of juveniles with rapid growth. The GRTO for these regions was low (0.2-0.3/d); the higher values may have been high enough to affect the phytoplankton growth. The data were not consistent enough to say that *Potamocorbula* benefitted or was hurt following wet years, but the GRTO values in October (medians of 0.4 and 0.6/d) were sufficient to reduce phytoplankton growth given low turbidity and residence time common in fall.

Droughts – Three years of Critically Dry and Dry Years (2007-2009,2013-2015)

There were positive and negative effects of the droughts on these two invasive species. We can assess years 2 and 3 of two drought periods but year one comparison is hampered by the lack of bivalve data in the dry year 2013. *Potamocorbula* biomass increased from May to October in the second and third year of both droughts similar to what occurs in non-drought years and were a significant grazing presence by October of those years. *Corbicula* biomass was much lower in the second drought (2013-2015) than the first drought (2007-2009) with SR South, Old River, and East Slough areas showing much smaller biomass in the second drought (Figure 2). It is not clear if *Corbicula* at those locations were particularly susceptible to reduced flow or to some other environmental stressor. The second drought was more severe than the first drought possibly leading to some threshold of an unknown environmental stressor. *Corbicula* GRTO values during both droughts were ~0.1/d. This means it would take 10 days for the *Corbicula* to totally filter the water column. GRTO values at this level are essentially zero as the assumptions, that the water column is stationary and well mixed are unlikely to be true for 1 day much less 10 days.

Summary

1. Some basic patterns of bivalve occurrence are consistent within all hydrographic water years. *Corbicula* biomass is larger than *Potamocorbula* in most instances. *Corbicula* biomass is greater in May than October whereas *Potamocorbula* biomass is larger in October than May. The two species overlap in the X2 region.
2. (2) Bivalves can limit phytoplankton growth in shallow water with long residence times. *Potamocorbula* May GRTO values show that some spring grazing is high enough to challenge phytoplankton in spring. However, the very large grazing rates in October (GRTO 0.5 – 1/d) will almost always limit a fall bloom in a well-mixed water column. *Corbicula* probably lives in many shallow habitats in the Delta that were not sampled for logistical reasons. The shallowest areas, Franks Tract and Mildreds Is., did experience periods when the GRTO of *Corbicula* was high enough to challenge the phytoplankton but those conditions did not persist throughout the study period.
3. (3) San Pablo Bay has a non-persistent *Potamocorbula* population that has potentially large effects when present. Biomass and GRTO is very low in Potamocorbula in May when they are present. However, GRTO values increase to ~1/d in October. These bivalves may be capable of controlling the phytoplankton growth, at least on the broad shoals in October of the years they are present (2010-2011, 2017-2018 in this study).
4. (4) The best example of a conduit between phytoplankton producer areas and the broader system are the large sloughs in Suisun Marsh. These areas have high GRTO values (0.5-1/d) in all years except 2007-2008 and 2018. In most years the grazing is sufficiently high to reduce our enthusiasm for these sloughs as conduits being a safe harbor for phytoplankton. Other conduits are likely present in the Delta but the sampling, although remarkably broad, did not include everything e.g., Yolo Bypass.

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6. How Aquatic Vegetation Affects and is Affected by the Delta Ecosystem and Food Web

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Introduction

Floating and submerged aquatic macrophytes are widespread in the Sacramento – San Joaquin Delta (Delta) and currently occupy approximately a third of the waterways (Ustin et al. 2015, 2020). Submerged Aquatic Vegetation (SAV) constitutes about 80% of this invaded area while Floating Aquatic Vegetation (FAV) occupies the rest. In 2004, less than 20% of the waterways were invaded by SAV and FAV and cover dropped to just 10% in 2008. During the drought years, their cover continued to increase, reaching a peak in 2017 at 43% of waterways (Ustin et al. 2008, 2015, 2019, 2020). This increase in invaded area has brought significant changes to the Delta ecosystem. This review describes i) the SAV and FAV community in the Delta and their invasion history, ii) how the physical environment affects floating and submerged species, iii) how they, in turn, change the habitat through positive feedbacks to facilitate their own spread and persistence, and finally, iv) how they interact with and impact other trophic levels of the aquatic food web such as phytoplankton, zooplankton and fish.

The aquatic vegetation community

Table 1 summarizes the SAV and FAV native and non-native species found in the Delta. One of the earliest aquatic macrophyte invaders in the Delta was *Eichhornia crassipes* (recently renamed to *Pontederia crassipes*) which arrived more than a century ago (Finlayson 1983). The most recent invader is *Alternanthera philoxeroides* which was first discovered in the Delta in 2017 (Calflora 2020). Three of the four most common SAV species in the Delta are invasive: *Egeria densa*, *Myriophyllum spicatum*, and *Cabomba caroliniana* (Table 1). The most common native SAV species is *Ceratophyllum demersum*, which has benefitted from its association with *E. densa* (Santos et al. 2010). Non-native species comprise 75% of total SAV cover (Table 1). A new invasive first recorded in 2017 (but likely present since 2014) has been identified as *Vallisneria australis*. *V. australis* has a very dense growth form and has the potential to seriously impact the Delta ecosystem if it spreads over greater areas. Among floating macrophytes, the two most common invaders, *P. crassipes* and *Ludwigia* spp. comprise most of the total FAV cover. This may change as the two new invasive FAV species, *Limnobium laevigatum* and *A. philoxeroides* become more established in the Delta.

Table 1: Native and non-native submerged and floating aquatic species found in the Delta and the likely year of colonization for non-native species. Relative cover of SAV species is with respect to the SAV community recorded at a field data location and FAV species with respect to the FAV community at its respective field data location. **Hydrilla* is a potential invader which is already present upstream of the Delta but is not in the Delta yet. $^{+}$*A. philoxeroides* is a very recent invader and insufficient data is available to estimate its relative cover in the Delta.

Common name (Scientific name)	**Status (year of invasion in Delta)**	**Relative cover of species in 2019**
Brazilian waterweed (*Egeria densa*)	**Non-native SAV (1946)**	**51.9%**
Watermilfoil (*Myriophyllum spicatum*)	**Non-native SAV (1979)**	**12.6%**
Fanwort (*Cabomba caroliniana*)	**Non-native SAV (1980)**	**6.7%**
Curly leaf pondweed (*Potamogeton crispus*)	**Non-native SAV (1946)**	**3.0%**
Ribbon grass (*Vallisneria australis*)	**Non-native SAV (~2014)**	**< 1%**
Waterthyme (*Hydrilla verticillata*)	**Non-native SAV (1976 upstream of Delta)**	**0%***
Coontail (*Ceratophyllum demersum*)	**Native SAV**	**13.4%**
Sago pondweed (*Stuckenia pectinata*)	**Native SAV**	**4.0%**
American pondweed (*Potamogeton nodosus*)	**Native SAV**	**< 1%**
Richardson's Pondweed (*Potamogeton richardsonii*)	**Native SAV**	**4.0%**
Waterweed (*Elodea canadensis*)	**Native SAV**	**3.2%**
American pondweed (*Potamogeton nodosus*)	**Native SAV**	**< 1%**
Southern Naiad (*Najas guadalupensis*)	**Native SAV**	**< 1%**
Upright Burhead (*Echinodorus berteroi*)	**Native SAV**	**< 1%**
Water primrose (*Ludwigia* spp.)	**Non-native FAV (1949)**	**67.5%**
Water hyacinth (*Pontederia crassipes*)	**Non-native FAV (1904)**	**24.4%**
Spongeplant (*Limnobium laevigatum*)	**Non-native FAV (2008)**	**< 1%**
Alligator weed (*Alternanthera philoxeroides*)	**Non-native FAV (2017)**	**NA$^+$**
Water pennywort (*Hydrocotyle umbellata*)	**Native FAV**	**< 1%**
Duckweed (*Lemna* spp.)	**Native FAV**	**< 1%**
Mosquito fern (*Azolla* spp.)	**Native FAV**	**3.9%**

Impact of the environment on SAV and FAV

Variable flow and water levels

All three major floating invasive species, *P. crassipes*, *Ludwigia* and *A. philoxeroides*, are somewhat resistant to variability in water levels. Both *A. philoxeroides* and *Ludwigia* can tolerate periodic flooding and drying (Shen et al. 2005; Thouvenot et al. 2013; Chen et al. 2013). *P. crassipes* is a true floating plant but when lower water levels strand a patch on land, it develops roots and survives. If the water level then goes up and submerges the entire patch during active growth, it redevelops floats and floats back to the surface. If the water levels rise too rapidly after a dry period, the plant can drown before it develops floats but that would be rare in an estuary like the Delta (Penfound and Earle 1948). *P. crassipes* needs a lot of sunlight to sustain its high growth rate hence years with more cloud cover through the wet season are known to depress growth of this species (Williams et al. 2005).

During wet years, SAV might be relatively more resistant to high flows because SAV species are rooted. However, niche occupancy studies indicate that both SAV and FAV are limited by depth and velocity while SAV is also limited by turbidity (Durand et al. 2016); Khanna et al. unpublished data). During high flows in wet years, velocity, depth, and turbidity all rise, leading to decrease in SAV and FAV. During dry years, lower velocities, depth, and turbidity allow both SAV and FAV to increase their niche space and colonize new areas. These areas (depending on duration of the drought or dry period) can then be subject to positive feedbacks by these species leading to continued colonization even after conditions have changed (Kimmerer et al. 2019). Some proof of this response in the Delta comes from the recent California drought. Both FAV and SAV expanded in cover during the drought years increasing the total area of waterways invaded to almost 40% (Khanna et al. 2015; Ustin et al. 2015). Higher salinity during the drought did not have much impact on SAV extent, although it possibly changed the community composition in some areas (Kimmerer et al. 2019).

High and low temperatures

All three FAV invasive species are sensitive to below freezing temperatures but *Ludwigia* likely has the highest tolerance and is known to survive temperatures of -10°C (Sainty et al. 1997; Wilson et al. 2005; Armitage et al. 2013; Thouvenot et al. 2013). *Ludwigia* optimum growth happens between 20-30°C while *A. philoxeroides* shows strong growth between 10-35°C (Shen et al. 2005; Thouvenot et al. 2013). *P. crassipes* optimal growth is at approximately 26°C, it can tolerate temperatures between 1-40°C but cannot tolerate below freezing and > 34°C temperatures for extended periods of time (Penfound and Earle 1948; Wilson et al. 2005). Among SAV species, temperate climate species are more tolerant of cold temperatures and show strong growth between 10-25°C for *S. pectinata* and *M. spicatum* and 13-27°C for *C. caroliniana* (Madsen. J. D. and Smith. D. H. 1997; Pilon and Santamaria 2002; Wilson et al. 2007). Optimal temperature for *E. densa* is 21-23°C but growth reduces if there is sustained increase in temperature over 21°C (Barko and Smart 1981; Borgnis and Boyer 2016). Temperatures above 30°C are stressful for *E. densa*, especially at higher salinities (Borgnis and

Boyer 2016). That is why *E. densa* phenology in the Delta generally shows a dip in peak summer (Santos et al. 2010). *M. spicatum* is susceptible to extended periods of below-freezing temperatures (Aiken et al. 1979) but *C. caroliniana* and *E. densa* are resistant to low temperatures (Wilson et al. 2007).

Impact of SAV and FAV on the environment

Hydrology and substrate

Aquatic invasive species have had a major impact on the Delta ecosystem by changing both the physical environment and the food web interactions in the Delta. SAV and FAV have modified channel bathymetry, water temperature, velocity, turbidity, and availability of light and dissolved oxygen in the water column (Wilcock et al. 1999; Dandelot et al. 2005; Nehring and Kolthoff 2011; Lacy et al. 2020). Through these impacts, it has directly affected ecosystem services such as nutrient cycling, sedimentation, succession, and carbon sequestration (Cook and Urmi-König 1984; Drexler et al. 2020). Submerged and floating species do not affect the ecosystem in the same way. SAV, especially *E. densa*, has been shown to reduce water velocity through their mats by more than 90% (Lacy et al. 2020) leading to settling of sediment within the SAV mats and lower turbidity in the water column (Hestir et al. 2016). The settling sediment results in much finer grain substrate under the mats compared to within the channel and C accumulation (Drexler et al. 2020; Lacy et al. 2020). The presence of SAV mats to some extent also deflects water into the main channel bypassing the mat leading to channel incision (Wilcock et al. 1999). The impact of FAV on velocity or turbidity is less clear. *Ludwigia* slows down water flow and accelerates sedimentation due to its huge biomass (Dandelot et al. 2005; Nehring and Kolthoff 2011) eventually leading to hyper-sedimentation, silting and much lower channel volume within the waterways, thereby increasing chance and frequency of flooding (Sears et al. 2006; Thouvenot et al. 2013).

Light availability and nutrient cycling

FAV and SAV can have opposite impacts on light availability in the water column. While SAV species can improve light availability in the first few feet of the water column by reducing turbidity, it can also reduce light within the mat due to shading (Pokorný et al. 1984). Whereas, FAV mats cover the water surface thus shading out the entire water column below the mat (Nehring and Kolthoff 2011; Hestir et al. 2016). Rake data collected in the Delta have shown that no SAV are able to survive below FAV mats (Khanna and Lay, personal observation). Studies have indicated that both SAV and FAV reduce Dissolved Oxygen (DO) in the water column (Penfound and Earle 1948; Grimaldo and Hymanson 1999; Dandelot et al. 2005; Nehring and Kolthoff 2011). FAV generally reduces DO by increasing microbial growth due to accumulation of organic matter thus inducing anoxic conditions detrimental to aquatic life (Penfound and Earle 1948; Dandelot et al. 2005). Consistent with these observed patterns, Tobias et al. (2019) found that after patches of *P. crassipes* were treated in the Delta, DO increased, relative to baseline values for the region. Reduced DO, in turn, mobilizes

Phosphorous (P) from the substrate making it available for uptake and changing nutrient cycling pathways in invaded areas (Aiken et al. 1979; Cook and Urmi-König 1984; Mazzeo et al. 2003).

Water temperature

Finally, both SAV and FAV also have an impact on water temperature which can affect fauna in higher trophic levels. *E. densa* and other SAV lead to higher temperatures in the top of the water column (Aiken et al. 1979; Grimaldo and Hymanson 1999; Wilcock et al. 1999) likely because water residence time is high and the sun has time to warm up the pocket of mostly stationary water. Penfound and Earle (1948) found that temperatures within a *P. crassipes* mat were more uniform than in open water. It is unclear whether FAV reduces or increases the water temperature because it likely increases water residence time but also shades the water column from solar radiation. There is some indication that evapotranspiration losses of water through FAV mats might be higher than loss of water through evaporation in open water areas (Penfound and Earle 1948) but more study is needed to disentangle the mechanisms involved.

SAV and FAV interactions with other trophic levels

Phytoplankton

Few studies in the Delta have focused on interactions between aquatic vegetation and phytoplankton. However, from other systems we know, aquatic vegetation can affect phytoplankton through a variety of direct and indirect pathways. The canopy formed by FAV and SAV can block light required by pelagic and benthic phytoplankton (Pokorný et al. 1984; Andersen et al. 2017). The structural complexity created by vegetation in the water column also reduces flow rates and turbulence of the water column (Marshall and Westlake 1990; Losee and Wetzel 1993; Work et al. 2020). Reduced turbulence can increase sedimentation loss of phytoplankton, particularly large-bodied taxa like diatoms (Reynolds 1987) but can also increase light penetration in the water column, which could benefit phytoplankton (Hestir et al. 2016). Vegetation provides zooplankton with a refuge from fish predation, which can facilitate top-down control of phytoplankton through zooplankton grazing (Timms and Moss 1984; Schriver et al. 1995). However, the strength of this top-down effect likely depends upon how much vegetation also serves as a refuge for zooplankton-feeding macroinvertebrates and fishes. Aquatic vegetation absorbs nutrients from both sediment and water column, reducing those available to phytoplankton (Denny 1972; van Donk et al. 1990, 1993; Sand-Jensen and Borum 1991), and provides surface area for epiphytic algae, which also compete with pelagic phytoplankton for nutrients (Sand-Jensen and Borum 1991). In addition, some aquatic plant species produce allelopathic chemicals that inhibit phytoplankton growth (Nakai et al. 1999; Dandelot et al. 2008; Hilt and Gross 2008; Vanderstukken et al. 2011). Some of the most dominant SAV species in the Delta are known to produce these allelopathic chemicals, including *Ceratophyllum demersum, Elodea canadensis, Egeria densa,* and *Myriophyllum spicatum* (Hilt and Gross 2008; Vanderstukken et al. 2011). Studies in other systems have demonstrated that phytoplankton biomass is negatively correlated with aquatic vegetation biomass and that aquatic vegetation can alter phytoplankton community composition (Jones 1990; Schriver et al. 1995; Barrow et al. 2019). It is likely that aquatic vegetation plays an increasingly important role in shaping phytoplankton communities in the Delta, given the rapid spread of vegetation in this ecosystem in recent years.

Zooplankton

Aquatic vegetation can affect the zooplankton community in a variety of ways. Aquatic vegetation, particularly FAV, can reduce dissolved oxygen levels, which can reduce abundances of some invertebrate taxa (Ceschin et al. 2020). Vegetation may also release allelopathic chemicals that have direct negative effects on zooplankton (Van Donk and Van de Bund 2002). Vegetation can affect zooplankton indirectly by reducing pelagic phytoplankton biomass and altering phytoplankton community composition, as mentioned above. However, aquatic vegetation can increase the structural complexity of the environment, which can reduce predation of zooplankton by fish (Timms and Moss 1984). Research in other similar environments has shown that zooplankton communities differ between open water and vegetation-dominated areas (Walseng et al. 2006; Declerck et al. 2007; Bolduc et al. 2016) . There have been few studies of interactions between aquatic vegetation and zooplankton in the Delta, but a pilot study comparing zooplankton in SAV versus adjacent open water showed that total zooplankton abundance was often higher in SAV. However, taxonomic composition of the two habitat types was similar, though it may due to close proximity of the habitats sampled (Rasmussen et al. 2020). Toft et al. (2003) showed that not only was the zooplankton community found in the native *H. umbellata* patches different than that found in *P. crassipes* patches, but the taxa found in *H. umbellata* were common in fish diets and taxa found in *P. crassipes* were not favored by fish. Thus, rapid spread of invasive FAV and SAV in the Delta has the potential to shift both the abundance and composition of the zooplankton community. Because the nutritional value of zooplankton can vary among different taxa (Kratina and Winder 2015), such shifts could potentially impact the diet of zooplanktivores like Delta Smelt.

Fish

The proliferation of invasive SAV has contributed to major changes in the Delta's shallow water fish community, leading to increased dominance of centrarchids that have their origins in the southeastern United States. These dominant non-native species - chiefly Largemouth Bass (*Micropterus salmoides*), Bluegill (*Lepomis macrochirus*), Redear Sunfish (*Lepomis microlophus*) - were introduced to the Delta for recreational fishing in the late 1800s, but their populations were relatively small until the late 1900s when SAV coverage was also expanding(Brown and Michniuk 2007). Today, the Largemouth Bass recreational fishery is world-renowned and large tournaments are frequent and a major component of the Delta economy (Frantzich 2013). The expansion of SAV provides habitat for juvenile Largemouth Bass, which are more abundant in SAV patches (Conrad et al. 2016) as it offers refuge from larger fish that would predate them (Ferrari et al. 2014). For adult Largemouth Bass and other fishes with a lie-in-wait predation style that relies on visual cues to locate prey, the structure of SAV and the associated increase in water clarity provides suitable hunting habitat. At a regional scale, the increase in SAV has meant an increase in biomass for the shallow water fish community (Nobriga et al. 2005), even as biomass in pelagic areas has declined. While both native and non-native fishes may be positively associated with SAV density, in general there is little overlap between them, as their respective microhabitats are also driven by other factors, with native fishes more common in areas with higher turbidity and salinity (Young et al. 2018).

However, the prevalence of SAV has implications for the food web structure of the Delta, and this is an area of current research and discovery. While some early research has suggested that pelagic and shallow-water habitats have functionally distinct food webs (Grimaldo et al. 2009), more recent work indicates a lesser degree of separation and the distinction may be habitat-dependent. Focusing on the North Delta region, Young et al. (2021) found little distinction between littoral and pelagic food webs, and suggest that where SAV is present and habitat diversity is high, SAV and phytoplankton-based trophic pathways may be mixed and inter-dependent. The evolving understanding of how SAV and other forms of aquatic vegetation contribute to food webs in the Delta will inform tidal wetland restoration (Brown et al. 2016), with early indications that supporting a diversity of trophic pathways will lend some ecological resilience, as multiple primary producers are contributing to contemporary Delta food webs (Young et al. 2021).

For Delta Smelt, a species that is unlikely to inhabit vegetated areas even under the immediate threat of predation (Ferrari et al. 2014), the expansion of SAV has meant a direct reduction in habitat area. In recent years, this reduction in habitat has been particularly apparent in the North Delta, a region known for its importance for Delta Smelt spawning and rearing (Hobbs et al. 2019), and where SAV and FAV has seen significant expansion (Ustin et al. 2019). In addition to direct reduction in habitat, the role of SAV in increasing water clarity in the Delta is also detrimental to Delta Smelt because the species relies on turbidity as a predation refuge and as juveniles, for locating food (IEP-MAST 2015). Because of the rarity of Delta Smelt, it is unlikely and uncommon to find evidence of Delta Smelt as dietary items for potential predators that are highly associated with SAV (Schreier et al. 2016; Weinersmith et al. 2019), but SAV expansion and the associated rise of predators are implicated as important factors contributing to the decline of Delta Smelt in system-scale analysis (Mac Nally et al. 2010).

Control of invasive FAV and SAV

As the spread of invasive vegetation in the Delta became more rapid and started affecting the health of the ecosystem and ecosystem services in the 1990s, the need for a control program became more urgent. The California State Parks, Division of Boating and Waterways (DBW) was given the responsibility for controlling invasive aquatic vegetation in the Delta (DBW 2017; Conrad et al. 2020). The control program was mandated in 1982 to control *P. crassipes* in the Delta and Suisun Marsh. DBW began treating *P. crassipes* and *E. densa* in 2001 (Carruthers et al. 2013). The primary objectives of the control program were to improve the ecosystem services of Sacrament-San Joaquin Delta. By controlling the spread of invasives, their impact on navigation, recreation, and water diversions for urban and agricultural needs would be reduced. Benefits to reducing the spread of SAV and FAV in the ecosystem were connected to improving water quality and improving conditions for native species. The control program mainly uses chemical herbicides with some investment in biocontrol and mechanical control and costs about $12-13M annually (Carruthers et al. 2012; Conrad et al. 2020). Under its updated Biological Opinions that require coordination between eight state and federal permitting agencies, DBW is authorized to treat a total of 15,000 acres of combined SAV and FAV (Madsen 2019). Restrictions on locations and timing of treatment make it harder to achieve effective control. Studies that have examined the efficacy of SAV control over the years have found the program to be ineffective in achieving long-term reduction in invasive species (Santos et al. 2009; Rasmussen et al. 2020). A couple of studies of FAV control found similar results soon after the program was implemented (Santos et al. 2009), but a recent study on FAV efficacy is showing promising results, although research is ongoing (Khanna, unpublished data).

The mixed results in the control program bring into focus the strategy of the treatment program and its potential impacts. Field studies are limited but several laboratory studies have been conducted to look at the impacts of the herbicides and their adjuvants on water quality (Tobias et al. 2019) and the foodweb (Hasenbein et al. 2017a, b; Jin et al. 2018; Stillway and Teh 2020). Dissolved oxygen and turbidity increased to ambient conditions following treatments (Tobias et al. 2019). The herbicides used in the program are not equally effective on different invasive species (Ta et al. 2017) and also have impacts on phytoplankton, invertebrates, and fish (Hasenbein et al. 2017a, b; Jin et al. 2018; Stillway and Teh 2020). Results suggest that there were little to no acute impacts at the concentrations detected after herbicide application but several sublethal impacts were detected. These studies were conducted in a controlled setting and can only have some resemblance to the field conditions. A variety of interactions could lead to some additional effects given the complexity of the contaminants in the field and the various sensitivities of a variety of organisms that are found there compared to the controlled test species in the laboratory studies. Further studies should be conducted to examine the costs and benefits of the treatment program and the potential for long-term reduction in invasive aquatic species.

Management and Climate Change

In recent years, flow alteration actions have been considered in order to improve survivability of endangered fish species in the Delta (Kimmerer et al. 2019; Sommer et al. 2020). For example, the Suisun Salinity Marsh Control Gate (SSMSG) action implemented in 2018 was geared towards increasing low-salinity habitat for the endangered delta smelt by keeping the Suisun Marsh fresher during the critical August month (Sommer et al. 2020; Beakes et al. 2021). Most invasive SAV and FAV species are freshwater species hence an increase in fresher habitat can potentially increase the habitat available for colonization, but a corresponding increase in turbidity could minimize that risk. The location of the gates is near propagules of invasive species hence a monitoring program to remain vigilant for increased colonization of both SAV and FAV and keeping an eye on entry of invasives through the control gates is recommended. The drought barrier installed in 2015 during the peak of the last drought is another example of a flow alteration mechanism intended to prevent salinity intrusion into the Delta. This management tool has been installed again in 2021 due to the current drought. Kimmerer et al. (2019) showed that the installation of the drought barrier at the mouth of Frank's Tract in False River in the Delta did have the intended consequence of preventing salinity intrusion in the central Delta, however, it also reduced tidal pumping through Frank's Tract allowing SAV to establish in areas of the tract that had stayed clear for decades. Thus, any flow alteration measures employed by managers in the Delta need to consider the unintended consequences of the actions on invasive SAV and FAV species and the long-term impact on the Delta ecosystem.

Climate change will further complicate control efforts in the Delta and will require a treatment program that is agile and adaptable to changing conditions. Early spring onset will lead to longer growing seasons and likely more SAV and FAV cover in the Delta. Taking clues from the most recent severe drought, drier conditions might also favor increase in area invaded by SAV and FAV in the Delta (Kimmerer et al. 2019). Higher temperatures in summer might depress growth of SAV and FAV (Penfound and Earle 1948; Madsen. J. D. and Smith. D. H. 1997; Shen et al. 2005; Wilson et al. 2007; Thouvenot et al. 2013) but a rise in winter temperatures might offset that by removing the greatest vulnerability some of these invasive species have to below-freezing temperatures (Sainty et al. 1997; Wilson et al. 2005; Armitage et al. 2013). Overall, the rise in year-round temperatures will likely lead to easier overwintering survival and higher growth. More severe storms could help flush out both SAV and FAV because they are sensitive to water velocity (Penfound and Earle 1948; Durand et al. 2016). But the storms alone would likely not be sufficient to reduce invasive species cover in the long run. The ubiquity of SAV and FAV mats surrounding remnant marshes in the Delta and their ability to prevent sediment from reaching the marsh will also make it difficult for marshes to keep up with future sea level rise (Drexler et al. 2020). In conclusion, keeping a check on invasive species spread and persistence in the Delta will require an adaptive management framework that considers the challenges of changing climate.

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7. Range, Distribution, Survival and Population Growth of Delta Smelt

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Introduction

Delta Smelt (*Hypomesus transpacificus*) is an annual fish species endemic to the tidal freshwater and brackish portions of the upper San Francisco Estuary, occurring mostly in the region of low-salinities (0.5 – 6.0) (Bennet 2005; IEP 2015; Hobbs et al. 2019); known as the low salinity zone (LSZ) (MacWilliams et al. 2015). The limited historical distribution of Delta Smelt, along with their short life span, low fecundity, selective feeding, and water quality requirements make this species particularly sensitive to habitat loss and alteration, including water diversions, introduced species, contaminants, food limitation, and other stressors (e.g., Moyle et al. 1992; Bennett 2005; Brooks et al. 2012). Although salinity is considered the most important variable controlling the physical habitat of pelagic estuarine organisms (Dege and Brown 2004; Kimmerer 2004), the LSZ is also historically associated with optimal turbidities for Delta Smelt (Hasenbein et al. 2013) and is relevant to X2, an ecological metric that reflects the influence of outflow on the position of the salinity field along the main axis of the estuary (the distance in km from the Golden Gate bridge to the location where the near bottom salinity is 2) (Jassby et al. 1995; Brown et al. 2014). The location, area, volume, and average depth of the LSZ varies non-monotonically with X2; with such variation being greatly influenced by geometry of the estuary (MacWilliams et al. 2015).

Long-term monitoring of juvenile and subdadult Delta Smelt suggests the population began to decline in the 1980s (Moyle et al. 1992; Moyle et al. 2016) and its low population levels in the 1990s led to both state and federal listings as threatened species, coinciding with increased water diversion during a period of extended drought (Moyle et al. 1992). The invasion of *Potamocorbula amurensis* eliminated summer phytoplankton blooms since 1987 (Kimmerer 2006) but decreases in biomass of mesozooplankton and most fish were somewhat muted. The zooplankton community changed in the late 1980s, coincident with invasion of *P. amurensis*, resulting in decreased abundance of prey historically important to Delta Smelt and other fishes (Winder and Jassby 2011; see FLOAT MAST Delta Smelt Diet Whitepaper for more details.) As a result, the distribution of Northern Anchovy (*Engraulis mordax*) shifted downstream and such shift may have mitigated some of the phytoplankton productivity losses (Kimmerer 2006).

A regime shift occurred in the early 2000s involving steeper population declines of numerous pelagic species, including Delta Smelt, in the upper estuary (Cloern 2007; IEP 2015; Sommer et al. 2007). The Delta Smelt was up-listed to endangered status under the California Endangered Species Act in 2009. Federal up-listing was determined to be warranted but precluded due to other listing priorities (Federal Register 2010). Further declines in the numbers of Delta Smelt caught across all IEP survey since 2013 indicate the population is not meeting distribution and abundance recovery criteria (USFWS 1995), and the species faces increasing risk of extinction unless concerted efforts are taken to improve multiple habitat conditions for this species (e.g., Moyle et al. 2016, Hobbs et al. 2017).

Range & Distribution

Historically, Delta Smelt were observed in all major regions of the estuary covering an area of 51,800 hectares (see Fig. 2 in Merz et al 2011; Bennett 2005). This historical range went as far west as Berkeley in San Francisco Bay, as far north as the confluence of the Sacramento and Feather Rivers (Wang 1991; Sweetnam and Stevens 1993), and as far south as the San Joaquin River near Stockton (Moyle et al. 1992) and inhabited the South Delta year-round (Erkkila *et al.* 1950). They were also found in the tributaries of Napa River, Cache Slough, American River, Mokelumne River, and Calaveras River in the east as well as seasonally flooded habitat in the Yolo Bypass (Fig. 1; Merz et al. 2011; Mahardja et al. 2019).

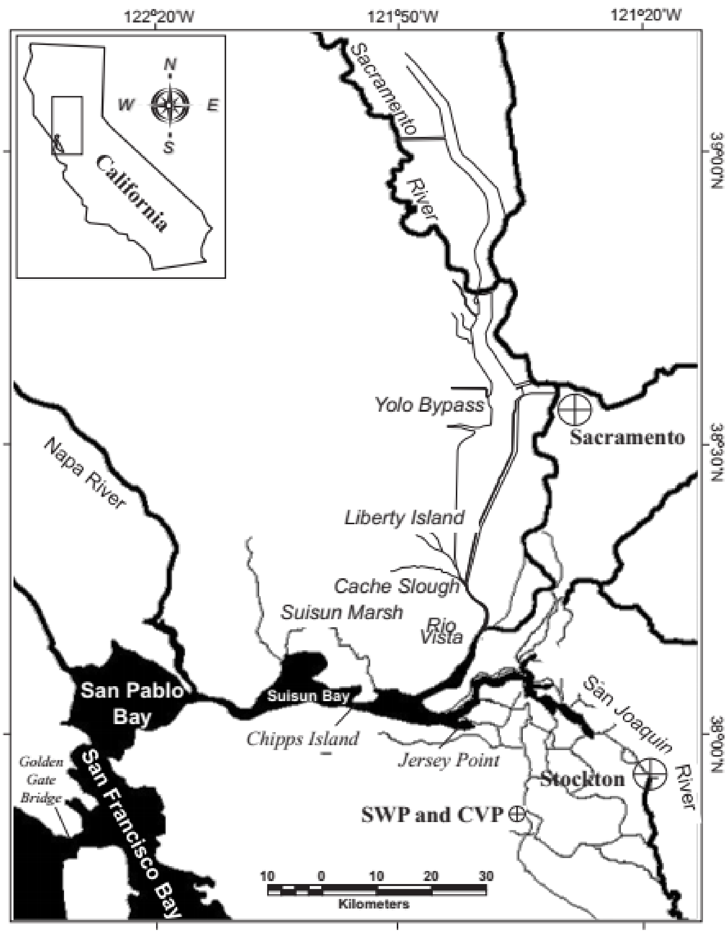

Figure 1. The San Francisco Estuary including key landmarks noted in the text. The Sacramento-San Joaquin Delta is the area between Chipps Island, Sacramento, and just south of Stockton. Image from Sommer and Mejia 2013.

Various meta-analysis of long-term IEP monitoring survey data have shown Delta Smelt are semi-anadromous (Bennett et al. 2002; Dege and Brown 2004; Hobbs et al. 2007; Grimaldo et al. 2009; Sommer et al. 2011) and occupy different habitats of tidal fresh and brackish waters (Bennett 2005; IEP 2015; Moyle et al. 2018; Hobbs et al. 2019). Their habitat varies by life stage (Merz et al. 2011; Sommer and Mejia 2013) and is influenced by freshwater outflow (Sweetnam 1999; Moyle 2002). Analyses of IEP monitoring surveys suggested a year-round segment of the Delta Smelt population in the central region of the lower Sacramento River (Moyle et al. 1992; Dege and Brown 2004) to Suisun Bay (Moyle et al. 1992; Sommer and Mejia 2013), Cache Slough and the Sacramento River Deepwater Ship Channel (Grimaldo et al. 2009; DSC 2010; Sommer et al. 2011). Other portions of the population migrate in the spring for spawning in upstream regions of Napa River, Suisun Marsh, the upper Sacramento River and Cache Slough and mature in the area between Grizzly Bay and the lower Sacramento River (Merz et al. 2011; Sommer et al. 2011). By fall, the highest juvenile and sub-adult densities were usually found further east in the confluence of the Sacramento and San Joaquin Rivers (Merz et al. 2011).

Location of Delta Smelt spawning is associated with freshwater outflow, with spawning occurring mainly above the entrapment zone (Wang 2007). Hence, habitat tends to be more upstream for adults and more seaward for larval and juvenile stages (Sommer and Mejia 2013). Younger planktonic and pelagic life stages tend to occur in low salinity habitats (Dege and Brown 2004; Sommer et al. 2011), and their habitat shifts more upstream of Suisun Bay in drier years (Sommer and Mejia 2013), and periodically use Napa River (Hobbs et al. 2007; Merz et al. 2011; Sommer and Mejia 2013) and San Pablo Bay (Moyle et al. 1992) during wet years. Juvenile delta smelt densities were significantly higher in shallow water in Honker Bay and Sherman Lake than in adjacent channels, indicating that they used shallow areas in bay and flooded island environments as nursery habitats (Aasen 1999), with the North Channel of Suisun Bay acting as critical nursery habitat by providing better feeding and growing conditions than the South Channel (Hobbs et al. 2006). The unique chemical signature in the otoliths of Delta Smelt suggests that this periodic habitat use during high outflow years can be substantial (Hobbs et al. 2007) and suggests they can take advantage of a range of life histories which include freshwater spawning/ freshwater rearing, freshwater spawning/brackish rearing, and brackish spawning/brackish rearing with multiple variations in the specific timing (Hobbs et al. 2010). Semi-anadromous Delta Smelt also have four distinct life-history phenotypes that vary by natal origin, dispersal age, and adult salinity history (Hobbs et al. 2019).

In recent decades there have been major changes in habitat throughout the estuary, including rapid expansion of invasive aquatic weeds (Jassby and Cloern 2000) with an associated decrease in water turbidity (Durand et al. 2016; Hestir et al. 2016, Cloern 2019). This may have contributed to seasonal reductions in habitat suitability for Delta Smelt in the southern Delta (Nobriga et al. 2008) and in area where X2 is located upstream of the Suisun region (Castillo 2019). Since the 2012-2017 drought, Delta Smelt are rarely caught by IEP monitoring programs, with catches mainly limited to the regions around Cache Slough and the Sacramento River Deepwater Ship Channel (Murphy and Weiland 2019; U.S. Fish and Wildlife Service 2021, Tempel et al. 2021).

Drivers of Smelt Distribution

The distribution of Delta Smelt depends on interactions among abiotic and biotic conditions across their life cycle, with most studies focusing on abiotic factors. Salinity (usually measured as specific conductance) influences the distribution of the larval (Mahardja et al. 2017), juvenile (Nobriga et al. 2008), subadult (Feyrer et al. 2007) and adult stages (Castillo et al. 2018). Based on the 10th and 90th percentiles of salinity distribution for Delta Smelt and nine other estuarine species including fishes and invertebrates, Delta smelt exhibited the narrowest optimum salinity range (0.3 - 1.8) at the larval and juvenile stages (Unger 1994). For both juvenile and subadult stages however, Bennett (2005) reported that >90% of the catch occurred at salinities below 6 ppt. Adult Delta Smelt predominated at a salinity of 1.32 ± 1.94 ppt (mean ± sd) (Castillo et al. 2018).

The 50% and 100% cumulative catch of juvenile Delta Smelt in Summer Tow Net Survey (June-August) occurred at temperatures of c.a. 21.5°C and 27°C (Bennett 2005, his figure 5). In contrast, the 50% and 100% cumulative catch of subadult in the Fall Midwater Trawl survey (September–December) occurred respectively at lower water temperatures (16°C and 22.5 °C). Adult Delta Smelt caught in the Spring Kodiak Trawl Survey (January-May) predominated at a temperature of 11.2 ± 2.4 °C (mean ±sd) (Castillo et al. 2018).

High summer water temperatures during the high flow year 2017 could have limited recruitment success of Delta Smelt during the fall (IEP 2021). For Juvenile Delta Smelt acclimated to 11.9, 15.7 and 19.7 °C, Komoroske et al. (2014) reported juvenile Delta Smelt had a critical thermal maximum (CTmax) of 27.1, 28.2 and 28.9 °C. Those CTmax values are consistent with the results of Davis et al. 2019 under single and multiple stressor tests. These experimental results, along with cumulative catch of juvenile Delta Smelt as a function of temperature (Bennett 2005, Komoroske et al. 2014) suggest an earlier estimate of CTmax (25.4 °C; Swanson et al. 2000) underestimates juvenile Delta Smelt tolerance to high temperatures. Nevertheless, comparative thermal physiology (Swanson et al. 2000; Davis et al. 2019) suggest

Delta Smelt may also have disadvantages to cope with introduced species interactions under climate change.

Delta Smelt generally occurred at intermediate levels of turbidity or Secchi depth, including the larval (Mahardja et al. 2017), juvenile (Nobriga et al. 2008, Hasenbein et al. 2013), subadult (Feyrer et al. 2007) and adult stages (Castillo et al. 2018). Turbid conditions are important for feeding of larvae and juveniles (Baskerville et al. 2004; Hasenbein et al. 2013), with a long-term increase of Secchi depth (decreased turbidity) linked to reduced habitat quality for juvenile (Nobriga et al. 2008), and subadult Delta Smelt (Feyrer et al. 2007). The limited Delta Smelt occurrence at low turbidities may involve several non-mutually exclusive factors, including poor abiotic habitat, increased predation risk, and low food availability (IEP 2015; Hestir et al. 2016).

Analyses of multiple abiotic variables revealed that water temperature and turbidity are important predictors of occurrence for young-of-year Delta Smelt. Occupancy probability increases with turbidity, and Delta Smelt occur more often at locations with lower spring and summer temperature (Mahardja et al. 2017). Feyrer et al. (2007) modeled subadult Delta Smelt presence/absence as a function of electrical conductivity (EC), temperature, and Secchi depth. Their models showed EC and Secchi depth were more important than temperature. Although no clear thresholds for “suitable” abiotic habitat components were evident, fish occurrence increased at Secchi depth below 1 m while occurrence reached a peak at EC ~5000 µS cm^{-1}. Predicted fish occurrence declined progressively at EC > 12000 µS cm^{-}1 compared to EC < 5000 µS cm^{-1}. Nobriga et al. (2008) modeled juvenile Delta Smelt presence/absence as a function of EC, temperature, and Secchi depth, and indicated all these covariates were important, with highest probability of occurrence at EC 1000-5000 (c.a. salinity 0.6-3.0), Secchi depth <40 cm, and temperatures less than 24^{o}C. Subadult delta smelt seems to use selective tidal movements to either maintaining position or moving upriver on flood tides and minimizing advection down-estuary on ebb tides (Bennett and Burau 2014). Such fish movement could minimize the energy spent swimming and limit predation risk by remaining in turbid water in response to lateral gradients in water turbidity between the near-shore and mid-channel habitats (Bennett and Burau 2014).

Survival and Population Growth

The 98% reported reduction of adult Delta Smelt during 1995-2015 shows the population is experiencing long-term negative growth, implying unfavorable ecosystem conditions to support robust spawning or over-summer survival of new recruits (Smith et al. 2021). This decline is consistent with the long-term decline in habitat quality and increase in stressors for Delta Smelt (IEP 2015; Moyle et al. 2016; Hobbs et al. 2017; Castillo et al. 2018). No-long term association was detected between juvenile Delta Smelt relative abundance based on the 1959-2000 STN surveys and X2 (Kimmerer 2002). However, a negative relation for these variables was suggested during years 1988 and 2000 and such change apparently occurred well before the step change at the base of the food web attributed to *P. amurensis* (Kimmerer 2002). Reduced fall outflow (i.e., increased X2) was also linked to reduce abiotic habitat and abundance of subadult Delta Smelt (Feyrer et al. 2011), with such association remaining significant over the period 1967 to 2017 (Castillo 2019). Since 2000, the occurrence of years where the average position of X2 in September–October was ≤ 75 km has greatly declined (11.1%) compared to the period 1967–1999 (39.4%) (Castillo 2019). Hence, the long-term increase in X2 position seems a key consideration when evaluating the population response of Delta Smelt to X2 over different timescales. The USFWS's Delta Smelt Life Cycle Model (USFWS LCM) fit to observations from years 1995-2015 did not support a fall X2 effect on Delta Smelt survival (Smith et al. 2021), but it supported a summer outflow effect which contributes to the position of fall X2 at the scale that could limit smelt mortality. Consistent with the general understanding of fish survival across different life stages (Houde 2008), and the estimated Delta Smelt abundance over time and life stages (Bennett 2005; IEP 2015), the USFWS LCM results suggested most of the Delta Smelt mortality occurs prior to the fall. Yet, unlike previous studies for Delta Smelt, the USFWS LCM divided the life cycle using 20mm, TNS, FMWT, and SKT data and estimated mortality across different life stages. Kimmerer et al. (2013) reported an inverse relation between a Delta Smelt habitat index (catch per trawl in the FMWT) and X2, but the slope of this association overlapped the lower 95% confidence limit of the abundance–X2 relation. The slopes for other habitat indices of Delta Smelt (20-mm, STN) to X2 were below their corresponding 95% confidence limits. However, for the period 2003-2013, significant negative associations were apparent between abundance indices for larval-juvenile Delta Smelt and the position of X2 during February-June (IEP 2015), implying that lower February-June X2 favors stronger recruitment of Delta Smelt.

A relevant aspect of historical Delta Smelt catch is the overlap of low salinity, low maximum velocity, and low Secchi depth regions (Bever et al. 2016), with such overlap occurring in Suisun Bay during 2011, coinciding with higher Delta Smelt abundance in 2011 compared to 2010 when the favorable ranges of these metrics did not overlap in Suisun Bay (Bever et al. 2016). Community modeling further suggested the interplay of high fall outflow and community interactions across salinity and spatial gradients across the upper San Francisco estuary tends to favor higher abundance of subadult Delta Smelt when the position of X2 is ≤ 74 km compared to X2 is located at 81 km or 85 km (Castillo 2019).

The USFWS LCM suggested Delta Smelt entrainment mortality is related to environmental conditions used to manage entrainment (south delta turbidity, OMR flow), and recruitment and natural mortality were related to temperature, outflow, food, and predators (Smith et al. 2021). Moreover, entrainment mortality was significantly greater during the late 1990s and early 2000s, compared to mid-1990s and all years after 2006. Declining entrainment mortality in recent years was attributed to control of OMR to more positive than –5,000 cfs during most periods and a long-term trend of less turbid water in the south delta. Although entrainment mortality has been low in recent years, it may have been the dominant source of winter mortality during the early 2000s (Smith et al. 2021), prior to the current entrainment management regime. Smith et al. (2021) also reported recruitment of late-spawned fish was associated with average April-May water temperature, with warm years 2012-2015 showing lower recruitment of late post-larvae compared to most of the earlier years. Estimated post-larvae survival during June to August decreased significantly as delta outflow declined over 1995-2015. Though outflow was the covariate tested, it was considered a multivariate index reflecting factors like food availability, water temperature, and the position of the low salinity zone.

Given the long-term decline of habitat quality indicators for Delta Smelt (Feyrer et al. 2007; Nobriga et al. 2008), the potential for synergistic drivers of population decline is likely increased (e.g., Brook et al. 2008, Castillo 2019). For example, the predominance of years with low Delta outflows or droughts could compound such synergistic effects (e.g., Castillo et al. 2018; Mahardja et al. 2020). Moreover, salinities downstream of the LSZ could impose osmoregulatory costs that limit Delta Smelt ability to acclimate and exploit higher salinity habitats even under more favorable temperatures (Komoroske et al. 2016). Considering that extinction can be driven by amplifying feedbacks and depensatory processes that can be disconnected from the original cause of decline (Berek et al. 2006; Brook et al. 2008), some of the reported stressors during the life cycle of Delta Smelt (IEP 2015; Moyle et al. 2016; Hobbs et al. 2017) are likely self-reinforced by long-term habitat degradation, hydrological and food web alterations, contaminants, introduced species and increased drought severity attributed to climate change (e.g., Nichols et al. 1986; Moyle et al. 2010; IEP 2015; Griffin and Anchukaitis 2014; Mahardja et al. 2020). For example, Delta Smelt was among the species showing a negative association between the FMWT abundance indices and pyrethroid use in the Delta (Fong et al. 2016), and population trends of several pelagic species in the SKT survey, including Delta Smelt, were associated with overall salinity increases due to winter-spring water diversions, both within the Delta and the entire watershed (Castillo et al. 2018). Under these scenarios, mitigation actions only targeting entrainment drivers such as OMR and turbidity may prove insufficient due to cascading unmanaged synergies influenced by stressors and sustained perturbations (e.g., Bennett and Moyle 1996; Castillo 2019). This is consistent with simulation results showing limited probability of population growth under standard management actions (Smith et al. 2021).

Conclusion

The once abundant Delta Smelt has faced dramatic population declines over the past few decades and are now rarely caught in IEP surveys. Their historical range and distribution used to span most freshwater and brackish regions of the estuary but are now mostly limited to a few areas in the Sacramento River, Cache Slough, and the Sacramento River Deepwater Ship Channel. This is likely due to several interacting factors, including entrainment mortality, water contaminants and diversions, reduced zooplanktonic prey, and introduced species, which have resulted in cumulative decline of multiple habitat conditions due to anthropogenic impacts. Standard management actions are now unlikely to improve the Delta Smelt population and the lessons learned from their population collapse should be used to improve management for this species, other declining species, and future species of concern.

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8. Delta Smelt Diet

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Introduction

Zooplankton are important prey for many young fishes in the San Francisco Estuary (SFE), including the endangered Delta Smelt (*Hypomesus transpacificus*). Delta Smelt is a small (usually < 80mm fork length (FL)) fish endemic to the SFE that has experienced considerable declines in the past couple decades (Bennett and Moyle 1996, Bennett 2005, Moyle et al. 2016). Delta Smelt are visual predators that consume zooplankton and feed during the day. Their diet is based on the zooplankton available in the environment, which varies by season, region, and environmental conditions (Hobbs et al. 2006, Slater and Baxter 2014, Sullivan et al. 2016). Young Delta Smelt show preference for herbivorous calanoid copepods (Nobriga 2002, Slater and Baxter 2014), which consume phytoplankton. Significant decreases in phytoplankton biomass and resulting changes to the food web occurred after the invasion of the overbite clam *Potamocorbula amurensis* in 1986 (Nichols et al. 1990, Brown et al. 2016). *P. amurensis* is an efficient suspension feeder consuming large amounts of phytoplankton and has caused a 5-fold decrease in phytoplankton biomass after its introduction in this region (Alpine and Cloern 1992; see Phytoplankton and Bivalve whitepapers for more detail). Decreases in phytoplankton have impacts to higher trophic levels (i.e., zooplankton and fish) by directly or indirectly reducing the amount of food available at these levels. Food limitation is hypothesized to be one of many factors contributing to the decline of Delta Smelt in the SFE (Bennett and Moyle 1996, Bennett 2005, Sommer et al. 2007, Moyle et al. 2016). This is especially the case spring through fall during the critical foraging period for Delta Smelt development. The following summary focuses on Delta Smelt diet specifics and how changes to the lower food web in the SFE have impacted Delta Smelt feeding success and diet composition.

Feeding at Different Life Stages

Feeding success, prey size and prey abundance are important for all fish life stages, especially in the vulnerable larval stage. Houde (1987) showed the importance of adequate food abundance during larval stages of five species of fishes, indicating there may be 10-fold fluctuations in fish recruitment from subtle changes in growth or duration of early life stages. Periods of low prey concentration and the resulting reduction in feeding success can lead to a decrease in growth rate and therefore longer durations in early life stages. This leaves fishes in vulnerable life stages for longer and increases their susceptibility to predation thus lowering the possibility of survival (Houde 1975, 1978, 1987). This can be further precipitated by other confounding factors such as unfavorable environmental conditions (e.g., high temperatures). Observed Delta Smelt larval survival rates have fluctuated from 0.01 to 0.85 over the past 25 years (Polansky et al. 2019) indicating that the success of this life stage is highly variable. To realize the upper end of this range, the feeding success and survival of Delta Smelt is dependent on adequate zooplankton abundance and species composition, especially during the most vulnerable early life stages.

Delta Smelt feeding success and diet composition varies by life stage, season, and region of the SFE. Copepods dominate Delta Smelt diets at all life stages, with the dominant species changing seasonally based on zooplankton abundance and availability. At all life stages Delta Smelt positively select for the calanoid copepods *Pseudodiaptomus forbesi* and *Eurytemora affinis* and switch to cyclopoids or other calanoids when *P. forbesi* and *E. affinis* are low in abundance (Lott 1998, Slater and Baxter 2014, Slater et al. 2019). In addition, prey size increases with fish size (Nobriga 2002, Slater and Baxter 2014, Hammock et al. 2017, Slater et al. 2019). Delta Smelt larvae begin feeding within a week post-hatch at 5-6mm total length (Mager et al. 2004) and consume mostly copepod nauplii, the smallest stage of copepods, during that time (Nobriga 2002). At this time larvae capture prey by encounter as opposed to exhibiting coordinated predatory behavior (Nobriga 2002, Bennett 2005), thus feeding success largely depends on prey densities at hatching. In addition, small larval fishes can have a difficult time keeping prey items in their mouths due to the inability to overcome water viscosity (China et al. 2017). As a result, larvae have been shown to have high instances of empty stomachs when prey densities are low. For example, Nobriga (2002) found that 50% of larvae had empty stomachs and low amounts of prey in those fish with food in their stomachs. Other studies found similar results with low gut fullness occurring in winter to spring in freshwater (<0.5 ppt) (Hammock et al. 2017, Slater et al. 2019). This could be due to the reduced availability of calanoid copepods such as *P. forbesi*, during this time (see Zooplankton White Paper for more detail). Reduced feeding success does not necessarily result in starvation; however, it may decrease growth, condition, and prolong the larval stage thereby increasing vulnerability to predation (Houde 1975, 1978, 1987, Nobriga 2002, Hammock et al. 2015).

As larval fish grow, prey encounter rates increase due to higher swimming speeds (Hunter 1981). At this time, larval Delta Smelt begin feeding on later stages of calanoid copepods, switching to juvenile (i.e. copepodids) and adult copepods after 13mm FL (Lott 1998, Nobriga 2002, Sullivan et al. 2016). Despite the switch to larger copepods, Lott (1998) still found high instances of empty stomachs in later fish life stages with an increase in empty stomachs and reduced feeding success at the 20-24mm size range. This is considered a critical foraging period when larval Delta Smelt are transitioning to a juvenile life stage, and low feeding success could result in greater mortalities during this stage (Lott 1998, Mager et al. 2004, Moyle 2002). During this period (June to August), Delta Smelt diet composition continues to consist mostly of copepods, with *P. forbesi* dominating diets in freshwater (Slater et al. 2019). Diet composition in the low salinity zone (LSZ) is more variable during this time with Delta Smelt supplementing *P. forbesi* with the small cyclopoid copepod *Limnoithona* spp. and larger prey items such as mysids, amphipods, larval fish, and predatory calanoid copepods (i.e., *Acartiella sinensis*, *Tortanus* spp.) (Moyle et al. 1992, Lott 1998, Slater and Baxter 2014, Slater et al. 2019). This is likely due to both the increased size of Delta Smelt allowing for predation on more diverse prey, and the increased mortality of *P. forbesi* in the LSZ (Kayfetz and Kimmerer 2017, Kimmerer et al. 2018) making it less abundant in this region.

Fish size has a large influence on feeding success, due to the increase in mouth gap, as well as an increase in prey detection, swimming maneuverability, and aim as fish grow (Sullivan et al. 2016). This allows larger fish to detect and consume bigger, more diverse prey items. In addition, Hammock et al. (2017) found that adult Delta Smelt had a higher feeding efficiency (i.e., higher proportion of available prey consumed) despite decreased zooplankton abundance in some areas. Number of prey consumed also increases as Delta Smelt grow from juveniles to adults (Slater et al. 2019). This is dependent on prey size as fish will consume more as prey size decreases to achieve the same stomach fullness. However, a high number of smaller prey would result in increased foraging and amount of energy expended to achieve the same gut fullness as a low number of large prey. In fall, *P. forbesi* still dominates diets with some fish also feeding on other copepods such as *A. sinensis* and *Limnoithona* spp., as well as mysids and amphipods. Slater et al. (2019) noted an increase in the consumption of amphipods in recent years compared to the findings in other studies (Lott 1998, Moyle et al 1992, Hammock et al 2017), especially in fall 2017. Over the study period, Delta Smelt consumed mostly juvenile Corophium amphipods, *Americorophium* spp., and *Gammarus daiberi,* with *G. daiberi* becoming more common in diets after 2017 (CDFW Diet Study data; Slater et al. 2019). Amphipods are large prey items which typically indicate a higher caloric value than smaller prey such as copepods. However, amphipods have a high amount of chitin which is not assimilated by predators (Vijverberg and Frank 1976) and therefore a stomach full of amphipods may not be as beneficial to Delta Smelt as the high fullness value suggests.

In winter and spring, when *P. forbesi* is low in abundance, adult Delta Smelt diets are more variable switching to other prey types that vary by salinity and year (Lott 1998, Slater et al. 2019). In freshwater these include the cladocerans *Daphnia* spp. and *Ceriodaphnia* spp., the calanoid copepod *Sinocalanus doerrii*, Corophium amphipods, and larval fish (Slater et al. 2019). Adult diets in the LSZ consist of mainly *E. affinis* and the cyclopoid *Acanthocyclops* spp., along with *Daphnia* spp. and other cyclopoid copepods (Slater et al. 2019). Delta Smelt were shown to consume larval fish in previous studies (Lott 1998); however, Slater et al. (2019) found higher instances of larval fish in adult guts than previously reported, with consumption occurring mostly in spring. Of the larval fish that could be identified, Pacific Herring (*Clupea pallasii*) and Prickly Sculpin (*Cottus asper*) were the most common species consumed (Slater et al. 2019). Larval fish present a rich caloric meal for Delta Smelt compared to smaller prey items (e.g. copepods or mysids) during the spawning period when energy expenditure is increased (Damon et al. 2016). Larval fish provide a particularly important component of the diet in Suisun Bay and near tidal wetlands, with Delta Smelt collected in areas close to tidal wetlands being six times more likely to have larval fish in their guts (Hammock et al. 2019). Slater et al. (2019) also found adult Delta Smelt consumed terrestrial insects (e.g. ants, flies, chironomids), particularly in areas with extensive emergent vegetation (Whitley and Bollens 2014), indicating the versatility of Delta Smelt to consume prey based on availability in their environment.

In addition to life stage and season, foraging success can also vary by region. Lott (1998) found that Delta Smelt in Suisun Bay had the poorest feeding success, and fish in Grizzly Bay had the greatest. This is similar to results found by previous studies where fish in Suisun Bay also had the lowest fullness values (Slater and Baxter 2014, Hammock et al. 2015), and fish from the Sacramento River (Slater and Baxter 2014) and Suisun Marsh (Hammock et al. 2015) had the highest gut fullness. Other studies found the opposite trend in that fish in the LSZ had the highest feeding success overall (Hammock et al. 2017, Slater et al. 2019), despite decreased zooplankton densities (Hammock et al. 2017, 2019) compared to other salinity regions (i.e., <0.5 and >6 ppt). This trend switches in summer when freshwater fish have higher feeding success than those in the LSZ (Hammock et al. 2017). Therefore, although Delta Smelt can be food limited from summer to fall (Bennett and Moyle 1996, Bennett 2005), there are spatial differences in foraging success, and the effects of reduced zooplankton abundance during that time can also vary by year.

Many studies have shown interannual variation in Delta Smelt diets and feeding success, however, there does not seem to be a consistent pattern between feeding success and water year type or outflow. Where most studies found that stomach fullness was not related to water year type (Nobriga 2002, Slater and Baxter 2014, Hammock et al. 2015, Hammock et al. 2019), others found the unexpected result of drought years having higher fullness values than previous wet years (i.e., 2013 vs. 2011) (Hammock et al. 2017). Slater et al. (2019) found the opposite trend with years with higher outflow (i.e., the wet year 2017) having the highest gut fullness. Thus, fullness seems to vary more based on month or season than entire years, likely due to strong seasonal trends in prey abundance and not consistent yearly trends. This could be the result of the dynamic habitat of the SFE and interannual variation in several environmental conditions, not just flow.

In summary, Delta Smelt feeding success varies by salinity range, season, life stage and year. Diet composition is also variable, but several trends are consistent: (1) copepods dominate diets at all stages, (2) larger fish consume larger and more diverse prey, (3) diets depend on prey resource availability and Delta Smelt switch to other available taxonomic groups when the calanoids *P. forbesi* and *E. affinis* are less abundant, and (4) foraging success in most life stages is dependent on zooplankton density, with success increasing with increased zooplankton.

Consequences of Zooplankton Community Changes

Species introductions have caused zooplankton declines and shifts in community composition in the estuary. The clam *P. amurensis* caused decreases in phytoplankton and zooplankton biomass due to suspension feeding, predation, and competition with copepods (Kimmerer et al. 1994, Brown et al. 2016). Shifts in zooplankton community composition began in the late 1980’s due to the introduction of several copepod and mysid species replacing natives (Orsi and

Walter 1991, Modlin and Orsi 1997, Orsi and Ohtsuka 1999, Winder and Jassby 2011, Avila and Hartman 2020) (See Zooplankton Whitepaper for more detail).

Although the nutritional value of most invasive and native zooplankton species are similar (Kratina and Winder 2015), introduced species can differ in their environmental tolerances, spatial distribution, and timing of peak abundance altering where, when, and if these species are available for predators. Historical data from the 1970's showed that the calanoid copepod *E. affinis* dominated Delta Smelt diets in June and July when *E. affinis* previously peaked in abundance (Lott 1998, Moyle et al. 1992). The calanoid copepod *P. forbesi* was introduced to the estuary in 1987 (Orsi and Walter 1991) and peaks in abundance during summer and fall (Hennessy 2018). Starting in 1988, after the introduction of *P. forbesi*, *E. affinis* decreased in overall abundance by 89 to 97% (Kimmerer and Orsi 1996) and shifted its timing of peak abundance to spring with sharp decreases in summer (Hennessy 2018). This shift, and significant decrease in *E. affinis*, created a mismatch between the Delta Smelt larval stage and the timing of high zooplankton abundance (*P. forbesi*) in summer (Nobriga 2002), limiting food resources available to larval fish. Despite this, *P. forbesi* is still an important component and dominates Delta Smelt diets from June to August (Hammock et al. 2017, Slater et al. 2019), indicating that increases in abundance of this invasive copepod may still be beneficial to fish.

The introduction and rapid proliferation of the cyclopoid copepod *Limnoithona tetraspina* in 1993 (Orsi and Ohtsuka 1999) added another copepod for Delta Smelt in the LSZ to consume when calanoid copepods are less abundant. However, *L. tetraspina* is considerably smaller than most copepod species in the SFE at approximately one-tenth the mass of *P. forbesi* and *E. affinis* (Bouley and Kimmerer 2006). Due to their smaller size, the consumption of higher numbers of *L. tetraspina* are needed for the same mass as calanoid copepods. To achieve similar gut fullness values as small amounts of larger copepods or mysids would achieve, Delta Smelt can have very large numbers of *Limnoithona* spp. in their guts (> 1000 individuals; CDFW Diet Study data, Slater et al. 2019). Due to their small size, *Limnoithona* spp. also have a higher chitin to volume ratio resulting in a lower nutritional value per individual (Vijverberg and Frank 1976). Despite *Limnoithona* spp*.* being the most abundant copepod in the estuary (Hennessy 2018), Delta Smelt select against it, meaning they eat fewer than expected given their availability, except when found in exceptionally high abundance (Slater and Baxter 2014). This is possibly due to their small size and relatively motionless behavior in the water column thereby making them difficult for visual feeders to detect (Bouley and Kimmerer 2006).

The abundance of mysids in the estuary also decreased overall after the introduction of the overbite clam, reducing the availability of this important food resource to young fishes in the SFE (Feyrer et al. 2003). To compound this, the invasive mysid *Hyperacanthomysis longirostris* was introduced in 1993 (Modlin and Orsi 1997) replacing the native *Neomysis mercedis* and quickly became the most abundant mysid in the estuary (Hennessy 2018). *H. longirostris* is smaller than *N. mercedis* (Avila and Hartman 2020), which further reduces the caloric value and availability of mysids to fishes. Slater et al. (2019) found limited numbers of native mysids in

Delta Smelt guts, and low amounts of mysids in guts overall compared to pre-clam diet values observed by Feyrer et al. (2003). Due to the reduced availability of mysids, Delta Smelt, as well as other fishes in the SFE, have shifted to consuming more copepods. This results in a need to increase the number of prey consumed to compensate for the reduced caloric value thereby increasing the energy expended to forage.

Overall, the changes and decreases in abundance in the zooplankton community have affected prey availability to fishes in the SFE, including Delta Smelt. Most of these changes have resulted in negative effects such as smaller, less available prey as well as a mismatch between vulnerable fish life stages and copepod peak abundance. This further supports the hypothesis that Delta Smelt are food limited in the SFE, which has contributed to their continued decline.

Management Implications and Usage of Data

Feeding success is dependent on zooplankton abundance and long-term declines in zooplankton have likely impacted Delta Smelt feeding success, especially at the larval stage. Management actions and recovery plans for Delta Smelt have recognized the importance of habitat conditions, including outflow and food, since listing of the species (USFWS 1995, Bennett and Moyle 1996). A renewed look at food limitation began with recognition of the Pelagic Organism Decline (POD) studies initiated by the Interagency Ecological Program (IEP) circa 2005 and the “Bad Suisun Bay” hypothesis (see 2005 IEP POD work plan). This evolved into the IEP Fall Low Salinity Habitat (FLASH) studies in 2011, developed from the 2008 USFWS Biological Opinion and “Adaptive Management of Fall Outflow for Delta Smelt Protection and Water Supply Reliability” plan, to look at Delta Smelt foraging success in the low salinity zone versus north Delta.

More recently in 2016, the CA Natural Resources Agency issued the Delta Smelt Resiliency Strategy (DSRS) to look at a suite of options to benefit Delta Smelt and related habitat conditions. The DSRS identified directed flow actions to increase zooplankton abundance and prey availability for endangered fishes such as Delta Smelt (CA NRA 2016, 2017). This includes flow pulses through the Yolo Bypass, coordinated flooding and draining of managed wetlands in Suisun Marsh (which are highly productive), and use of the Sacramento Deep Water Ship Channel for production of phytoplankton and zooplankton. Many of these strategies have also been included in the project description of the 2019 Reinitiation of Consultation on the State Water Project and Central Valley Projects, as well as the accompanying 2020 Incidental Take Permit (USFWS 2019, CDFW 2020). Diet data has been an important tool to measure the response of many management actions and is needed to inform future decisions to direct regions and months these actions may be the most beneficial.

Tidal wetland restoration is another strategy currently being conducted in the estuary and is aimed at increasing food resources and critical habitat for Delta Smelt (USFWS 2019, See Introduction and Abiotic Habitat White Papers for more detail on specific flow actions). Hammock et al. (2019) found that Delta Smelt gut fullness increased with increased tidal wetland area. Fish found in tidal wetlands were also 6x more likely to have consumed larval fish, a high value prey item (Hammock et al. 2019). Increased feeding success is just one of the many benefits of wetland restoration for Delta Smelt and other SFE biota.

The Flow Alteration (FLOAT) Management Analysis and Synthesis Team (MAST) Diet team examines recent trends in Delta Smelt diet by region, life stage, and time of year. This is work developed from the POD and FLASH studies, a continuum of IEP efforts (Brown et al. 2014, IEP-MAST 2015). We compare feeding success to varying environmental factors such as turbidity and salinity. Delta Smelt diet composition is compared to prey availability in the environment and the relationship to gut fullness. Our efforts are aimed at increasing our knowledge of Delta Smelt feeding habits, how feeding success affects health metrics (e.g. condition, contaminant stress) and recruitment, and to further examine the effect of flow and habitat restoration efforts on these factors.

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9. Delta Smelt Life History Diversity

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Introduction

Effective ecosystem management requires a robust understanding of the ecological processes driving changes in species, populations, and interactions among species assemblages across the diversity of habitats within the target ecosystem. In the Sacramento-San Joaquin Delta, ecosystem management in the form of freshwater flows has been the primary focus of resource managers for decades. For Delta Smelt, the decline in abundance has been attributed to multiple interacting factors including reduced freshwater flows, water diversion and entrainment, contaminants, food web collapse and overall habitat degradation (Baxter et al. 2010, Sommer et al. 2007). Physical habitat quality during the fall has diminished since the early 2000s due to changes in water project operations, resulting in the mandated fall flow management action (RPA-Fall-X2) in above normal and wet years (USFWS 2009). This management action is intended to improve rearing habitat quality by creating greater overlap of low-salinity water with dynamic physical habitat found in Suisun Bay and Marsh (Brown et al. 2014, FLOAT-MAST 2020, Shultz 2019). The prevailing hypothesis is that when the low-salinity zone occurs in Suisun Bay-Marsh, Delta Smelt have access to cool, turbid water with greater food availability resulting in faster growth rates, improved condition, health and survival, and greater reproductive potential. The Fall-X2 action was implemented during August and September of wet years 2011 and 2017, while in 2019 the management action was modified by operating the Suisun Marsh Salinity Control Gates to move freshwater into the marsh, allowing X2 to shift upstream of the RPA standard of 74km. To facilitate a greater understanding of how Delta Smelt responded to these actions, in this whitepaper, we provide a primer on life history diversity for resource managers and non-scientists. Using this primer and recent observations of Delta Smelt biology, we redefine the life history of the species and discuss how this revised life history model influences our understanding of how Delta Smelt respond to environmental variability and management actions.

What is “Life History”?

When one thinks about a species, we typically envision mature adult forms, as if the diversity of life could be distilled into a single form. However, fishes exhibit a variety of developmental stages, from eggs to small larval forms to mature adults that are products of environmental forces shaping the evolution of form and function. The Oxford dictionary definition of life history is “a series of changes or events undergone by an organism during its lifetime.” A broader evolutionary and ecological definition of an organism’s life history would include lifetime patterns of growth, development, movement, survival, and reproduction (Begon et al. 1996). Understanding a species life history provides a means by which expectations of a species response to changing environmental conditions and the selective forces of nature can be predicted. Furthermore, an understanding of a species life history can manifest expectations for management actions taken to improve a species status.

Fishes have evolved a diversity of life history responses (e.g., movement patterns and growth) to environmental variability that maximize an individual's contribution to the next generation and a diversity of life history pathways among species. For example, Tule Perch (*Hysterocarpus traskiii*) have a small home-range and produce a small number of young via live-birth, while Chinook Salmon (*Oncorhynchus tshawytscha*) are wide-ranging, migrating from the ocean to headwater rivers to produce many small eggs, thus life histories are written in the genome. However, within species, life histories can vary, for example *Oncorhynchus mykiss* can exhibit both freshwater resident (rainbow trout) and migratory forms (steelhead trout) in the same population. Indeed, understanding fish life histories can be critical for assessing the effectiveness of management actions taken to improve conditions for target species.

Attributes of Life History

As these examples demonstrate, species can differ in several different ways, from how many and what size of offspring they produce, to how often they reproduce, and how large they grow. The components of a species' life history are those attributes that are important in understanding how organisms reproduce, grow, and survive. These attributes are largely under genetic control and reflect the evolutionary history of species, yet within species attributes can exhibit variation or 'plasticity' in response to environmental variability. It is important to recognize that many life history attributes are correlated and represent trade-offs in resource allocation, such as energy allocation to somatic growth vs. reproduction and each species life history represents a unique optimization of resource allocation to maximize fitness.

Reproduction

Parental investment is a critical attribute of life history, for example, some organisms produce many small (*energetically cheap per capita*) offspring while other organisms produce fewer, larger offspring (*expensive per capita)* often in the form of life birth (viviparous) or produce eggs (oviparous) that are deposited into the environment, or that hatch within the mother and are later expelled as larvae (Ovoviparous). Investment in offspring can also include protecting offspring from predators and even procuring food for young. Ultimately, reproduction is an energetically costly endeavor that can come at the expense of maintaining body condition and stasis with the external environment.

There are several aspects of reproductive events that distinguish unique life histories. First, organisms can be largely classified as species that produce all offspring in a single relatively short productive period (semelparity) or produce offspring in a series of events separated by some period or stasis (iteroparity). Fishes can also vary in how energy is obtained, stored and allocated to reproduction. Capital breeders consume and store energy for reproduction prior to maturation, often occurring in separate habitats where spawning will occur, which is common in semelparous species. Income breeding allows for feeding during maturation and is more common in iteroparous species (McBride et al. 2015).

The process of oogenesis, whereby primary oocytes develop into secondary oocytes (vitellogenesis) and tertiary oocytes (hydration) and eventual ovulation can occur in three general patterns: synchronous, group synchronous (as a distinct batch) and asynchronous. Species that undergo only a single cycle of oogenesis and spawn only once, then die are synchronous, and as this process implies are semelparous. In iteroparous fishes, when discrete cohorts of secondary oocytes develop resulting in a hiatus between primary and secondary oocytes, this pattern is referred to as group synchronous, while asynchronous species exhibit overlapping size cohorts of primary and secondary oocytes that persist through the spawning season.

Independent of synchrony of secondary oocyte development, species can exhibit variation in the synchrony of ovulation. Total spawning refers to when secondary oocytes undergo hydration and ovulate in a single event. When secondary oocytes undergo ovulation in multiple, discontinuous events, this pattern is referred to as “batch spawning”. Importantly, iteroparity and batch spawning overcome the physical constraint of body size on egg production and promote a ‘bet-hedging’ strategy of spawning events by spreading out the risk of mortality over time, either within a spawning season or across spawning years (Stearns 1992). Lastly, species can vary in terms of fecundity. In some species fecundity is ‘determinate’ as with fishes with synchronous or group-synchronous oocyte development, while species that exhibit asynchronous oocyte development are said to be ‘indeterminate’.

Size

Body size is a critical component of life history. Large size affords greater survival for individuals by providing a competitive advantage over small individuals, decreases vulnerability to predation, facilitates more energy-efficient physiological homeostasis with the environment and ultimately higher production of offspring. However, a larger size can also come with greater costs. Larger individuals may require more energy for maintenance, growth and reproduction making them more susceptible to periods of food limitation, while some predators may exhibit stronger selection for larger individuals, thus the shape of selective pressures can result in variable size-based life history responses.

Individuals can achieve a larger size by starting life at a larger size, growing faster, or growing for a longer period. Size of mothers can dictate the size of offspring by providing greater nutrition to embryos resulting in larger size-at-birth (hatch from egg-bearing species), (Moussaeau and Fox 1998, Green 2008). In aquatic habitats, larger size-at-hatch can provide a distinct advantage over smaller individuals because water is viscous or ‘sticky’ for small aquatic organisms, limiting their ability to begin feeding and grow in the early-life stages (China and Holzman 2014, Holzman et al. 2015). Larger mothers can produce larger eggs and provide greater provisions of nutrition to offspring, given them a distinct advantage.

Since fish begin life at a small size relative to adult forms and many larger organisms consume early-life stages of fish, rapid growth in the early-life is critical for reaching a size at which predation pressure is reduced and mortality is stabilized – in fisheries we call this 'recruitment' (Miller et al. 1998). Indeed, variation in environmental factors encountered by early-life stages can result in orders-of-magnitude change in recruitment and year-class abundance, thus understanding how fish grow and survive the early-life in response to environmental variation is critical for managing fish populations (Houde and Hoyt 1987).

Longevity

The length of time an organism lives can vary greatly among different life histories. Organisms that are born, grow and mature and reproduce in a single year are considered annual species, while species that live more than one year are perennial. Species with a short life span (1 to 2 years) can be facultative annual species, where reproduction in the first year occurs in some and some can live a second year to reproduce, while species that only live one year are considered obligate annual species.

Dispersal and Migration

Dispersal is the process by which individuals leave their immediate environment by either active or passive movements. In larval fishes, dispersal is often inferred as a mechanism to reduce competition and avoid predation. Meanwhile, migration is most often taken to mean a mass directional movement of a large number or fraction of a population usually for reproductive purposes.

Diadromy is a term used to describe migrations of aquatic organisms between fresh waters and the ocean where organisms undergo physiological adaptations that occur at predictable times at characteristic life history phases and are often associated with reproduction. Diadromy occurs as at least three definitive forms; (1) anadromy, where feeding and growth occurs in the ocean prior to migration to freshwater to reproduce (e.g. Salmon), (2) catadromy, where the opposite pattern of anadromy occurs (e.g. Eels), and (3) amphidromy, where migration of larval (baby) fish to the ocean occurs soon after hatching to feed, grow and develop into a juvenile form prior to migration back to freshwater for prolonged feeding and growth to maturation and eventual reproduction. In addition to diadromous movements between fresh and saltwater, some aquatic species migrate entirely within freshwater habitats (potamodromy).

Studies of estuarine habitats have revealed many variations on the forms of diadromy and habitat use that are important for understanding how species respond to environmental variability and management actions (Elliot et al. 2007, Potter et al. 2015). Species that utilize estuarine habitats for part of their life cycles can be categorized by their dependence on estuarine habitats (full-dependence, opportunists or stragglers) and their habitat origins (marine or freshwater) and species that can complete their full life-cycle in estuarine habitats can be further categorized by their ability to complete their life cycle in estuarine and freshwater or estuarine and marine habitats (Potter et al. 2015). An accurate depiction of a species migratory life history can be critical for managers when assessing a species response to habitat alteration and loss and targeted management actions in only a subset of a species total habitat.

Life History Strategies

Attributes that make up a species life history are connected to form a specific strategy for maximizing lifetime fitness and the degree to which attributes are connected represent evolutionary trade-offs. For example, a species may maximize fitness (contribution to future generations) by increasing resource allocation into making more offspring; however, this investment in reproduction may come at a cost to surviving, as energy is diverted away from body growth and maintenance, otherwise all species would maximize their size, reproductive effort, and longevity to maximize fitness. Resource limitation often results in trade-offs among life history attributes. The study of life history theory seeks to understand how strategies have evolved as adaptive responses to environmental variation (Stearns 1992).

A prominent example of life history theory is *r/K*-selection (MarArthur and Wilson 1967). *K*-selected species possess a suite of life history attributes, such as delayed reproduction, low number of offspring, high parental investment in offspring and long lifespan that together afford higher fitness in response to environments with greater density-dependent effects on the juvenile life-stages (predation, competition) than species having the opposite *r*-selected life history attributes. Based on patterns of life history found in North American freshwater and marine fishes, Winemiller and Rose (1992) proposed a triangular model of life history evolution in response to environmental variation containing three primary life history strategies; 1) Opportunistic (short generation time, high reproductive effort, small body size, low batch-fecundity and low investment per offspring, 2) Periodic (long generation time, moderate reproductive effort, large body size, high batch-fecundity, and low investment per offspring and, 3) Equilibrium (moderate to long generation time, low reproductive effort, variable body size, low batch-fecundity, and high investment per offspring). The three life history strategies are considered evolutionary end points to environmental gradients. For example, the opportunistic strategists evolved in highly productive but also highly variable habitats where populations are largely driven by density-independent abiotic drivers.

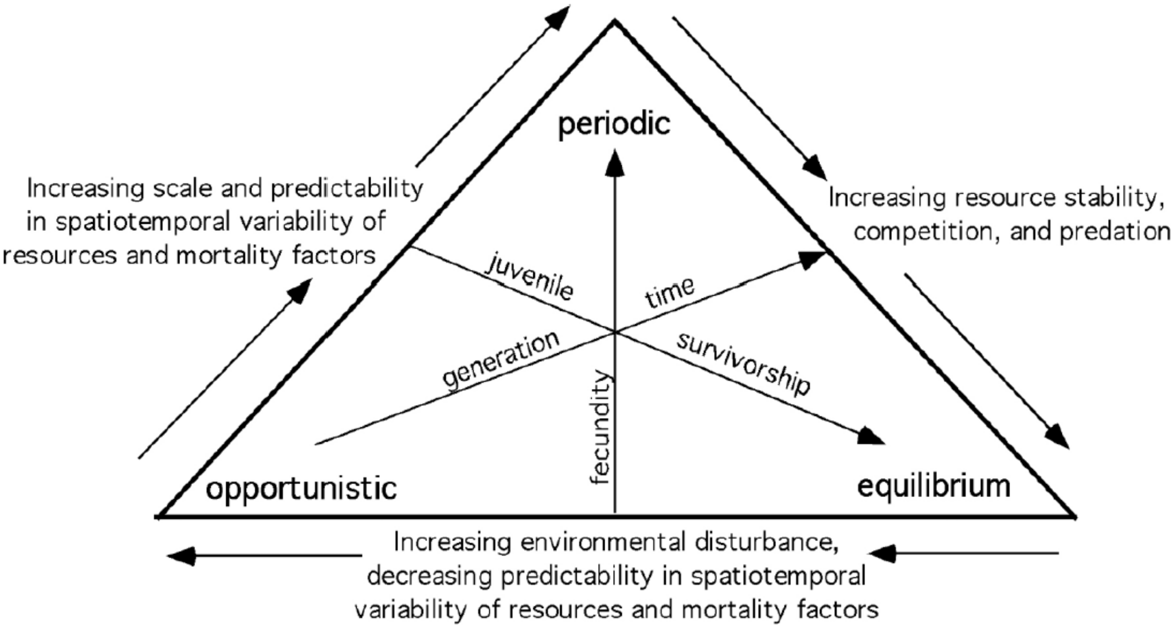

Figure 1. Triangular life history conceptual model illustrating how environmental gradients select for endpoint life history strategies defined by optimization of demographic parameters including generation time, stage-specific survivorship, or age-specific fecundity (from Winemiller 2005).

Delta Smelt (Hypomesus transpacificus)

The Delta Smelt was first described as a distinct species by McAllister (1963) through morphometric analysis with other species within the family Osmeridae. Its status as a distinct species was later confirmed through genetic techniques and it was found to be distinct from the invasive congener Wakasagi (*Hypomesus nipponensus*), which was introduced from Japan in 1959 (Stanley et al. 1995, Trenham et al. 1998). Delta Smelt are thought to have evolved from the marine congener Surf Smelt (*Hypomesus pretiosus*) during the Pleistocene when sea levels receded leaving Delta Smelt in isolated freshwater lakes (Ives and Tayler 2008). Later, when sea levels rose after the last ice-age, Delta Smelt regained connectivity with brackish habitats and began exploiting this productive habitat.

The life history of Delta Smelt was first described by Moyle et al. (1992) as a small (~80mm FL), semelparous, primarily annual species with low fecundity that spawns in the tidal freshwaters of the Delta in the late-winter to spring months and rears in the low-salinity mixing zone found in Suisun Bay and Suisun Marsh- semi-anadromous through fall. These life history components are consistent with the Opportunistic strategists as described by Winemiller and Rose (1992). This would suggest that Delta Smelt are adapted to a dynamic and highly variable environment and undergo large inter-annual population fluctuations in response to variation in the environment. Indeed, the population abundance of Delta Smelt exhibits high inter-annual variability, yet the mechanisms for such population fluctuations have remained poorly understood.

In a critical assessment of the Delta Smelt population, Bennett (2005) provided additional insights into the life history of Delta Smelt and questioned whether Delta Smelt fit the Opportunistic strategist life history strategy because Delta Smelt fecundity was relatively low and exhibited low reproductive effort (contrary to high reproductive effort), a pattern that would result in difficulty rebounding when environmental conditions were “good”. Bennett (2005) used information gained from laboratory culture studies and otoliths to refine Delta Smelt life history. He found that 1) Delta Smelt, as a population exhibited a protracted spawning period, lasting upwards of 5 months (nearly half the annual life span), 2) fish in culture readily lived two years and a small fraction of fish were likely living to age-2 in the wild, and 3) fecundity increased exponentially with body size, where two-year old females produced 2-4 fold more eggs than age-1 fish (*see also* Lindberg et al. 2013). Moreover, Bennett found a correlation in Delta Smelt abundance at a lag of 2 years suggesting fish living and reproducing in their second year may be important to recruitment, at least historically.

Field observations of gonads have identified both immature (oocytes) and fully mature (ripe-vitellogenic) eggs in individuals, suggesting Delta Smelt could produce more than one clutch of eggs within a single spawning season (Damon et al. 2016). In laboratory culture spawning studies, Delta Smelt were observed to undergo 1 to 10 spawning events with a refractory period from 35-45 days based on temperature (LaCava et al. 2015), and histological assessment of oocytes solidified that Delta Smelt can produce multiple batches of eggs within a single spawning season and that production of oocytes was consistent with group-synchrony (Kurobe et al. 2016). Interestingly, diet studies have also demonstrated that Delta Smelt continue to feed through the spawning period (Hammock et al. 2017) and that Delta Smelt do not appreciably change in body condition during the spawning season, despite drought conditions causing early maturation, smaller egg size, and lower batch-fecundity (Kurobe et al. 2021). This would suggest Delta Smelt may withhold some energy from reproduction to maintain somatic condition to facilitate a protracted spawning period, or to survive the spawning period of their first year to spawn in their second year. Bennett (2005) also postulated that Delta Smelt hatched at the end of the season may not have time to reach maturity in their first year, and instead devote energy to body maintenance to live and spawn in year two.

Following the expansion of long-term monitoring surveys year-round in the north Delta, Sommer et al. (2011) demonstrated that Delta Smelt underwent a “Spawning Migration” from the low-salinity habitats of Suisun Bay to the tidal freshwaters of the Cache-Slough Complex during the first flush of river flows in the winter and that some proportion of the population remained in freshwater habitats of the north Delta year-round (Sommer and Mejia 2013). Additional studies demonstrated that Delta Smelt exhibited a “tidal-surfing” behavior, whereby fish move from the open-water channels of the river to the shoals during ebbtides and moved back into the channels during flood tides to facilitate upstream movements (Bennett and Bureau 2015), cementing the notion that Delta Smelt undergo directed movements towards freshwater during the first flush. This was important because, fish making volitional movements upstream in winter months can become entrained in flows moving towards the water projects located in the south Delta. The mechanism by which Delta Smelt migrated upstream during the first flush also was significantly associated with salvage at the water projects (Grimaldo et al. 2009, Korman et al. 2021, Grimaldo et al. 2021). Yet, these observations do not explain the existence of individuals in freshwater year-round.

Using otolith strontium isotope ratios, Hobbs et al. (2019) demonstrated that Delta Smelt exhibit a complex life history with respect to their movements and habitat use. This study demonstrated that Delta Smelt consisted of at least three distinct life history patterns (phenotypes), where some Delta Smelt remained in freshwater through-out life (freshwater resident phenotype), some were hatched into low-salinity habitat and remained there through adult-hood maturing in low-salinity habitat (brackish resident phenotype) while the majority of fish were hatched in freshwater, reared in low-salinity and returned to freshwater during the spawning season (semi-anadromous phenotype). Examining year-classes of Delta Smelt from 2005 to 2014, Bush (2017) and subsequent analysis with additional years of data through 2017 (FLOAT-MAST 2020), inter-annual variability was relatively high, with the freshwater resident phenotype comprising >30% of the population in four of twelve year-classes examined and was associated with summer water temperature and Delta Outflow (Lewis et al. 2021).

Revised Delta Smelt Life History

Information on Delta Smelt life history gained since Bennett (2005) support the opportunistic strategist designation as described by Winemiller and Rose (1992). The species reproductive biology suggests high mortality during the egg and larval stage is minimized by spreading offspring across time and space by spawning multiple batches of eggs per season in both freshwater and brackish habitats. Moreover, adults continue to feed and capture larger more nutritious prey during the spawning season while maintaining somatic condition, allowing the population to rebound when environmental conditions support growth in the fall-winter months and potentially allowing individuals to survive to spawn in a second year of life. Given its evolutionary origins and greater reproductive output in freshwater, Delta Smelt could be described as a freshwater-linked migrant *sensu* Elliot et al. (2007) rather than an estuarine resident or anadromous species (Fig. 2). With this revised and expanded understanding of Delta Smelt life history, we revisit expectations for how Delta Smelt may respond to environmental variability to facilitate an improved understanding for how Delta Smelt respond to management actions.

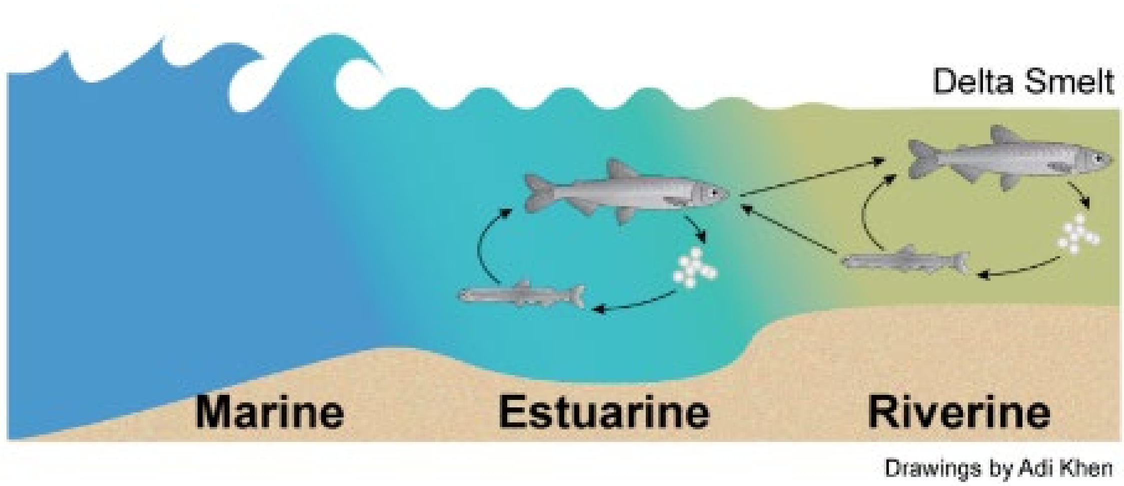

Figure 2. The Freshwater-linked migrant or opportunist can complete their life history in freshwater and low-salinity habitats with a large proportion of the population occupying estuarine waters during the juvenile rearing period and migrating slightly upstream to spawn.

Delta Smelt Life History Response to Management Actions

Recently, there have been several management actions taken to improve habitat conditions and feeding success for Delta Smelt in the summer-fall period, and looming efforts to supplement the wild population with cultured fish. Understanding Delta Smelt's life history strategy is important for predicting the species response to management actions. For example, management actions focused on improving conditions in the low-salinity zone may only benefit the semi-anadromous and brackish resident fish occupying low-salinity habitat but would have uncertain effects on the freshwater resident life history, while management actions in the North Delta may only benefit the freshwater resident life history. Thus, spatial or habitat specific management actions may only influence a part of the population. Here, we leverage our new understanding of Delta Smelts' life history to inform management of potential outcomes from ongoing and future actions to protect and restore Delta Smelt.

The Fall Actions

The Fall-X2 action managed Delta Outflow during the months of September and October (Above Normal and Wet year) to maintain the position of X2 downstream of 74-km from the Golden Gate Bridge, with the goal of improving rearing habitat for Delta Smelt (Brown et al. 2014, FLOAT-MAST 2020, Shultz 2019). This was hypothesized to increase overlap of low-salinity habitat with cool, turbid conditions found in Suisun Bay-Marsh, which would increase prey availability and improve feeding success, growth, condition, survival, reproductive output, and eventual recruitment in the next generation. In 2019, in lieu of implementing the Fall-X2, the Suisun Marsh Salinity Control Gate was opened in mid-August, which moves fresher water from the lower Sacramento River into Montezuma Slough and causes a 'freshening" of the eastern marsh. This action had similar hypothesized effects for Delta Smelt but restricted to fish occupying this region (Sommer et al. 2020, CRNA 2016). In 2016, DWR began the North Delta

Food Action which redirects agricultural drainage or Sacramento River water into the Yolo Bypass region for up to 2-4 weeks during the summer or fall to generate a flow pulse of 25-30 million m^3 to improve food quantity and quality in the North Delta (Twardochleb 2021). This action was also taken in 2018 and 2019

During the fall, juvenile Delta Smelt are transitioning from a period when fish are rapidly increasing length, to escape the mouths of predators, to the sub-adult life-stage, when fish begin to prioritize weight-gain, reflecting an ontogenetic shift of energy resources towards the maturation process. This transition is largely under genetic control reflecting a life history trade-off between size optimization and maturation but can also exhibit some degree of plasticity in response to environmental conditions. Actions that increase food resources prior to this life stage transition may result in longer fish and thus greater single-batch fecundity, while actions that occur after the transition may lead to heavier fish with greater energy storage for producing more batches of eggs and thus total fecundity. Importantly, the environmental conditions these fish experience during the following spring is likely an important factor in determining the optimal outcome. Fish that reached a longer length and greater single-batch fecundity may contribute more offspring in a warm-dry spring when the spawning-hatching window is short, while fish that maximized energy storage for producing multiple batches of eggs would benefit from a wet-cool spring.

Delta Smelt Experimental Release

The USFWS Biological Opinion for the Reinitiation of Consultation on Long-Term Operations of the Central Valley Project and State Water Project (USFWS 2019) proposed to establish supplementation as a project component of the permit. Due to the lack of wild broodstock available for the 2020 year-class, efforts to fast-track this effort have begun, with a target date of December 2021 to begin the experimental release phase of this plan.

Understanding the Delta Smelt life history strategy is going to be critical for setting expectations for supplementation of the wild population with hatchery fish. Delta Smelt are cultured at FCCL in freshwater conditions (Lindberg et al. 2013) and have been shown to undergo rapid domestication (Finger et al. 2018). Given the complex life history of this species, it is possible that domestication includes selection for the freshwater resident life history. If this component of the Delta Smelt life history is under genetic control and culture at FCCL is selecting preferentially for freshwater residence, the experimental release of Delta Smelt may benefit from release locations in freshwater habitats, but poor survival may be expected in brackish release sites. Furthermore, if experimentally released fish successfully spawn and recruit, offspring may also be freshwater resident fish.

Conclusion

Delta Smelt exhibit a complex life history strategy that affords opportunistic utilization of both freshwater and low-salinity productive habitats in the Sacramento-San Joaquin Delta. Effective ecosystem management requires a robust understanding of life history diversity contained within species, populations, and interactions with other species life histories, that co-occur across the diversity of habitats. While the recovery of this species is growing increasingly out of our control, we must take their demise as a lesson for the next species, as we are certain there will be more.

“Like winds and sunsets, wild things were taken for granted until progress began to do away with them. Now we face the question whether a still higher 'standard of living' is worth its cost in things natural, wild and free.”

Foreword, A Sand County Almanac, Aldo Leopold.

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10. Fish health

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Introduction

Why evaluate health?

Fish monitoring provides a necessary metric of distribution and relative abundance but may only offer limited information on the potential influence of lethal and sub-lethal stressors on fish populations (Maxwell and Jennings 2005). Abundance and distribution, though useful, are too coarse to identify and quantify the numerous stressors that fish experience. Evaluation of fish health as an indicator of environmental stress can provide a biological record of sub-lethal exposures, which has the potential to provide greater information than data on abundance and distribution alone (Stentiford et al., 2003; Ruiz-Picos et al., 2015).

What is a healthy fish?

Fish that can cope with daily environmental challenges, access resources, have normal organ function, and meet ecological expectations are considered healthy. A healthy fish with normally functioning organs is in homeostasis. Stressors in the aquatic environment such as exposure to natural and anthropogenic contaminants, food limitation, unfavorable temperature, etc., individually, or collectively, are factors that impose a challenge to the homeostasis of the fish. A fish is still considered healthy if it can adequately cope with these stressors and does not exhibit bioenergetic requirements that exceed its consumption of nutrients. Individuals that are unable to cope with a stress, resulting in reduced growth or impaired reproduction, are considered unhealthy.

How to determine if a fish is healthy

As health is a normative concept, establishing fish health is challenging and subjective without defined thresholds or measurements of normalcy. A variety of metrics have been developed to determine the health and condition of individual fish. These metrics span a range of organizational complexity from the molecular level to the whole organism. Metrics include an evaluation of biochemical/molecular, physiological, behavioral and/or histological/morphological changes. Biochemical changes include genomics, proteomics, and metabolomics (i.e., changes in gene expression, protein synthesis, and production of metabolites, respectively). Physiological changes include cell form, organ development, metabolic demand, and organ function. Behavioral changes include indices such as swimming ability and speed, predator avoidance, and feeding. Histological/morphological changes include cell and tissue integrity, functional status of the organ and condition, development of physical features, and the shape and size of the fish. At the lowest level of biological organization, biochemical changes can potentially cascade into physiological, behavioral, and histological changes, as stressors affect the fish.

Health Triad

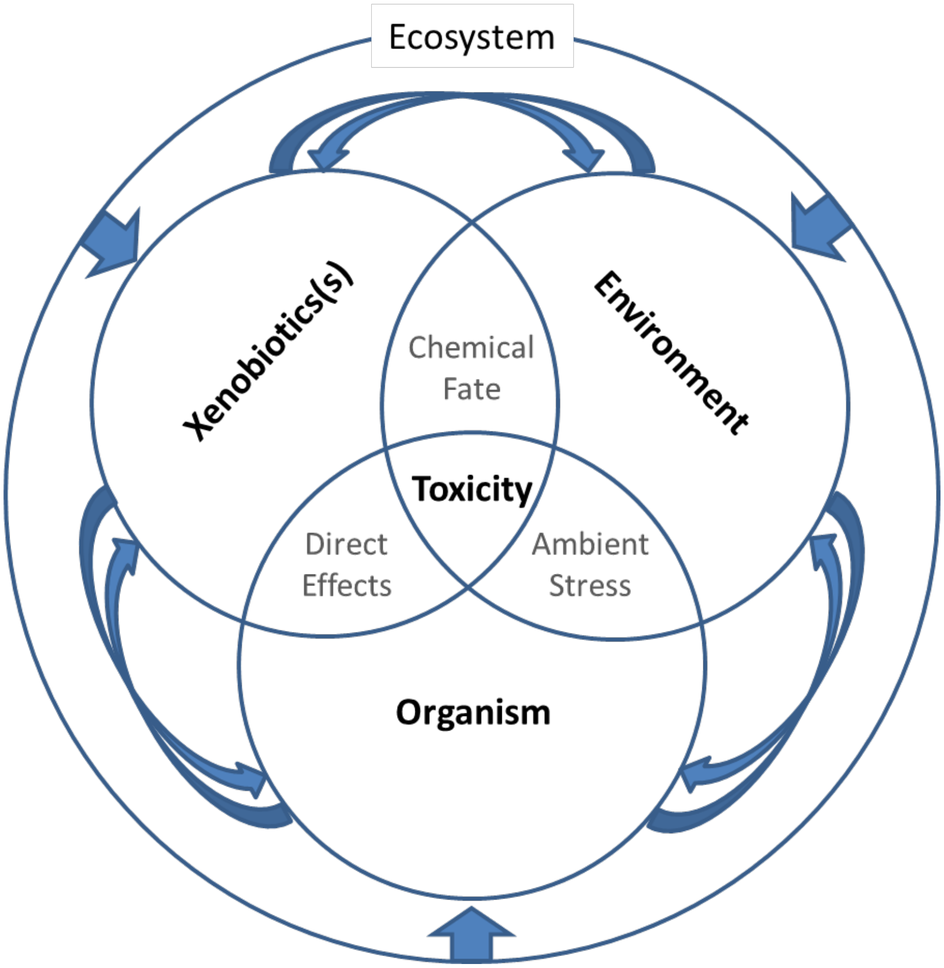

Figure 1. Toxicity Triad from the State and Federal Water Contractors conceptual model for the interactions of 1) Environment, 2) Organism, and 3) Xenobiotic (s).

A Health Triad (Figure 1) is a conceptual model that recognizes the equivalent importance of the health condition of the **Organism**, the status of the **Environment**, and the dynamics of the **Xenobiotic**. Organism condition includes the lifestage/development of the fish, its nutritional status, and whether it has been exposed to other stressors. For the status of the Environment, it is important to note whether the physical parameters such as habitat and water quality are either within an optimal range, within tolerance, or out of tolerance. In addition, the Environment would also include biotic interactions, such as with prey, competitors, and predators. A Xenobiotic is any natural and anthropogenic substance that is foreign to the organism that enacts a stress on that organism. Xenobiotics include chemical stressors such as contaminants, natural toxins, and physical stressors like microplastics. For the xenobiotic chemical it should be noted 1) what kind of chemical, 2) does the xenobiotic chemical co-occur in the environment, the diet of the fish or is it passed down from paternal exposure and 3) what concentration or rate of exposure If the Organism is in a stressed condition, and/or the Environment is not optimal, and if there is a significant presence of the Xenobiotic then it can cause toxicity in that organism. Toxicity can result in an unhealthy organism that could ultimately lead to increased mortality from acute toxicity, predation, and secondary stressors such as infections or food limitation.

Organism: Delta Smelt

Status and importance

The Delta Smelt (*Hypomesus transpacificus*) is a pelagic fish endemic to the fresh and brackish waters of the upper San Francisco Estuary (SFE) (Moyle 2002). Delta Smelt has exhibited a long-term decline in abundance which led to its listing as threatened under the Federal and California endangered species acts, and the up listing to Endangered by the State of California. A considerable amount of monitoring, research, and synthesis has been conducted on Delta Smelt to inform management of its life history requirements, and to understand how management actions affect its abundance and health (Baxter et al. 2010, Baxter et al 2015, Brown et al 2021, Hobbs et al 2017, Teh et al 2020).

Condition

Measuring condition or status of a fish allows for a greater understanding of the current capacity of the fish to respond to and cope with stress (Bolger and Connolly 1989, Connon et al 2019). A recent review by Connon et al (2019) details many of the components of fish condition, which can include the use of gross examination, necropsies, biochemical analyses, and behavioral studies. developmental stage (embryonic, ontogenic, and reproductive), morphometric condition (deformities, external lesions, and condition factor), somatic condition (hepatosomatic index, gonadosomatic index, visceral somatic index), growth, behavior (i.e., swimming and predation response), cellular and tissue damage (histopathology) and the condition of its normal molecular processes (i.e., gene expression and/or enzymatic activity). The evaluation of the condition or status can be from gross examination and observational data to more in-depth analyses mechanistic studies of biological processes (Blazer et al 2018, Connon et al 2019). When the fish’s condition is evaluated, the metrics recorded reflects the culmination of historic stress exposure up to that point (Teh et al 2020).

Alterations to the normal form of Delta Smelt can be detected superficially by gross examination. The use of gross examination can elucidate a variety of metrics of lifestage development, deformities, external damage, or lesions. Embryonic, ontogenic, and reproductive development can be evaluated and can reflect the health of Delta Smelt. Abnormal and/or delayed development can indicate an impaired individual. For example, musculoskeletal structural deformities were clearly identified in native Sacramento Splittail by gross examination (Stewart et al 2020). Larvae and spawning adults are more vulnerable than other life stages (Wendelaar Bonga 1997). Larvae are still developing, so have fewer defenses to stressors like osmotic or nutritional stress. Spawning adults are under more stress because their bioenergetic demands are greater and their potential for exposure to stresses changes as they disperse to spawn. Changes in length and/or weight can be used to evaluate growth. Stressors can increase bioenergetics costs and can reduce the available energy and nutrients for growth and development which ultimately affect reproduction (Steffens 1989). Length and weight can also be used to generate the Condition Factor. The Condition Factor is a common metric that is used to represent the relative index of health with larger values suggesting relatively “healthier” individuals, but it does not suggest the fish is “healthy” as it is relative. Further evaluations of how condition factor relates to physiological metrics of health, such as nutritional status or normally functioning metabolic process would need to develop to properly equate condition factor with “healthy”. This can be confounded by age, sexual development, impaired physiology, and sexual dimorphism. The presence of external lesions such as sores or laceration on the skin can also indicate impaired health.

Necropsies are necessary to identify internal lesions in small fish like Delta Smelt. Indicators of poor health can include alterations in internal anatomy, internal damage, parasites, tumors, and cysts. Somatic indices like Hepatosomatic index and Gonadosomatic index can give an indication of health as they use the relative weight of the organ (liver and gonads, respectively) to indicate health. The rationale for hepatosomatic index that healthier fish will generally have heavier livers, because the liver is a major site of energy storage (e.g., glycogen). As fish mature, gonadal size increases resulting in increasing gonadosomatic index. The use of Gonadosomatic index (GSI) can be used to understand the reproductive health of Delta Smelt as elevated GSI can indicate mature gonadal tissue and greater capacity for gametes while controlling for body weight (Kurobe et al 2016). Visceral fat can also indicate nutritional status, a component of health.

Histopathology can be used to evaluate cellular alterations (lesions) and has been used extensively on Delta Smelt. Fish histopathology, in which thin sections of tissue slides are examined under light microscope, was introduced recently by Teh et al. (2020). The liver and gills of fish are commonly used organs for evaluation (Mallatt 1985, Hinton et al 1992, Poleksic and Mitrovic-Tutundzic, 1994; ICES, 1997). The liver performs a variety of metabolic and detoxification functions (Schlenk and Benson 2003). The gills are directly exposed to stressors in the environment and responds more rapidly to exposure (Mallatt, 1985; Poleksic and Mitrovic-Tutundzic, 1994; Au, 2004). Cellular damage or lesions in these organs can indicate significant exposure to contaminants or physiochemical stressors (Poleksic and Mitrovic-Tutundzic, 1994, Schwaiger et al., 1997, Au, 2004). Histopathologic examination of Delta Smelt found that lesions were prevalent year-round in juvenile to spawning adult lifestages, generally increasing with maturity (Teh 2007, Teh et al 2020). Indicators of impaired health have been prevalent in multiple life stages throughout the distribution of its range.

Biochemical indices are the most sensitive of the biomarkers, and include genomic, proteomic and metabolomic indices. Several studies have been conducted to examine the relative change in gene expression (Connon et al 2009, 2011a, 2011b, Jeffries et al 2015, Hasenbein et al 2013, 2014, 2016, Komoroske et al 2016, Mundy et al 2020). Alterations in the expression or form of important molecules may not have a significant impact on the health of a fish but a culmination of these changes can reach thresholds that result in impaired physiological function. For example, expression of a gene involved in regulating toxicity may not be an indicator of physiological stress, but if it can be linked to significant changes to the physiology of the fish it may indicate a significant stress and can help identify the cause of the physiological changes. Additional biochemical indices used on wild Delta Smelt include RNA-DNA ratio and triglyceride concentration in muscle, with RNA-DNA ratio the more sensitive of the two to fasting (Hammock et al. 2015, 2020). A more comprehensive list of metrics is detailed in Connon et al (2019).

Behavior can also indicate the health status of Delta Smelt. Swimming trials, shoaling behavior, predation response, and foraging behavior are all typical endpoints used to evaluate fish behavior. Behavior studies on Delta Smelt include swimming trials (Swanson et al 1998, 2000, 2002, Connon et al 2009, 2011a), light/dark behavior (Young et al 2004, Mundy et al 2020), shoaling behavior (Davis et al 2019b) and predation studies (Ferrari et al 2014, Davis et al 2019b).

Environment: Upper San Francisco Estuary

The environment Delta Smelt inhabit consists of the upper San Francisco Estuary (Figure, Moyle et al 2018). The San Francisco Estuary (SFE) is formed by the convergence of the Sacramento and San Joaquin rivers, and numerous tributaries such as Coyote Creek and the Napa River, with the Pacific Ocean. It is the largest estuary on the Pacific coast of the Americas (Moyle, 2002). The SFE has highly altered geomorphology and hydrodynamics to accommodate agriculture, urban development, and water diversion. Numerous natural and anthropogenic contaminants drain into the SFE (Brooks et al 2012, Fong et al 2016, Teh et al. 2020). The watershed for the SFE consists of over 75,000 miles of natural, urban, industrial, and agricultural land.

The historic distribution of Delta Smelt occupies a significant portion of the SFE from San Pablo Bay through the North and South Delta. Recent distributions have been predominantly within what has been labelled the Delta Smelt Arc (Moyle et al 2016). This Arc consists of the upper reaches of the Cache Slough Complex, through the lower Sacramento, south of the confluence with the American River, to the confluence with the San Joaquin River, to Suisun Bay and Marsh, to the Carquinez Straits, and into Napa River and the eastern portion of San Pablo Bay. Delta Smelt are rarely seen in the south Delta today (Sommer and Meija 2013).

The Arc environment includes dead end sloughs, open water, tidal wetlands, managed wetlands (duck ponds and floodplains), shallow shores with riprap channels, and sandy shoals. Many of these habitats are heavily invaded and altered by aquatic weeds. The habitat spans both fresh and low salinity habitat and consists of historically turbid and temperate water, which has become less turbid and warmer (Moyle et al 2016). Other factors such as wind, outflow, and precipitation influence the extent of biotic and abiotic habitat attributes, as do anthropogenic factors such as reservoir releases and freshwater export rates.

What is a stressful environmental factor?

When an environmental factor is out of the optimal range for an organism it is stressful. How a species responds to the stressful condition varies both physically and behaviorally. If the organism is not able to cope with the stressor it may lead to an unhealthy organism. For example, under decreased dissolved oxygen conditions a fish has a variety of physical and/or biological responses. Fish may increase respiration, reduce bioenergetic demand, or increase the production of hemoglobin. If these responses are not able to cope with the stress of reduced dissolved oxygen, then health is reduced. The many factors in the environment, including both transient (salinity, prey densities, floating aquatic weeds, etc) and stationary (open water, wetland habitat, shallow water, etc), have significant spatial and temporal dynamics. A mixture of laboratory and field studies can be used to determine how Delta Smelt will respond to changes in the environment. Laboratory studies can be expensive and their applicability to the wild population can be uncertain, but they provide a valuable indication of how a species will respond. Field studies can help validate laboratory studies (and vice versa) and provide more realistic response but the information can be confounded by a variety of uncontrollable variables. Fortunately, Delta Smelt have had a variety of laboratory and field studies to evaluate their responses to the environment described below.

What environmental conditions are favorable?

As an imperiled species, and an indicator of ecosystem health, Delta Smelt have undergone several studies to determine the range of environmental factors it prefers. Field analyses have identified several key factors, including water temperature, salinity, and turbidity (Feyrer et al 2011). There have also been several laboratory, field, and modeling studies to evaluate the influence of prey. Less is known about how Delta Smelt interact with competitors, predators, and invasive plants.

An initial temperature tolerance study on Delta Smelt found that the Critical Thermal Max (CT_{Max}), a temperature at which there is significant impaired movement leading to death, was 25.4°C (Swanson et al 2000). More recent studies using higher acclimation temperatures found that the CT_{Max} for adults was 27.1°C (acclimation at 12.4 °C); 28.4°C (acclimation at 15.3 °C); 28.3°C (acclimation at 18.7°C; Komoroske et al 2014). In addition, it was determined that CT_{Max} varies ontogenically (Komoroske et al 2014). Larvae were found to have greater CT_{Max} (29.9°C) than juveniles (28.9°C) and adults (28.3°C), and post spawners were found to have the lowest CT_{Max} (27.1°C), indicating that older lifestages of Delta Smelt are more susceptible to high temperatures. Delta Smelt have limited capacity to respond to changes in temperature. Heat shock proteins, which are chaperone proteins that facilitate normal metabolic process, were found to have diminished capacity compared to similar temperate species (Komoroske et al 2015). Komoroske et al (2015) concluded that temperatures within 4-6 °C of the CT_{Max} would be stressful. Delta Smelt are projected to more frequently encounter higher temperatures and stressful conditions in the coming years due to climate change (Brown et al 2016). Although incubating Delta Smelt in different temperatures did not result in changes to changes to salinity tolerances (Davis et al 2019a), found that the temperature dynamics experienced by Delta Smelt can impact its predation risk (Davis et al 2019b). Sustained elevated temperatures (21^{o}C) resulted in continuous swimming velocities >20 cm/s (Davis et al 2019b), which may significantly reduce endurance (Swanson et al 1998). The warm temperature also resulted in elevated predation and injury (Davis et al 2019b).

Laboratory salinity studies demonstrate that Delta Smelt tolerate salinities as high as 19.1 ppt without significant impacts on their health (Swanson et al 2000, Komoroske et al 2016, Kammerer et al 2016, Hammock et al 2017). However, Delta Smelt are rarely collected near salinities greater than 12 ppt (Komoroske et al 2016), indicating that their seaward range is limited by factors besides salinity. Gene expression, cellular change, and metabolism under high salinity conditions were found to be like other euryhaline species (Komoroske et al 2016, Kammerer et al 2016). Davis et al (2019a) found that incubating Delta Smelt in different salinities did not result in changes to CT_{Max}. Also, bioenergetic studies found that there was no effect on Delta Smelt resting metabolic demand up to 12 ppt (Hammock et al 2017), and when challenged with salinity exposure Delta Smelt quickly acclimated (Komoroske et al 2016). Exposure to 34 ppt resulted in reduced condition factor, impaired metabolic processes, and impaired gene expression that corresponds to a very stressed condition. High salinities may be stressful, especially between 19.1 and 34 ppt (Komoroske et al. 2014).

Turbidity is important for Delta Smelt. At early life stages, clear water reduces foraging success (Baskerville-Bridges et al 2004) and has been found to increase predation (Ferrari et al 2014). Turbidity reduces visibility, allowing pelagic species to hide from predators. It may also improve visual acuity of Delta Smelt, leading to improved foraging success (Baskerville-Bridges et al 2004). Several studies associate turbid water with increased detection of Delta Smelt (Feyrer et al 2011 Sommer and Meija 2013). Also, turbidity has been found to improve predictions of the movement and distribution for Delta Smelt (Gross et al in review). Hasenbein et al (2013, 2016) found that turbidity has a quadratic relationship with several Delta Smelt responses. Stress responses were found at both low (≤ 25 NTU) and high turbidities (≥120 NTU) for juveniles and adults. Hammock et al. (2019) found that foraging success was reduced above 80 NTU but was not influenced by turbidities from 0 to 80 NTU. This is consistent with recent studies suggesting that for adults, turbidity may be more involved in predation than foraging (Latour 2016, Peterson and Barajas 2018). Although turbidity can be one of the indicators for favorable environmental conditions, low turbidity can also potentially allow the Delta Smelt to detect the nets, reducing detection efficiency of the survey. Detection bias, improved foraging success, and predation avoidance should be considered when evaluating whether water clarity is stressful.

Biotic factors like prey availability, competition, and predation are difficult to evaluate due to the complex set of interactions. There are numerous studies that have found that prey is important for Delta Smelt abundance and survival (MacNally et al 2010, Thomson et al 2010, Maunder and Deriso 2011, Miller et al 2012, Hamilton and Murphy 2018, Simonis and Merz 2019, Polansky et al 2019). Competition for available resources like prey could be a significant factor. There are few studies on Delta Smelt examining this relationship. More studies have been conducted on predation. Predation pressure in the environment may be significant, as predators like Striped Bass (*Morone saxatilis*) and Largemouth Bass (*Micropterus salmoides*) are prevalent. Striped Bass was found to correlate with the dynamics in Delta Smelt densities suggesting an historic predator/ prey relationship even before the long-term surveys like the Fall Midwater Trawl began (Nobriga and Smith 2020). Largemouth bass predation on Delta Smelt was found to increase under low turbidity conditions (Ferrari et al 2014) and high temperature (Davis et al 2019b). Reductions in sediment transport and increases in invasive aquatic weeds have reduced turbidity in the habitat of Delta Smelt, possibly increasing predation pressure (Ferrari et al 2014). For example, Mississippi Silversides (*Menidia audens*) had increased prevalence of Delta Smelt DNA in their guts in clearer water and offshore habitat than nearshore and turbid habitat (Schreier et al. 2016). Increased predation pressure poses not only a direct risk to survival but increased bioenergetic costs via indirect predation effects. In conjunction with reduced prey availability from increased competition and habitat degradation, the increased energetic cost of avoiding predators can increase the stress of any environment.

Pathogens are another component of an Environment that could be impacting Delta Smelt. Pathogens are well known to influence population dynamics in other fishes. In salmonids for example, there are concerns for survival and growth from diseases like Whirling Disease, *Ceratonova shasta*, and *Parvicapsula minibicornis* (Foott et al 2020, Lehman et al 2020). For Delta Smelt there is less information, but several studies have found a variety of pathogens that could be an issue given the right combination of factors. Pathogens have been detected on Delta Smelt from both hatchery and wild origin and may be cause for concern (Antonio et al 2000, Foott and Bigelow 2010). Diseases like Mycobacteria are highly prevalent in wild Delta Smelt with over 50% infected with the pathogen (Baxa et al 2015) and have been shown to significantly impact swimming performance (Swanson et al 2002). In addition, Helminth parasites were also detected in less than 10% of cases (Foott and Bigelow 2010).

Bioenergetics

Impacts of abiotic stressors can impact the bioenergetics of an organism. The stress may require elevated activity of metabolic processes and behavior that would increase bioenergetic needs. Studies by Jeffries et al (2016) and Hammock et al. (2017) examined the bioenergetic costs of temperature and salinity, respectively. Temperature is a known driver of bioenergetic costs as fish are poikilotherms and increase their activity and energy demands with increasing temperature. Larvae were incubated at cool (14°C) and warm (20°C) temperatures. Warmer temperatures resulted in significantly elevated metabolic rate and gene expression involved in increased metabolism (Jeffries et al 2016). Surprisingly, for Delta Smelt acclimated to a wide range of salinities (0.4 to 12 ppt), no change in bioenergetic demand was detected (Hammock et al 2017). Rose et al (2013) included temperature, turbidity, and salinity in an individual based model that included a bioenergetic component modified from Rainbow Smelt (*Osmerus mordax*). Consistent with the empirical bioenergetic work, the model found support for temperature, prey, and turbidity being major factors, while the inclusion of salinity did improve model.

Xenobiotics

Together, 'naturally' and anthropogenically derived xenobiotics are a source of stress in the SFE. The types and forms of these xenobiotics vary both spatially and temporally and can be chemical and/or physical stressors. Physical factors like wind, precipitation, and hydrology can also affect the loading and sources of xenobiotics. In addition, anthropogenic sources depend on land use type, with urban settings contributing an array of xenobiotics that partially overlap with the suite of agricultural xenobiotics. Point sources include wastewater treatment plants and agricultural drains while non-point sources include atmospheric deposition and runoff. Classifications of xenobiotics in the SFE include metals, metalloids, cyanotoxins, pesticides, persistent organic pollutants, industrial chemicals, and pharmaceutical and personal care products. Only a handful of xenobiotics have been examined for toxicity to aquatic organisms in the SFE (Fong et al 2016).

Naturally occurring xenobiotics include metals and metalloids, with human activities often increasing concentrations. Metals and metalloids have had a long history in the SFE with metals like Mercury and Copper resulting from historic land use (Buck et al 2007, Conaway et al 2008). Mercury was used extensively in gold mining and there are leachates from those mining activities as well as from mercury mines themselves that have resulted in a legacy of this metal (Gehrke et al 2011). Copper has been used to remove or control pest species for years and is still being used in antifouling paint and to control pests like aquatic weeds. Copper was found to cause reduced swimming speed and altered gene expression in Delta Smelt, suggesting an impaired immune system (Connon et al 2011a). Microbial metabolic processes have been found to reduce the availability of copper in the environment (Buck et al 2007), but metabolic processes could also increase the bioavailability of mercury (Marvin-DiPasquale and Agee 2003). Mercury control is an active consideration when dealing with the contaminant in managing wetlands, restoration, and fish consumption. The primary metalloid of concern is selenium, which has a variety of effects on development and reproduction (Teh et al 2002; 2004). Selenium, in its various forms, is a natural constituent of water bodies, both freshwater and marine, and is derived from natural processes such as erosion of ore-bearing rocks. Anthropogenic activities such as burning of coal and other fossil fuels, agricultural and industrial sources, and mining constitute an increasingly important source of Se in the aquatic environment (USEPA 1987). Evidence of selenium harm to wildlife has been noted for Sacramento Splittail (*Pogonichthys macrolepidotus*) as evidence by deformed juveniles collected in the estuary (Stewart et al 2020).

Cyanobacteria are another source of naturally occurring xenobiotics and were first detected in the SFE in 1999 (Lehman et al. 2005). These xenobiotics may pose a threat to fish by directly or indirectly altering the foodweb. In the SFE, *Microcystis* and some other cyanobacteria have been shown to form toxic blooms during the hotter parts of the year. The toxins produced, predominantly microcystin, can have negative impacts on fish species. For Delta Smelt, it has not been established whether there is significant exposure, but it is likely as they co-occur with *Microcystis*. Studies on Sacramento Splittail and Threadfin Shad (*Dorosoma petenense*) have shown that exposure through the diet can result in impaired health with an increase in liver lesions and loss of weight (Acuña et al 2012a, 2012b). Like Delta Smelt, Threadfin Shad is a pelagic zooplanktivore that feeds on a variety of prey and is exposed in the wild to these harmful algal blooms (Acuña et al 2020). These blooms and their grazers (like copepods) have been shown to contain toxic levels of microcystin (Lehman et al 2008). Co-exposure of Delta Smelt embryos to *Microcystis* and the pathogen *Aeromonas* resulted in reduced growth (Kurobe et al 2018).

Due to the SFE having a variety of land use types (Whipple et al 2012), there are a number of contaminants that are present from industrial, agricultural, and urban sources (Brooks et al 2012). Anthropogenic contaminants, not including metals and metalloids, include a variety of sources and effects. The entire watershed of the SFE collects and transports chemicals from agriculture and urban environment as well as from other land use types like flame retardants from private, state, and federal forests (Sutton et al 2019). From the agriculture setting comes a mixture of pest management chemicals and fertilizers (Brooks et al 2012, Fong et al 2016, Wang et al 2019). In the urban setting, there is an even greater variety from pest control and fertilizers to pharmaceuticals and industrial chemicals (Brooks et al 2012, Fong et al 2016, Overdahl et al 2021). Routine monitoring has detected contaminants from metals, to pesticides, to pharmaceuticals with various individual chemicals exceeding EPA Aquatic Life Benchmarks (Brooks et al 2012, Jabusch et al 2018, De Parsia et al 2018, 2019). Seasonal variation is also a concern as runoff and pesticide management can vary through the year, resulting in a seasonally dynamic mixture of contaminants (Brooks et al 2012, Jabusch et al 2018, De Parsia et al 2018, 2019). Contaminants occur both in the aqueous form and can partition into the sediment (Bolotaolo et al. 2020). Fish can also experience contaminant exposure via their diet (Acuña et al 2020).

Studies on contaminants present in the SFE have found that toxicity is a ubiquitous stressor (Weston et al 2015, Brandt et al 2018, Teh et al 2020). Delta Smelt have lesions that are likely associated with contaminant toxicity throughout their range and during each life stage (Teh 2007, Hammock et al 2015, Teh et al 2020). Field-collected water has caused significant toxicity in Delta Smelt (Hasenbein et al 2014, Stillway et al *in progress*). Studies on pesticides for aquatic weed control have found impacts of impaired immune response, neurotoxicity, and endocrine disruption (Jin et al 2018). A variety of responses were detected from gene expression to liver damage (Hasenbein et al 2014, Stillway et al *in progress*). Pyrethroids are insecticides that are highly prevalent and in common use in agriculture and urban environments, were found to be toxic at very low concentrations to Delta Smelt larvae and the effects were found to be non-monotonic on gene expression affecting expression of genes involved in neuromuscular activity and immune response (Connon et al 2009, Jeffries et al 2015, Mundy et al 2020, 2021, Segarra 2021). At higher concentrations neurotoxicity was detected such as reduced swimming speed and at lower concentrations exposures resulted in endocrine toxicity and reproductive impairment across generations that could have population level impacts (Brander et al 2016, DeCourten et al 2020). The correlation and the known impacts of pyrethroids on reproduction suggest that pyrethroids pose a significant threat to Delta Smelt The recent declines in Delta Smelt was significantly correlated with pyrethroid use in the environment (Fong et al 2016).

Nutrients in the environment may be naturally occurring or anthropogenic. Phosphorous and nitrogen are the primary nutrients of concern, with the latter being a recent focus for evaluating environmental impact. Nitrogen is naturally cycled in the environment as an essential nutrient for primary productivity but is also artificially introduced to the SFE via runoff from urban and agricultural sources as well as point source discharge from agriculture and wastewater treatment plants. Nitrites, nitrates, and ammonia are of concern as the SFE is at eutrophic nutrient concentrations, despite low pelagic productivity. Ammonia has been found to be significantly toxic to copepods and Delta Smelt at levels found near or around the Sac Regional Wastewater Treatment Plant (Teh et al 2010, 2011, Hasenbein et al 2014). Also, the eutrophic conditions along with high temperatures and residence time contribute to cyanobacteria blooms (Lehman et al 2013, 2015).

Summary

Fish health is an important assessment of how well a fish responds to its environment. Abundance based occupancy models can be misleading because organisms frequently occupy detrimental habitat, so information below the scale of an individual can provide key information. Using metrics to evaluate the health of Delta Smelt can be useful as they can more clearly link observed patterns of abundance to a causal factor. Several studies have shown that multiple factors interact significantly with abundance or survival (Feyrer et al 2011, MacNally et al 2010, Thomson et al 2010, Maunder and Deriso 2011, Miller et al 2012, Hamilton and Murphy 2018, Polansky et al 2019). Three major factors of the Health Triad, the Environment that Delta Smelt occupy, the Condition of the Delta Smelt, and the status (i.e., type, presence, concentration, etc.) of the Xenobiotics will interact to affect Delta Smelt health. Suboptimal environmental parameters (i.e., water quality out of tolerance range) and the presence of xenobiotics (i.e., pesticides, nutrients, cyanotoxin, etc.) at harmful levels will be stressful for the fish. A fish that cannot cope with stressful conditions due to poor nutritional status, prior stressful condition, and/or being at a vulnerable developmental stage will result in an unhealthy fish (Lusardi et al 2020). If enough individuals are unhealthy than this could reduce abundance. Metrics that cover the three components of the health triad should be examined to identify any causal factors for management and recovery of the species.

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11. Fish Assemblage

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Introduction

The Delta Smelt (*Hypomesus transpacificus*) is a declining, San Francisco Estuary-endemic fish species and focal target of California water management. While much has been learned about Delta Smelt habitat and environmental drivers over the past few decades (Feyrer et al. 2007b; Nobriga et al. 2008; Bever et al. 2016; Polansky et al. 2020), there is still a lot we do not fully understand regarding the interactions between Delta Smelt and other fish species. The continued decline of Delta Smelt abundance has also exacerbated the challenge of evaluating how the species responds to targeted management actions (Frantzich et al. 2018; Beakes et al. 2020; Sommer et al. 2020), especially now that the population has declined to such low levels beyond the detection capability of most long-term fish monitoring programs. For these reasons, evaluating the larger San Francisco Estuary (estuary) fish assemblage may enhance our understanding of Delta Smelt population dynamics and its potential response to environmental change such as variation in freshwater flow.

Large ecosystem shifts have been observed by studying multiple fish species or fish communities (Kimmerer 2006; Brown and Michniuk 2007; Thomson et al. 2010; Mahardja et al. 2017a). Further, some estuary community constituents are expected to directly or indirectly impact Delta Smelt, and thus the status and trends of these other species are important to evaluate. For example, Delta Smelt are exposed to predation throughout their life cycle by piscivorous fishes and possibly introduced shrimp (Schreier et al. 2016). In addition, under conditions in which food is limiting, Delta Smelt compete with other planktivorous fish species that occur in similar habitat (Feyrer et al. 2003; Whitley and Bollens 2014). Some of the more common pelagic fish species (e.g., Threadfin Shad *Dorosoma petenense*, juvenile Striped Bass *Morone saxatilis*) that co-occur with Delta Smelt may be used as a surrogate for Delta Smelt and their responses may provide insight into the success or failure of certain flow actions or events. Some of these species share similar overall diet with Delta Smelt and their abundance trends mirrors that of Delta Smelt to some extent, as they experienced a steep decline during the Pelagic Organism Decline (POD) event in early 2000s alongside Delta Smelt (Thomson et al. 2010).

In this whitepaper, we provide an overview of how the fish assemblage of the upper estuary has changed over time, as well as highlight key similarities and interactions between Delta Smelt and other fish species that make up the majority of the estuary's fish biomass.

Executive Summary of Major Changes to the Estuary's Fishes

Prior the late 1800s, the pelagic forage fishes of the estuary are thought to have consisted of native species that were partitioned by salinity. Northern Anchovy (*Engraulis mordax*) and Pacific Herring (*Clupea pallasii*) dominated the marine and brackish portion of the estuary and Longfin Smelt and Delta Smelt dominated the brackish and freshwater portion of the estuary.

Of the non-native pelagic fishes now commonly found in the upper estuary, American Shad was the first to be introduced in 1871 (Dill and Cordone 1997). This introduction was quickly followed by another, when Striped Bass were introduced in 1879 (Stevens et al. 1987). Around this time, the upper SFE also experienced the large-scale conversion of wetlands and floodplains into agricultural tracts that resemble the modern day Sacramento-San Joaquin Delta (Delta) (Whipple et al. 2012). Although estimates of American Shad and Striped Bass numbers from the late 1800s and early 1900s are not available, both species were abundant enough to support commercial fisheries during this time period (Skinner 1962). Adult Striped Bass are largely piscivorous, leading some to believe that Delta Smelt numbers were suppressed long before the establishment of many monitoring programs key to the listing of this native species (Nobriga and Smith 2020). Another key species was added to the pelagic fish assemblage of the upper estuary when Threadfin Shad were introduced into the system in 1959. Threadfin Shad quickly became one of the most abundant fish species in the pelagic fish surveys of the upper estuary, and because Threadfin Shad share similar diet patterns with the Delta Smelt (Feyrer et al. 2003), it has been suggested that it is a competitor to Delta Smelt. Since the 1960s, Striped Bass, Threadfin Shad, American Shad, Longfin Smelt, and Delta Smelt make up the majority of catch in pelagic fish surveys within the freshwater to brackish portion of the estuary.

The introduction of the overbite clam (*Potamocorbula amurensis*) in 1987 caused another significant shift in the estuary's pelagic food web with consequences to the fish assemblage (see bivalve white paper). Since its establishment, chlorophyll levels declined to consistently low concentrations, and the abundance of multiple phytoplankton and zooplankton species was similarly reduced (Kimmerer et al. 1994; Lehman 2000), including herbivorous calanoid copepods and mysids recognized as important prey to native fishes (Feyrer et al. 2003; Winder and Jassby 2011; Slater and Baxter 2014). There was no apparent decline in Delta Smelt abundance immediately after the introduction of overbite clam, likely due to the shift of Northern Anchovy towards higher salinity waters that mitigated the effects of lower food availability in the low salinity zone often occupied by Delta Smelt (Kimmerer 2006).

Another shift to the ecosystem occurred in 2002, when Delta Smelt, Longfin Smelt, age-0 Striped Bass, and Threadfin Shad experienced a simultaneous steep decline in abundance often dubbed as the Pelagic Organism Decline (POD) (Sommer et al. 2007). Most studies concluded that the POD event was caused by multiple, interacting environmental factors (increased summer temperature, increased water clarity, reduction in chlorophyll levels, etc.) given that these pelagic fish species exhibit different life histories (Mac Nally et al. 2010; Thomson et al. 2010). Since the POD, Delta Smelt has been the rarest pelagic fish in the upper estuary and has continued to decline (Moyle et al. 2016). The sole exception was the wet year of 2011, which saw the highest abundance of Delta Smelt in almost two decades and similarly high numbers for other pelagic fishes. However, the increased abundance of the 2011-year class was short-lived, as it was followed by drought conditions during 2012-2015 which was thought to contribute to further declines in pelagic fish abundance indices (Brown et al. 2014). Since the 2012-2015 drought, Delta Smelt numbers have become increasingly low and they are now consistently below the detection level of multiple long-term surveys, while the remaining pelagic species continued to be detected at a new lower baseline level.

While pelagic productivity in the upper estuary has declined over time, the nearshore littoral food web of the Delta appears to have thrived in recent years. Although Delta Smelt generally do not occupy the littoral habitat, changes that have occurred here can have widespread effects beyond the littoral zone. Non-native submerged, emergent, and floating aquatic vegetations have rapidly expanded to many parts of the Delta with severe consequences (Santos et al. 2011; Khanna et al. 2018). Non-native aquatic plant species in the estuary have been demonstrated to reduce water velocity, increase sedimentation, and alter dissolved oxygen levels (Hestir et al. 2016; Tobias et al. 2019). These non-native aquatic vegetation species have also facilitated the increase of non-native fish species such as Largemouth Bass (*Micropterus salmoides*) in the Delta, by fueling a different primary productivity pathway in the food web and by offering suitable structured habitat (Conrad et al. 2016; Young et al. 2020). Overall, fish biomass in the littoral zone of the Delta may have doubled in the post-POD period (Mahardja et al. 2017). Although some native fish species may have benefited from this novel littoral habitat (Mahardja et al. 2017; Young et al. 2018), the changes that have occurred in this littoral habitat are likely detrimental to Delta Smelt, which do not appear to utilize habitat dominated by submerged aquatic vegetation (Ferrari et al. 2014).

Link Between Flow and Pelagic Fishes

Flow may affect fish species with considerable influence on Delta Smelt population as well as species that can potentially serve as surrogate for Delta Smelt. As such, it is important to understand how flow can directly impact these fish species. Multiple relationships between pelagic species abundance and flow have been evaluated and reported in the past (Turner and Chadwick 1972; Kimmerer 2002; Nobriga and Rosenfield 2016; Tamburello et al. 2019; Grimaldo et al. 2020; Mahardja et al. 2021). However, just as with Delta Smelt, there is no clear, single established mechanism described for many of these relationships due in part to species-specific interactions between flow, water quality (e.g., temperature turbidity), food-web productivity, and the system's state prior to high-flow events. Although the mechanism underlying abundance-flow relationships may vary considerably between species, assessment of the status of these pelagic fishes and their responses to flow actions may provide insight into their successes, failures, or how magnitude or timing of these actions change their impacts. This has become especially crucial now that Delta Smelt numbers have become low enough that assessing their response can be difficult. Two major hypothesized mechanisms behind some flow-fish abundance relationships are described below.

Physical Habitat

Higher freshwater flow in the estuary has been linked to increased abundance of American Shad, Striped Bass, and Longfin Smelt (Stevens and Miller 1983; Kimmerer 2002). Similar to Delta Smelt, age-0 Striped Bass, Threadfin Shad, and Longfin Smelt are associated with brackish to freshwater habitat in the estuary and are more often found in turbid waters (Feyrer et al.

2007; Mahardja et al. 2017). It has been hypothesized that expansion of low-to-moderate salinity and high turbidity waters in wet years may increase access to suitable habitat for these pelagic species (Feyrer et al. 2011; Bever et al. 2016; Grimaldo et al. 2017, 2020). Certain management actions, such as the Suisun Marsh salinity control gate operation in the summer-fall period is intended to increase suitable abiotic habitat for Delta Smelt in the summer and fall (Sommer et al. 2020), and it stands to reason that we would also see a change in distribution of other estuarine-dependent pelagic fish species as a result of such action (Beakes et al. 2020).

Food Availability

The decline in pelagic food productivity due to the introduction of invasive overbite clam, *Potamocorbula amurensis,* in 1987 has been implicated as one of the main drivers of decline in pelagic fishes (Brown et al. 2016). Individual-based model constructed for Delta Smelt also indicate that increased food availability should lead to subsequent increase in the abundance of Delta Smelt (Kimmerer and Rose 2018). This is in addition to long-term advective loss of phytoplankton, zooplankton and larval fish biomass at the water projects (Arthur et al. 1996; Hammock et al. 2019). Because higher freshwater flow into the estuary has been linked to an increase of phytoplankton biomass to some extent (Lehman 2000) and higher abundance of some zooplankton species (albeit prior to the POD) (Jassby et al. 1995; Kimmerer 2002), it has been hypothesized that wet years would lead to higher food-web productivity in multiple regions within the estuary. Brown et al. (2014) and Kayfetz and Kimmerer (2017) demonstrated that distribution of certain key phytoplankton and zooplankton taxa change with water year type. Management actions, such as the pulse flow into the Yolo Bypass Toe Drain in the summer and fall, were taken to increase food availability for Delta Smelt (Frantzich et al. 2018). Given that there is a considerable overlap in diet between Delta Smelt and certain pelagic fish species (e.g., Threadfin Shad) (Feyrer et al. 2003), we can expect an increase in food availability to benefit multiple pelagic fish species and not only Delta Smelt.

Predators of Delta Smelt

Predators are a natural biological component of ecosystems, and most organisms are exposed to predation during some part of their lives. The commonly found piscivorous fishes in the upper estuary are largely non-natives: Striped Bass, black bass (*Micropterus* spp.), crappie (*Pomoxis* spp.), and catfish (White Catfish *Ameiurus catus*, Channel Catfish *Ictalurus punctatus*) (Grossman 2016). Sacramento pikeminnow, *Ptychocheilus grandis*, a native piscivorous fish species, also occurs throughout the upper estuary and may have predated on Delta Smelt prior to the introductions of non-native fishes.

Piscivorous juvenile Striped Bass often co-occur with Delta Smelt, and can predate on Delta Smelt (Brandl et al. 2021). Striped Bass is an opportunistic predator and Delta Smelt is unlikely to be a main prey item; however, predation impacts from Striped Bass likely occurred prior to the inception of existing monitoring programs (Nobriga and Smith 2020). Largemouth bass populations have increased in the Delta (Brown and Michniuk 2007; Mahardja et al. 2017a) and may prey on Delta Smelt particularly at the interface between littoral areas with submerged aquatic vegetation and the open water favored by smelt. Although Largemouth Bass predation on Delta Smelt has not yet been observed in the wild, it has been documented in mesocosm experiments (Ferrari et al. 2014). Mississippi Silverside (*Menidia audens*), may be an intraguild predator of Delta Smelt due to their fairly broad niche and distribution throughout the estuary (Bennett 2005; Mahardja et al. 2016; Schreier et al. 2016). Mississippi silversides appear to prey on larval Delta Smelt in the spring (Baerwald et al. 2012; Schreier et al. 2016), but are too small to prey on juvenile and sub-adult Delta Smelt in the fall and winter. Overall, predator abundance and associated predation risk for Delta Smelt generally could be high depending on condition (e.g., turbidity, temperature) and location. Much uncertainty remains, however, about the role and magnitude of predation on Delta Smelt. Furthermore, monitoring of large piscivorous fishes in the upper estuary has been inconsistent. Only the relative abundance of Mississippi Silverside can easily be evaluated on an annual basis (Mahardja et al. 2016).

Competitors of Delta Smelt

The reduction in the estuary’s phytoplankton productivity increase competition for food resources between Delta Smelt and other planktivorous fishes (Bennett 2005). Threadfin Shad possess a diet quite similar to Delta Smelt (Feyrer et al. 2003), and larval and early juvenile Striped Bass feed on the same copepods that Delta Smelt consume (Nobriga and Feyrer 2008). Non-fish species such as introduced jellyfish species may also consume similar prey items to Delta Smelt (i.e., calanoid copepods) (Wintzer et al. 2011), particulary in areas of high-quality habitat such as Suisun Marsh (Beakes et al. 2020). Overlap in diet does not necessarily indicate competition for resources, but it can occur when resources are scarce. Competition is difficult to evaluate in the field and will not be measured directly in these reports.

Fish Species of Interest

Here we highlight a few species that may be important to consider when evaluating Delta Smelt response to increased freshwater flow or a flow action. Generally, our criteria when selecting fish species to evaluate are as follows:

1. Non-Delta Smelt fish species that are ecologically similar to Delta Smelt in some manner, and therefore can potentially be used as surrogates for Delta Smelt.
2. Fish species that may have considerable impact on Delta Smelt population

Striped Bass (age-0)

Evaluating age-0 Striped Bass response to flow actions meant for Delta Smelt can be useful because Striped Bass was also part of the POD along with Delta Smelt and the two species share similar habitat (Feyrer et al. 2007b; Thomson et al. 2010; Mahardja et al. 2017b). Additionally, work on the Delta Smelt life cycle model indicated that abundance of age-0 Striped Bass correlate positively with Delta Smelt abundance (Polansky et al. 2020). Striped Bass are planktivorous in their first year of life and increased in abundance at Suisun Marsh due to the reduced salinity during the Suisun Marsh Salinity Control Gate action in 2018 (Beakes et al. 2020).

Threadfin Shad

Threadfin Shad is the most frequently caught species in the brackish to freshwater habitat of the estuary by pelagic fish surveys today (USFWS et al. 2019; Stompe et al. 2020). Feyrer et al. (2003) found that Threadfin Shad share similar diet with Delta Smelt. Given the rarity of Delta Smelt in the past few years, monitoring Threadfin Shad may be useful for evaluating flow action intended to increase food availability for Delta Smelt. However, it is important to note that Threadfin Shad differs from Delta Smelt in many fundamental ways. For example, they spawn later than Delta Smelt and unlike Delta Smelt, Threadfin Shad are often found in the South Delta where turbidity is low (Feyrer et al. 2009).

Wakasagi

Wakasagi (*Hypomesus nipponensis*) is a non-native congener to Delta Smelt, introduced from Japan to California reservoirs between 1959 and 1973. Wakasagi has since expanded their distribution to additional reservoirs (e.g., Folsom and Oroville reservoirs) and parts of the estuary. This species can negatively influence Delta Smelt through hybridization and potentially competition (Fisch et al. 2014; Benjamin et al. 2018). Spawning timing and diet of Wakasagi are similar to Delta Smelt (Moyle 2002). Prior to 2017, Wakasagi have been observed mostly in reservoirs and tributaries to the Sacramento River (e.g. Feather River, Lake Oroville) with few catches downstream; however, more recent survey data indicate that their occurrence in the upper estuary has increased (USFWS et al. 2019). A study in progress has indicated that the timing of spawning, diet, and abiotic habitat of these two congeners are similar (Brittany Davis et al., unpublished data). Evaluation of Wakasagi catch in the estuary may provide further insight into the success and/or failures of certain flow actions or events.

Mississippi Silverside

Multiple studies indicate that survival of Delta Smelt from egg to post-larvae may be reduced by predation and competition with the invasive Mississippi Silverside (Bennett 2005; Schreier et al. 2016; Hamilton and Murphy 2018; Polansky et al. 2020). Mahardja et al. (2016) found a negative correlation between Mississippi Silverside catch and freshwater inflow in the Delta, but regular assessment of Mississippi Silverside abundance and distribution can provide a better understanding of Delta Smelt response to certain flow actions or events.

Acknowledgments

Larry Brown provided text and comments to an earlier draft of this article prior to his passing. We thank Frederick Feyrer and Peter Nelson for their helpful suggestions and comments. The findings and conclusions of this article are those of the authors and do not necessarily represent the views of our respective agencies.

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