RESEARCH

Dry Me a River: Ecological Effects of Drought in the Upper San Francisco Estuary

Rosemary Hartman*[1], Elizabeth B. Stumpner[1], David H. Bosworth[1], Amanda Maguire[1], Christina E. Burdi[1,2], Interagency Ecological Program Drought Synthesis Team

ABSTRACT

Droughts have major effects on estuaries because freshwater entry is one of the defining features of an estuary, and freshwater flow is an important variable that determines the interannual change in the environment. In the upper San Francisco Estuary (the Sacramento–San Joaquin Delta, Suisun Bay, and Suisun Marsh), the Mediterranean climate includes frequent multi-year droughts. To assess ecosystem responses to droughts in the upper estuary, the Interagency Ecological Program Drought Synthesis Team assembled a set of flow, water quality, chlorophyll, zooplankton, and fish data from 1975 to 2021 to test for differences between multi-year droughts and multi-year wet periods and tested for linear relationships between each variable and the Sacramento Valley Hydrologic Index (see definitions and relationships as outlined in Appendix A). Our models showed droughts *decreased* Delta outflow, project exports, zooplankton in Suisun Bay, and some fish species. We also found that droughts *increased* water clarity, salinity, nutrients, chlorophyll in the South Delta, zooplankton in the South Delta, and water residence time. Although our analyses only tested correlations, we hypothesized that most of the food-web responses could be traced to increased residence time, decreased transport rates, or both. However, some responses may have been caused by secondary effects, including shifts in salinity gradients, regional changes in water quality, or differences in top-down effects of increased predation and grazing rates. With increased frequency of droughts in the future, this increasingly low-outflow, warming, clearing estuary—which is invaded by non-native species and has low pelagic fish production—is rapidly becoming the new "normal."

KEY WORDS

INTRODUCTION

California's San Francisco Estuary (hereafter, estuary), including the Sacramento–San Joaquin River Delta (hereafter, Delta) is a hub of water supply and economic activity. This watershed supplies water to approximately 30 million

people and irrigates more than 6 million acres of farmland across California (Gartrell et al. 2022). However, the estuary is also home to a diverse array of native fishes and wildlife species that evolved in a highly variable climate (Hanak et al. 2012). This Mediterranean climate is characterized by hot, dry summers and cool, wet winters with little to no rainfall for 6 to 9 months of the year (Andrew and Sauquet 2017). This region also has high interannual variability in rainfall, with average precipitation varying from a low of 23.8 cm in 1924 to a high of 105.8 cm in 2017, usually driven by a few large storms each year (Dettinger 2011). This high variability leads to floods and multi-year droughts that result in substantial year-to-year changes in the aquatic community and changes in the ability of managers to provide water for consumptive use. Droughts in the estuary are frequent, affect all aspects of the ecosystem, and often drive conflict between human and environmental uses.

As a result of California's high interannual variation in precipitation and well-developed water storage and conveyance infrastructure, a single dry year does not necessarily constitute a drought. Droughts may be classified based on meteorology (a period of low precipitation), hydrology (period of low in-stream flows), or sociology (a shortage of water supply for human use). While there is no agreed-upon definition for "drought," droughts in California generally consist of multiple consecutive years of low precipitation resulting in a water supply shortage (CDWR 2020). Similar to Mahardja et al. (2021), in this paper we define "drought" as 2 or more consecutive years with a Sacramento Valley Hydrologic Index (hereafter, Sacramento Valley Index) of Below Normal, Dry, or Critical (see "Sacramento Valley Index Calculation" in Appendix A). We compared multi-year drought periods to multi-year wet periods (consecutive years of a Sacramento Valley Index classification of Wet or Above Normal) and "neutral" periods, which are neither part of a drought period nor wet period.

Previous droughts in recent history include the dry periods of 1929–1937, 1944–1950, 1959–1962, 1976–1977, 1987–1992, 2001–2002, 2007–2010,

and 2012–2016 (Figure 1). In contrast, no wet periods have occurred in the past 20 years, the most recent being 1995–2000 (Figure 1). In pre-historical periods, tree-ring analysis shows droughts lasting decades to hundreds of years (Stine 1994). Climate change could bring increased frequency of major floods and droughts, which will stress California's environment and economy (Swain et al. 2018). The 2020–2022 drought, during which this study was conducted, resulted in record low stream flows, groundwater reserves, and reservoir levels, which resulted in extremely dry soils, and inadequate water supply for wildlife and human demands.

The influence of annual freshwater flow on water quality, productivity, and fishes of the estuary is relatively well-studied, though predicted responses frequently have high uncertainty. There are well-established relationships between freshwater flow and population levels of certain biota, most notably the Longfin Smelt (*Spirinchus thaleichthys*) which has increased abundance and recruitment during high-flow conditions (Nobriga and Rosenfield 2016; Kimmerer and Gross 2022) and the copepod *Pseudodiaptomus forbesi*, which increases in abundance in downstream regions during high-flow conditions (Kimmerer, Ignoffo et al. 2018).

Multi-year droughts have received less study than low seasonal or annual outflow. The 2012–2016 drought provided the impetus for a number of studies and reports that gave us a basis for predictions of major ecosystem changes expected during a drought (Lehman et al. 2017; Jabusch et al. 2018; Singer et al. 2020; Mahardja et al. 2021), but droughts are related to complex combinations of physical, chemical, and biological changes that are difficult to capture in detailed statistical models. To fill this gap, the Interagency Ecological Program (IEP) Drought Synthesis Team was formed in 2021 in response to the extremely dry water year. The team analyzed the relationship between drought and a broad suite of environmental parameters, from hydrology to water quality, to phytoplankton, to invertebrates, to fishes. This paper, one of a series that came out of the project, is a synthesis of all the parameters
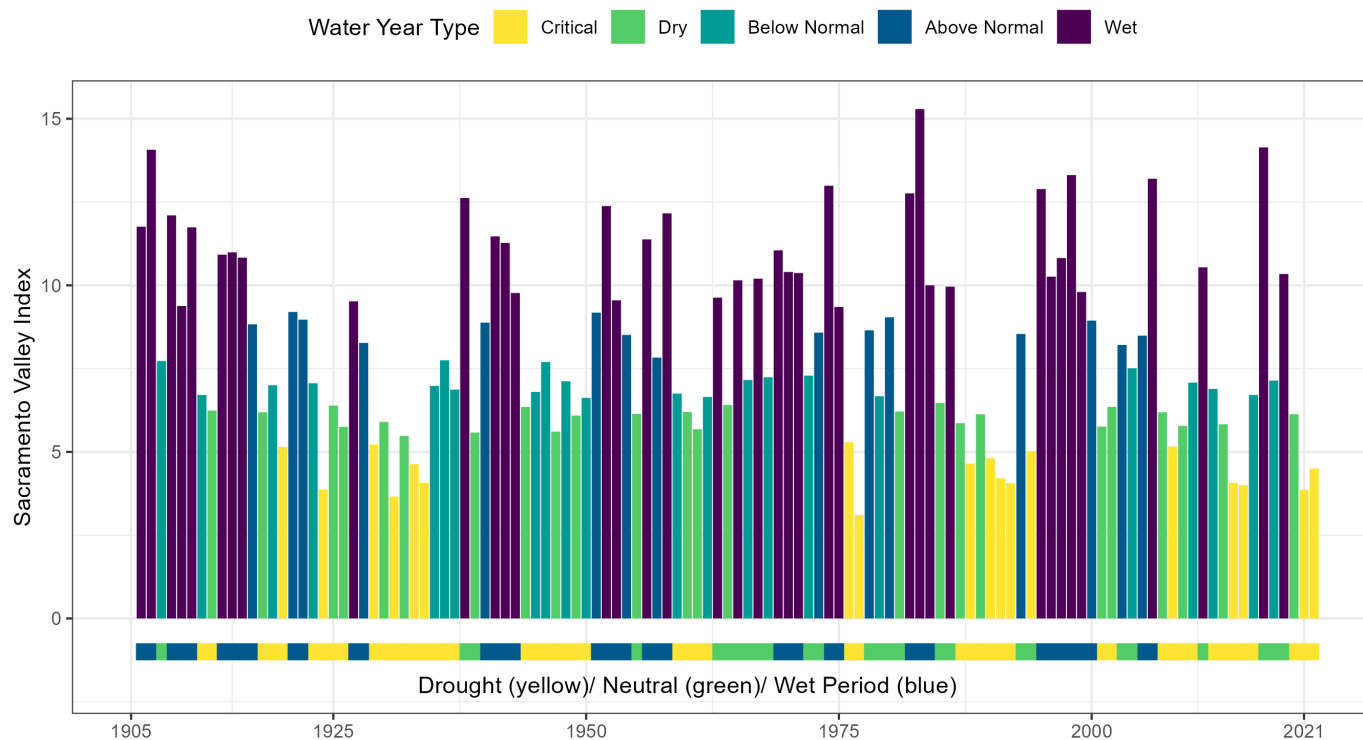
Figure 1 Water year indices for the Sacramento Valley from 1905 to 2022. Periods classified as "drought periods" (consecutive Dry, Critical, and Below Normal years) are highlighted by *yellow bars* below the *x*-axis. Periods classified as "wet periods" (consecutive Wet and Above Normal years) are highlighted with *blue bars* below the *x*-axis. "Neutral" periods (neither drought nor wet period) are highlighted in *green* below the *x*-axis.

analyzed by the IEP Drought Synthesis Team. Each paper in this series can stand alone, but many of the papers refer to each other and provide complementary information.

The IEP Drought Synthesis Team developed a conceptual model of the effects of drought on the ecosystem of the Delta, Suisun Bay, and Suisun Marsh (together the "upper estuary") (Figure 2), as predicted by the wealth of literature on how flow affects the ecosystem. We tested for correlations between ecosystem drivers that change during droughts, intermediate drivers that are directly affected by the major drivers, and ecosystem responses across the regions of the estuary. In many cases these analyses confirm that the relationships between flow and environmental factors previously tested by other research hold for muti-year droughts as well. Our analyses focused on correlations between variables, not mechanisms behind the correlations; however, our conceptual model

presents a framework for the hypothesized mechanisms that connect prolonged decreases in flow with ecosystem change.

CONCEPTUAL MODEL

Drivers

We hypothesized that the main driver during drought periods is reduced freshwater flow, which directly results in increased water residence time and decreased transport. Freshwater flow is also how resource managers can alter conditions in the Delta for beneficial uses, although managers are limited in how much they can control flow (Schoellhamer et al. 2016; Hutton et al. 2019;). In the upper estuary, tidal flow, rather than freshwater inflow, is the main determinant of water velocity and transport (Schoellhamer et al. 2016; Hutton et al. 2019). However, reduced freshwater flow will also increase water residence time (Hammock et al. 2019), alter transport between naturally connected hydrological
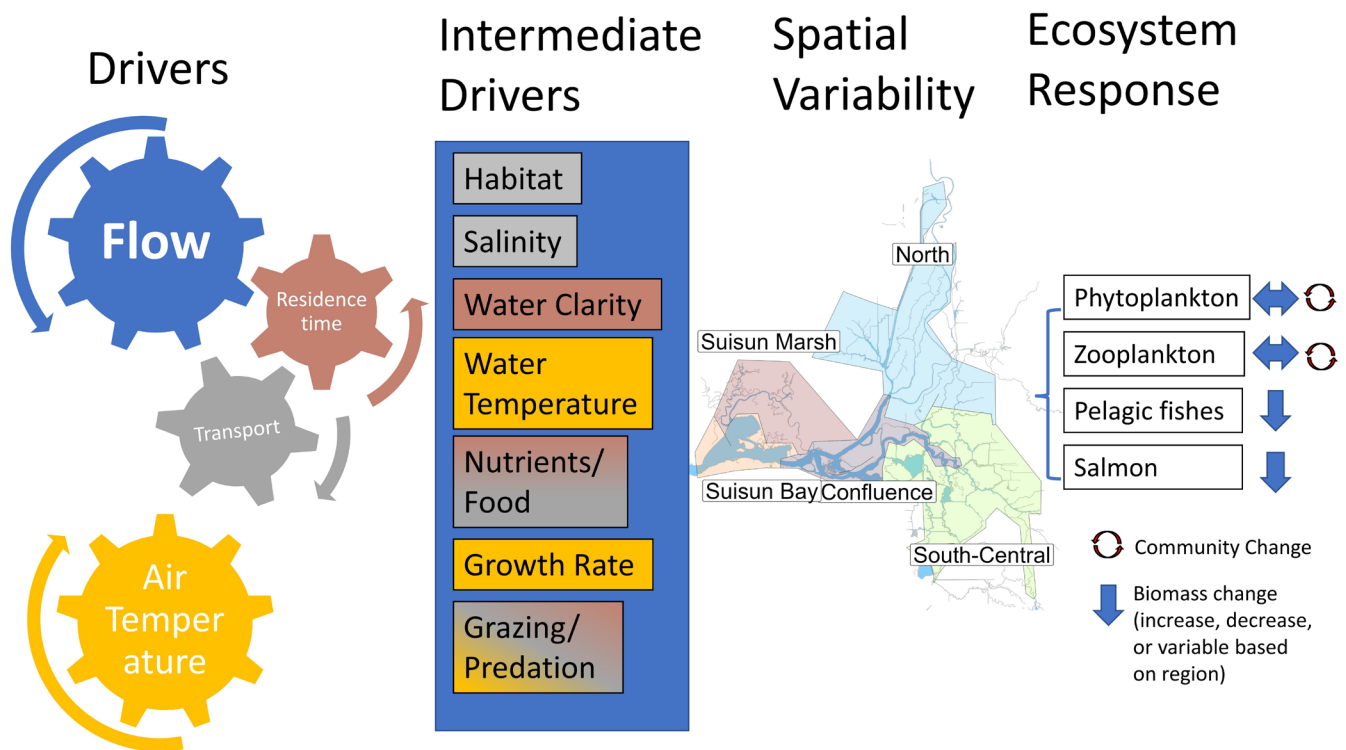
Figure 2 The conceptual model for how drought impacts the ecosystem of the upper estuary. This model provided the framework for hypothesized relationships between drought and ecosystem change. Decreases in flow and increases in air temperature drove changes to water quality, nutrients, and habitat, which, when distributed across different areas of the estuary resulted in different ecological outcomes.

habitats (Keeley et al. 2022), and reduce transport between terrestrial and aquatic systems (Saleh and Domagalski 2015; Weston et al. 2015).

We also hypothesized that water temperature would increase during droughts. This is especially true for the most recent droughts (2012–2016 and 2020–2022), as climate change effects have increased temperatures in recent years (Bashevkin, Mahardja et al. 2022). While air temperature is considered the primary driver of water temperature in the Delta (Vroom et al. 2017), researchers have also identified a negative correlation between flow and water temperature (Nobriga et al. 2021; Bashevkin and Mahardja 2022).

Intermediate Drivers

We hypothesized that changes to flow and the resulting changes to transport and residence time would affect many biogeochemical and physiological processes in the estuary. We

hypothesized that decreased flow would cause an increase in salinity (as described in Andrews et al. 2017; Ghalambor et al. 2021).

We hypothesized that increased residence time would cause an increase in water clarity as sediment drops out of the water (Livsey et al. 2021). In some regions, with sufficient light and nutrients, higher residence time may allow greater phytoplankton and zooplankton production (Glibert et al. 2014), though in other regions increased residence time will allow increased time for benthic grazing to reduce biomass (Lucas and Thompson 2012).

We hypothesized that decreased transport would cause a decrease in inputs of nutrients and sediment from upstream regions (Domagalski and Saleh 2015; Saleh and Domagalski 2015; Stern et al. 2020), as well as a decrease in connectivity between upstream and downstream habitat, increasing the time taken for organisms to move

to suitable habitat (Hance et al. 2022) and dividing populations separated by high-salinity areas (Feyrer et al. 2010).

We hypothesized that increased air temperature and water temperature would result in increased productivity and growth rates (Lehman et al. 2008; Paerl and Huisman 2008; Gearty et al. 2021), but also increased predation and grazing rates (Nobriga et al. 2021; Zierdt Smith et al. 2023), and in some cases may exceed species' optimal temperatures (Brown et al. 2016; Yanagitsuru et al. 2021).

Spatial Variability

We divided the upper estuary into five regions based on their salinity regimes, hydrologic influences, and hypothesized differences in response to droughts (Figure 3). Suisun Marsh, an area of extensive tidal and managed wetlands with little direct freshwater input, has been considered important native fish habitat because of its complex channel network, high turbidity (low water clarity), and high productivity (Moyle et al. 2013; Moyle et al. 2014). Suisun Bay, an area of extensive shoals and high turbidity, was also historically productive native fish and invertebrate habitat (Jassby et al. 1995; Carlson and Matern 2000; Hanak et al. 2012; Bever et al. 2016). The confluence of the Sacramento and San Joaquin rivers (confluence) is dominated by deep, armored channels, but there are also wetland islands such as Brown's Island and Sherman Lake (Figure 3). The South-Central Delta is a large network of small, interconnected channels lined by rip-rap and dominated by relatively slow-moving, warm, clear water even during wetter years, and is therefore considered poor habitat for pelagic fishes such as Delta Smelt, Longfin Smelt, Threadfin Shad, and American Shad (Stompe et al 2023). The North Delta is influenced by the Sacramento River and the Yolo Bypass flows, and tends to have lower temperatures, higher turbidity, and higher native fish populations (Hanak et al. 2012; Bashevkin, Mahardja, et al. 2022; Stompe et al. 2023).
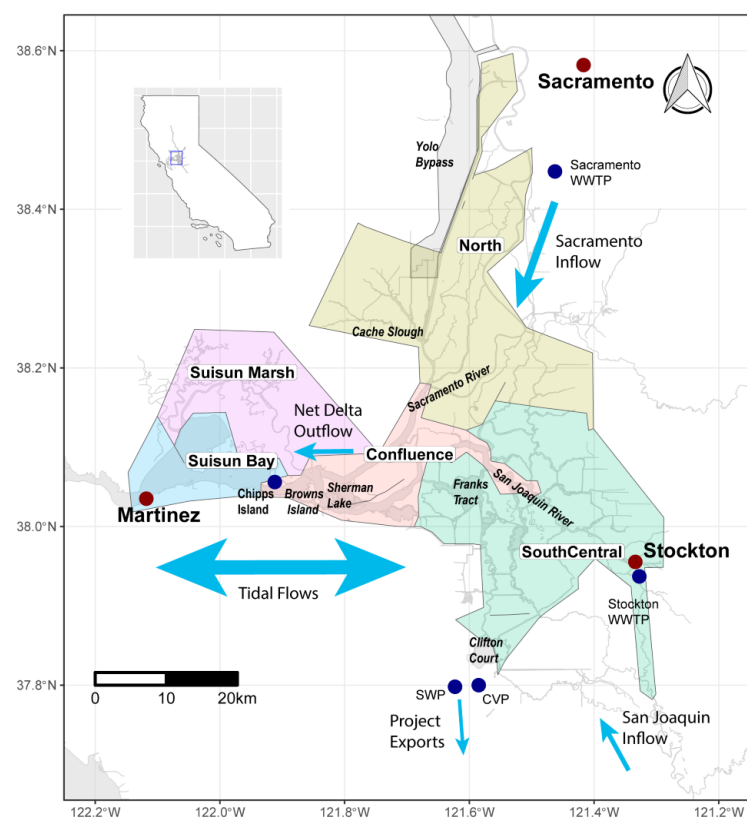

Figure 3 Map of the upper estuary delineating regions used in analysis, important rivers and islands, Central Valley Project (CVP) water export facility, State Water Project (SWP) water export facility, the Stockton Wastewater Treatment Plant (WWTP), the Sacramento WWTP, and major cities. *Blue arrows* represent major flow parameters (not to scale). Regions were chosen based on similar salinity regimes and hydrologic influences.

Drought Responses

We developed hypotheses for how populations of major classes of organisms would react to ecosystem changes across these regions. Changes in salinity alter the available habitat for estuarine species adapted to a specific salinity range (Kimmerer et al. 2013; Sommer and Mejia 2013; Hammock et al. 2015). Brackish-water species such as jellyfish and clams will shift their distribution further upstream, causing increased grazing pressure in the confluence (Crauder et al. 2016; Hartman, Twardochleb et al., this issue). Increased residence time, water clarity, and water temperature may result in phytoplankton blooms in the South Delta, but increased benthic and zooplankton grazing rates and decreased downstream transport may cause overall decreases in Suisun Bay and Marsh. Lack of appropriate salinity, turbidity, and temperature may cause a decrease in resident fish populations (Mahardja et al. 2021), while decreased connectivity may decrease native migratory fish survival (Hance et al. 2022). Conversely, higher temperatures can favor some fish species, such as introduced Threadfin Shad (Feyrer et al. 2007).

To test our conceptual model of drought effects, the IEP Drought Synthesis Team put together an integrated dataset of the major ecological metrics in the upper estuary and tested how they responded to drought periods. We also compared multi-year drought periods to the linear effect of flow within a given year to see whether multi-year droughts have different properties from overall flow effects.

Research Questions

- How does the ecosystem of the upper estuary respond to multi-year droughts?

- How does the effect of multi-year droughts differ from the effect of flow in a particular year?

- What correlations in ecosystem responses to droughts may indicate causal relationships?

METHODS

Drought Determination

To determine when drought periods occurred over the historical record, we used the Sacramento Valley Hydrological Index and associated classifications to define water-year types, with the water year beginning on October 1st of the previous year and ending on September 30th. This index is based on modeled unimpaired flow in the major rivers of the Sacramento Valley, and each year is classified as "Critical," "Dry," "Below Normal," "Above Normal," or "Wet," depending on the index value (see Appendix A for details on index calculation and classification). The indices and associated classifications for 1975 to 2021 were downloaded from the California Department of Water Resources website (CDWR 2022).

Actual flows in the upper estuary (as opposed to unimpaired runoff) are highly dependent upon water management that includes dam operations, exports and diversions, and environmental flows (Hutton et al. 2017; Durand et al. 2020). To visualize the effect of water management on the relationship between precipitation and flow from the Delta on an annual time-step, we compared a linear model of Delta outflow versus the Sacramento Valley Hydrological Index (as described above) with a generalized additive (non-linear) model. Annual average Delta outflow was modeled as a smooth function of annual Sacramento Valley Hydrological Index using the *gam* function from the 'mgcv' package in R (Wood 2017). Daily Delta outflow was modeled by the CDWR's Dayflow model (described below under Environmental Data Collection).

We assigned 2 or more years in a row that were classified as "Critical," "Dry," or "Below Normal" as "drought periods," 2 or more years in a row that were classified as "Above Normal" or "Wet" as "wet periods," and periods that switched from Dry to Wet as "neutral periods." It is important to recognize that "neutral" periods can contain extremely wet and extremely dry years, but they do not contain multiple consecutive Wet years or multiple consecutive Dry years.

Residence Time

To estimate residence time (the length of time a particle of water remains in the upper estuary), we replicated the methods used by Hammock et al. (2019). In brief, we obtained monthly residence times for the Sacramento and San Joaquin river corridors from Hammock et al. (2019) for 1991, 1996, 1998, 2005, and 2009 and then fit statistical models of residence time versus inflow, project exports, and in-Delta agricultural diversions, then used the best model to predicted residence time for all years not modeled by Hammock et al. (2019) (See Appendix A for more information).

Environmental Data Compilation

We developed an integrated dataset of environmental parameters derived from IEP long-term monitoring datasets from 1975 to 2021 (Table 1). Data from these surveys were averaged by region (Figure 3), and season (with Winter including December, January, February; Spring including March, April, May; Summer including June, July, August; and Fall including September, October, November). This seasonal definition meant that the "Fall" season straddled 2 water years. Because ecological conditions in the Fall are usually more dependent on conditions from the previous winter–spring than any early Fall rain, we adjusted the water year to begin on December 1 of the previous year and end on November 30, instead of October 1 through September 30. However, we still used the water-year index assigned to the water year from October through September. We then took the regional average across seasons for chlorophyll and zooplankton biomass to get a single data point for each region and year. For other variables, we averaged across both season and region to get a single data point for the entire year. Some variables (such as Delta outflow) did not have a regional component, and some variables (such as the fish indices) used established summary methods instead of regional averages (See Table 3 for details).

Delta Outflow, and SWP and CVP Water Exports

Net Delta Outflow Index and combined water exports from the State Water Project (SWP) and Central Valley Project (CVP) came from the CDWR's Dayflow model (CDWR 2002). (See Appendix A for data sources and how outflow is calculated.) All data are published annually after input data have undergone quality-control procedures on the California Natural Resources Agency Open Data Portal[1].

Water Quality, Nutrients and Chlorophyll

Water temperature, salinity, Secchi depth, dissolved ammonium, dissolved nitrate + nitrite, dissolved orthophosphate, and chlorophyll-*a* were assembled as for Bosworth et al. (this issue). In brief, data from 16 monitoring surveys were integrated into a discrete water-quality dataset available on the Environmental Data Initiative repository (Bashevkin et al. 2023). This dataset contains water quality, nutrient, and chlorophyll data collected by long-term monitoring surveys that sample approximately monthly at locations throughout the upper estuary. We obtained data collected by 12 surveys that have at least 20 years of data between 1975 and 2021 within our study area in the upper estuary (Figure 3). All water-temperature and salinity measurements were typically collected at a depth of 1 meter, and the nutrient and chlorophyll samples were collected at various depths less than 5 m from the surface. For more information on data-collection methods, refer to the metadata in Bashevkin et al. (2023).

To ensure spatial and temporal balance across the dataset, we selected only one sample per station per day, and restricted the dataset to include sub-regions that had data for at least 35 out of the 47 years for all four seasons. Sub-regions were defined by polygons from the 'deltamapr' package in R (Bashevkin 2021). Before aggregating the nutrient and chlorophyll data, we substituted the values below the reporting limit with simulated values between zero and the reporting limit based on a uniform distribution. We ran one simulation for each parameter and set a seed before running the simulation to ensure reproducibility. For more information on data cleaning and aggregation, see Bosworth et al. (this issue).

---

1. *https://data.cnra.ca.gov/dataset/dayflow/resource/776b90ca-673e-4b56-8cf3-ec26792708c3*

Table 1 Metrics and data sources

Metric	Dataset used	Summary method	Definition
Net Delta Outflow Index (Outflow)	Dayflow	Annual average	Model estimate of net flow past Chipps Island, in cubic feet per second (cfs). (CDWR 2002).
Project Exports	Dayflow	Annual average	Average State Water Project and Central Valley Project export rate in cfs.
Residence Time	Model based on Hammock et al. (2019)	Monthly average	Number of days for 90% of particles to exit the estuary
Temperature	Integrated IEP dataset (Bashevkin et al. 2023)	Annual average	Water temperature as measured within one meter below the surface at discrete stations sampled by IEP's long-term monitoring programs.
Secchi Depth	Integrated IEP dataset (Bashevkin et al. 2023)	Annual average	Secchi depth in cm at discrete stations sampled by IEP's long-term monitoring programs.
Salinity	Integrated IEP dataset (Bashevkin et al. 2023)	Annual average	Salinity (practical salinity units), converted from measured specific conductance at discrete stations sampled by IEP's long-term monitoring programs.
Nutrients	Integrated IEP dataset (Bashevkin et al. 2023)	Annual average	Dissolved nitrate + nitrite, dissolved ammonium, and dissolved orthophosphate concentrations in the water as measured by EMP and USGS discrete monitoring programs.
Chlorophyll	Integrated IEP dataset- (Bashevkin et al. 2023)	Regional average, log-transformed	Chlorophyll-a concentration as measured by EMP, NCRO, and USGS discrete monitoring programs.
Zooplankton	Environmental Monitoring Program (Bashevkin, Hartman, et al. 2022)	Regional average, log-transformed	Total biomass of zooplankton per cubic meter of water (BPUE) for taxa most important to pelagic fishes from Environmental Monitoring Program.
Delta Smelt	CDFW's Fall Midwater Trawl indices	Annual index, log-transformed	Annual population index as calculated by the FMWT survey.
Longfin Smelt	CDFW's Fall Midwater Trawl indices	Annual index, log-transformed	Annual population index as calculated by the FMWT survey.
Striped Bass, age-0	CDFW's Fall Midwater Trawl indices	Annual index, log-transformed	Annual population index as calculated by the FMWT survey.
American Shad	CDFW's Fall Midwater Trawl indices	Annual index, log-transformed	Annual population index as calculated by the FMWT survey.
Salmon Cohort Replacement Rate	GrandTab (see Azat 2021)	Annual index	Average of the annual cohort replacement rate for Central Valley spring-run Chinook Salmon, and Central Valley fall-run Chinook Salmon.

Zooplankton

Zooplankton data were collated as for Barros et al. (this issue). In brief, zooplankton Catch Per Unit Effort (CPUE, organisms m^{-3}) data for the Environmental Monitoring Program were downloaded using the 'zooper' package, an R package that synthesizes zooplankton data from multiple IEP studies (Bashevkin, Hartman, et al. 2022). We used CPUE data from either the macronet (500- to 505-µm mesh), mesonet (150- to 60-µm mesh), or micronet (43-µm mesh), depending on which net sampled each taxon most efficiently. We focused on dominant taxa that are most frequently found in the diets of Delta

Smelt and Longfin Smelt: the cladocerans *Bosmina longirostris*, *Daphnia* sp., *Diaphanosoma* sp.; the copepods *Acartia* sp., *Acartiella sinensis*, *Eurytemora affinis* (adults and copepodites), *Limnoithona tetraspina* (adults), *Pseudodiaptomus forbesi* (adults and copepodites), *Tortanus* sp. (adults), and the mysids *Hyperacanthomysis longirostris*, *Neomysis kadiakensis*, and *Neomysis mercedis*. We then calculated biomass per unit effort (BPUE, mg C m^{-3}) utilizing the conversions in Bashevkin et al. (2022) for meso and micro zooplankton (copepods and cladocerans) and the BPUE for macro zooplankton (mysids) using length to weight equations (Burdi et al. 2021)

for the years of 1975 to 2021. BPUE converts the zooplankton data into a "common currency" relevant to estuarine productivity and food availability for fish consumers. We excluded winter months (December through February) because of inconsistent historical winter sampling and excluded data from the North Delta region because of the lack of consistent long-term zooplankton sampling in the region.

Fall Midwater Trawl Indices

Data on population abundance of pelagic fishes (age-0 Striped Bass (*Morone saxatilis*), American Shad *(Alosa sapidissima)*, Delta Smelt (*Hypomesus transpacificus*), Longfin Smelt (*Spirinchus thaleichthys*), and Threadfin Shad (*Dorosoma petenense*), came from the Fall Midwater Trawl Survey (FMWT) conducted by the California Department of Fish and Wildlife (CDFW) (White 2021). Annual abundance indices were obtained from the CDFW website (*https://filelib.wildlife. ca.gov/Public/TownetFallMidwaterTrawl/*). The FMWT conducts stepped-oblique trawls at 100 index stations throughout the upper estuary once per month in September, October, November, and December of each year. The annual index for each species is calculated based on weighted catches from each of 17 areas over the 4-month sampling period (September through December). Details for the calculations, as well as the complete catch data from this program, are available from the CDFW website.

Salmon Cohort Replacement Rate

The combined cohort replacement rates for fall-run Central Valley Chinook Salmon and spring-run Central Valley Chinook Salmon (*Oncorhynchus tshawytscha*) were calculated as described in Appendix A). In brief, CDFW calculates annual escapement data based on watershed-wide surveys for salmon throughout their life cycle (Grandtab; Azat 2021). This dataset can be used to estimate a particular returning year class's contribution to the population's overall abundance. Year-over-year escapement can be used to calculate a population's "cohort replacement rate" (CRR), which is the measure of the number of spawners produced by the parental generation of spawners 3 years prior (see

Appendix A for details). We calculated the CRR for spring-run and fall-run Chinook Salmon and looked for effects of drought or water-year index on CRR for the year that the cohort out-migrated.

Data Analysis

Once data were organized and summarized, we modeled the effect of droughts in two ways:

1. To look for effects of extended, multi-year droughts, we performed a linear model on each metric that compared annual averages for drought periods versus wet periods. We calculated the effect size using the partial Cohen's F for the 'Drought' term in each model using the 'effectsize' package in R (Ben–Shachar et al. 2023). Because the FMWT fish indices have experienced a long-term decline over time, and depend on the number of spawners, we included year and the previous year's population index as terms in the model.

2. To test for a linear effect of flow, we performed a linear model on the annual average for each metric versus the Sacramento Valley Index. Year and the previous year's population size were included as terms in the models of FMWT species. Analyses were performed using the *lm* function in R (R Core Team 2022).

When necessary, data were natural-log transformed to meet assumptions of normality and homogeneity of variance (see Table 3 for transformations). In preliminary analyses, chlorophyll and zooplankton both showed major differences in response to flow and drought periods in different regions of the upper estuary, so we calculated annual averages by region instead of estuary-wide for these analyses. There were insufficient chlorophyll data to analyze the Suisun Marsh region, and insufficient zooplankton data to analyze the North region, so these were omitted from the analyses. We performed all analyses using the *lm* function in R, followed by the *anova* function for FMWT fish analyses (R Core Team 2022).

RESULTS

Residence Time

The best model as ranked by Akaike information criterion, with a correction for small sample sizes (AICc) for residence time on the San Joaquin River included San Joaquin River Flow, Agricultural Diversions, water exports, the interaction of Agricultural Diversions and River Flow, and the interaction of project exports and River Flow (see Table 2). The best model as ranked by AICc for residence time on the Sacramento River included Sacramento River Flow, project exports, and the interactions between Sacramento River Flow and project exports (Table 2).

Looking across time from 1975 to 2021, our statistical model of residence time predicts higher residence time during drought periods, with the peak residence time occurring after several dry years in a row (Figures 4, 5, and 6). The years of 1977 (second year of the 1976–1977 drought), 1992 (end of the 1987–1992 drought), 2009 (toward the end of the 2006–2010 drought), and 2015 (toward the end of the 2012–2016 drought) had particularly high residence times on both the Sacramento and San Joaquin rivers.

Flow and Water Quality Metrics

Net Delta outflow decreased significantly during drought periods, with one of the largest effect sizes of any parameter we analyzed (Figure 5 and 6, Table 3). It also had a strong positive relationship with the Sacramento Valley Index (Figure 8). A linear regression of Sacramento

Valley Index (based on unimpaired runoff) versus Delta outflow (which is highly managed) on an annual time-step fit very closely ($R^2 = 0.92$, Figure 9); however, a non-linear fit was slightly better ($R^2 = 0.97$, Figure 9), because of relatively small changes in Delta outflow per change in the Sacramento Valley Index at very low outflow levels.

Project exports also experienced large decreases during drought periods and a strong positive relationship with the Sacramento Valley Index (Figures 5, 6, and 8; Table 3), though the effect size was not as large as for outflow (Cohen's F of -0.93 and -2.9, respectively; Table 3).

Residence time on the Sacramento River significantly increased during drought periods and had a significant, negative relationship with the Sacramento Valley Index (Figures 5, 6 and 8; Table 3). Residence time on the San Joaquin River also had a significant, negative relationship with the Sacramento Valley Index, but the increase in residence time during drought periods was not significant ($p = 0.076$), and the effect size was smaller (Cohen's F of 0.63 and 2.5, respectively; Figure 6).

Annual average salinity, measured by IEP surveys, increased significantly during drought periods and had a significant negative relationship with the Sacramento Valley Index (Figures 5, 6 and 8; Table 3). Secchi depth and temperature also increased significantly during

Table 2   Results of top-ranked models for San Joaquin River and Sacramento River residence times

| River	Term	Estimate	SE	t value	p value
San Joaquin	(Intercept)	2.870	0.1470	19.52	< 0.0001
San Joaquin	River Flow	− 0.279	0.0316	− 8.83	<< 0.0001
San Joaquin	Ag Diversions	− 0.0047	0.0018	− 2.58	0.0114
San Joaquin	Exports	− 0.0049	0.0009	− 5.70	< 0.0001
San Joaquin	River Flow:Exports	0.0008	0.0002	4.16	0.0001
San Joaquin	River Flow:Ag Diversions	0.0010	0.0004	2.33	0.0219
Sacramento	(Intercept)	4.821	0.1970	24.47	< 0.0001
Sacramento	River Flow	− 1.278	0.0714	− 17.89	< 0.0001
Sacramento	Exports	− 0.0034	0.0013	− 2.69	0.0085
Sacramento	River Flow:Exports	0.0014	0.0005	3.07	0.0028
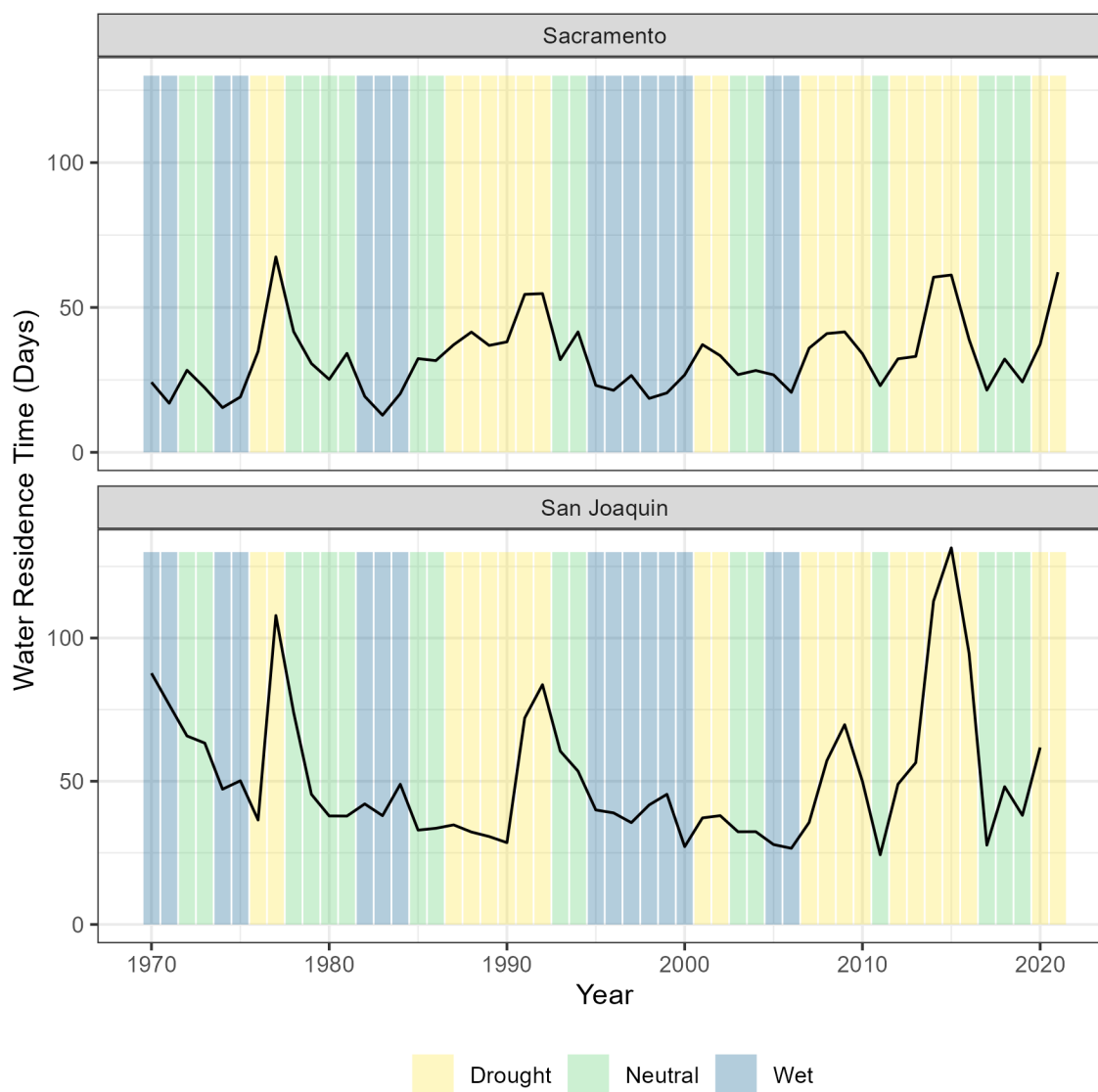
Figure 4 Predicted annual average residence time (days) for particles inserted at Sacramento (on the Sacramento River, *top panel*) or at Stockton on the San Joaquin River (*lower panel*). Drought periods are shown in *yellow*, wet periods in *blue,* and neutral periods in *green*.

drought periods and had a significant negative relationship with the Sacramento Valley Index (Figures 5, 6 and 8; Table 3).

All nutrients (ammonium, orthophosphate, and nitrate+ nitrite) had significant negative relationships with the Sacramento Valley Index, and orthophosphate and nitrate + nitrite also had significant increases during drought periods (Figures 5, 6 and 8; Table 3). Ammonium showed a trend toward increases during drought periods,

but it was not statistically significant (Figures 5, 6 and 8; Table 3).

Biological Metrics

Both chlorophyll and total zooplankton biomass failed to show clear relationships with drought periods or the Sacramento Valley Index when examined on an estuary-wide scale (data not shown); however; they did have strong relationships with the Sacramento Valley Index and drought periods when examined on a regional scale (Figure 7). In the South-

Figure 5 *Box plots* showing ecological metrics versus the drought, neutral and wet period classifications (D = Drought, N = Neutral, W = Wet). Units and transformations are as listed in Table 3. *Red asterisks* indicate parameters where there is a significant difference between drought periods and wet periods (* *p* < 0.05, ** *p* < 0.01, *** *p* < 0.001)

Central Delta, both chlorophyll and zooplankton increased significantly during drought periods and had a significant negative relationship with the Sacramento Valley Index, though this effect was stronger for zooplankton than chlorophyll (Figures 5, 6 and 8; Table 3). In Suisun Bay, zooplankton decreased significantly during drought periods and had a significant positive relationship with the Sacramento Valley Index. Chlorophyll showed trends in the same direction as zooplankton, but these were not significant (Figures 5, 6 and 8; Table 3). There were no significant relationships between chlorophyll or zooplankton and drought periods or the Sacramento Valley Index in the Suisun Marsh, confluence, and North Delta, with the trend varying by region.

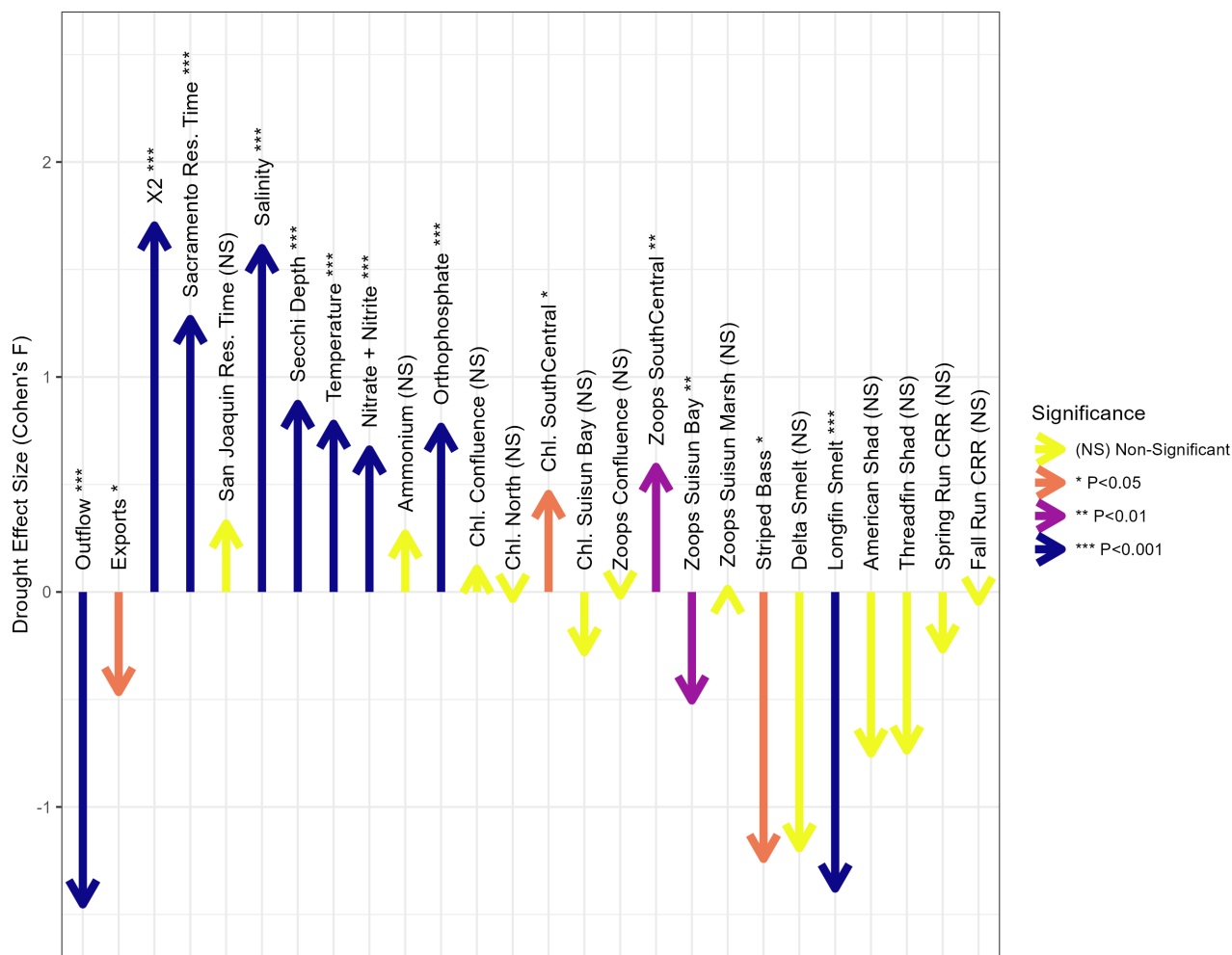All of the pelagic fishes showed decreasing trends in abundance during droughts (Figures 5 and 6;

Figure 6 Effect sizes (Cohen's F) for the factor characterizing the difference between drought periods and wet periods in a linear model for each ecological parameter. Large negative effects indicate greater decrease with drought period, larger positive effects indicate greater increases with drought period.

Table 3, Table A2); however, only Longfin Smelt and Striped Bass had statistically significant decreases once the long-term population trends were taken into account (Table A2). Longfin Smelt, Striped Bass, and American Shad also had significant positive relationships with the Sacramento Valley Index after long-term population trends were taken into account, whereas Delta Smelt and Threadfin Shad did not (Figure 8; Table 3, Table A2).

The cohort replacement rates for both salmon runs showed trends toward lower CRR when juveniles out-migrated during drought periods, but the trends were not statistically significant

(Figures 5 and 6; Table 3). Spring-run Chinook Salmon—but not fall-run—had a significant positive relationship with the Sacramento Valley Index in the year of out-migration (Figure 8; Table 3).

DISCUSSION

Freshwater flow into the estuary is one of the most important variables that determines interannual changes in the environment, and we identified many responses to multi-year droughts that most likely stem from changes to flow. Our models support our hypothesis that drought periods decreased inflow and increased estuarine
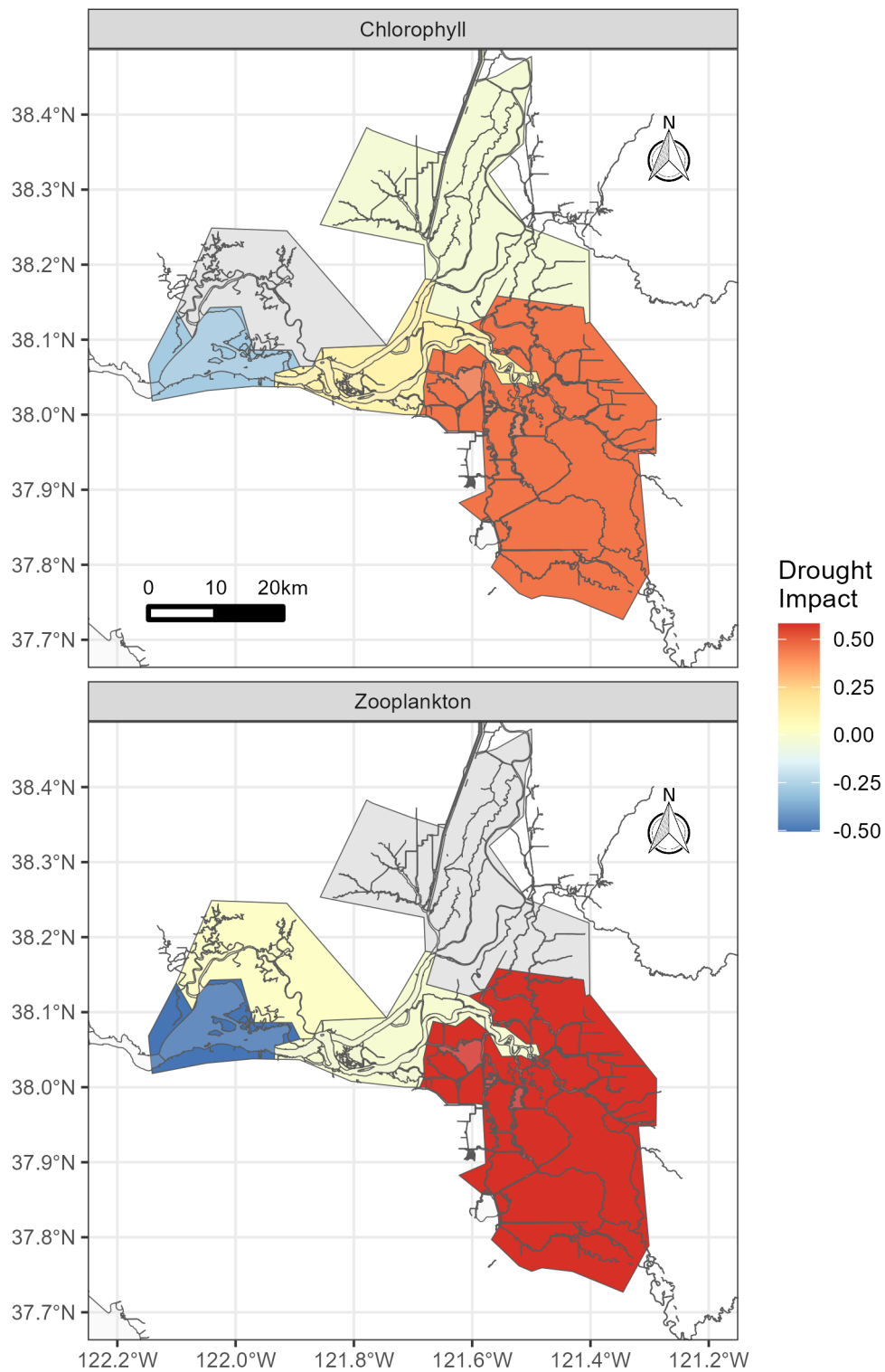
Figure 7 Map of zooplankton and chlorophyll drought period response across regions of the upper estuary. The Suisun Marsh region for chlorophyll, and the North region for zooplankton were omitted due to insufficient data.

Table 3 Ecological metrics, units, transformations (Trans), and regression parameters for regressions of metrics compared with the annual Sacramento Valley Index and the categorical Drought or Wet classification. FMWT indices also included the effect of year and the previous year's FMWT index (see Table A2). Negative Drought versus Wet model estimators indicate decreases during wet periods.

Metric	Units	Trans	Sacramento Valley Index model				Drought versus Wet model		
			Intercept	Slope	R^2	P value	Estimate	P value	Cohen's F
Delta Outflow	CFS	None	− 26667	6475.32	0.92	< 0.0001[c]	37012	< 0.0001[c]	− 1.453
Sacramento residence time	days	None	60.87	− 3.53	0.71	< 0.0001[c]	− 22.69	< 0.0001[c]	1.599
San Joaquin residence time	days	None	77.09	− 3.23	0.16	0.0033[b]	− 16.08	0.076	0.318
Project water exports	CFS	None	4286.5	293.50	0.25	0.0004[c]	1638.5	0.014[a]	− 0.465
Temperature	C	None	17.32	− 0.125	0.41	< 0.0001[c]	− 0.828	0.0001[c]	0.782
Salinity	PSU	None	4.051	− 0.271	0.83	< 0.0001[c]	− 1.728	< 0.0001[c]	1.599
Secchi Depth	cm	None	88.79	− 2.851	0.23	0.0002[c]	− 24.29	< 0.0001[c]	0.875
Ammonium	mg L^{-1}	ln(x)	− 1.986	− 0.035	0.09	0.0374[a]	− 0.207	0.141	0.271
Nitrate + Nitrite	mg L^{-1}	ln(x)	− 0.695	− 0.040	0.34	< 0.0001[c]	− 0.241	0.001[b]	0.663
Orthophosphate	mg L^{-1}	ln(x)	− 2.186	− 0.057	0.48	< 0.0001[c]	− 0.329	0.0002[c]	0.768
Chlorophyll Suisun Bay	µg L^{-1}	ln(x)	0.804	0.040	0.04	0.177	0.291	0.129	− 0.280
Chlorophyll confluence	µg L^{-1}	ln(x)	1.185	0.0018	< 0.0001	0.9362	− 0.104	0.552	0.108
Chlorophyll North	µg L^{-1}	ln(x)	0.691	0.0047	0.001	0.8348	0.032	0.861	− 0.032
Chlorophyll South-Central	µg L^{-1}	ln(x)	2.787	− 0.079	0.17	0.004[b]	− 0.518	0.016[a]	0.456
Zooplankton confluence	µg m^{-3}	ln(x)	8.78	0.01	0.003	0.7162	0.016	0.928	− 0.017
Zooplankton South-Central	µg m^{-3}	ln(x)	10.68	− 0.18	0.390	< 0.0001[c]	− 0.916	0.0033[b]	0.582
Zooplankton Suisun Bay	µg m^{-3}	ln(x)	7.88	0.13	0.30	0.0001[b]	0.650	0.0097[b]	− 0.505
Zooplankton Suisun Marsh	µg m^{-3}	ln(x)	9.11	0.01	0.004	0.6793	− 0.017	0.937	0.015
American Shad FMWT Index	unitless	ln(x)	5.71	0.18	0.30	< 0.0001[c]	0.644	0.056	− 0.752
Threadfin Shad FWMT Index	unitless	ln(x)	63.6	0.001	0.65	0.97	0.320	0.412	− 0.841
Delta Smelt FMWT Index	unitless	ln(x+1)	78.4	0.059	0.87	0.16	0.422	0.157	− 1.192
Longfin Smelt FMWT Index	unitless	ln(x)	110	0.37	0.73	< 0.0001[c]	0.685	< 0.0001[c]	− 1.380
Striped Bass, age-0 FMWT Index	unitless	ln(x)	147	0.11	0.84	0.03[a]	0.644	0.014[a]	− 1.242
Spring-Run Chinook CRR	unitless	none	0.321	0.14	0.10	0.032[a]	0.443	0.154	− 0.267
Fall-Run Chinook CRR	unitless	none	0.963	0.01	0.01	0.486	0.074	0.808	− 0.045

a. Significant at the $p < 0.05$ level.
b. Significant at $p < 0.01$ level.
c. Significant at $p < 0.001$ level.

residence time, aligning with previous studies of flow variation and residence time (Kimmerer and Nobriga 2008 and references therein). Decreased inflow and increased residence time were correlated with predictable changes in some parameters, whereas other parameters changed in very location-specific or species-specific ways, requiring a deeper understanding of how the ecosystem components interrelate. While we did not measure transport rates directly, we hypothesized transport of water—as well as sediment, nutrients, plankton, and fish—to be one of the major drivers behind drought effects, and changes to connectivity and transport explain many of these effects on the estuary.

Flow

Flow parameters decreased during drought periods; however, these effects were not always linear. At an annual time-step, mean
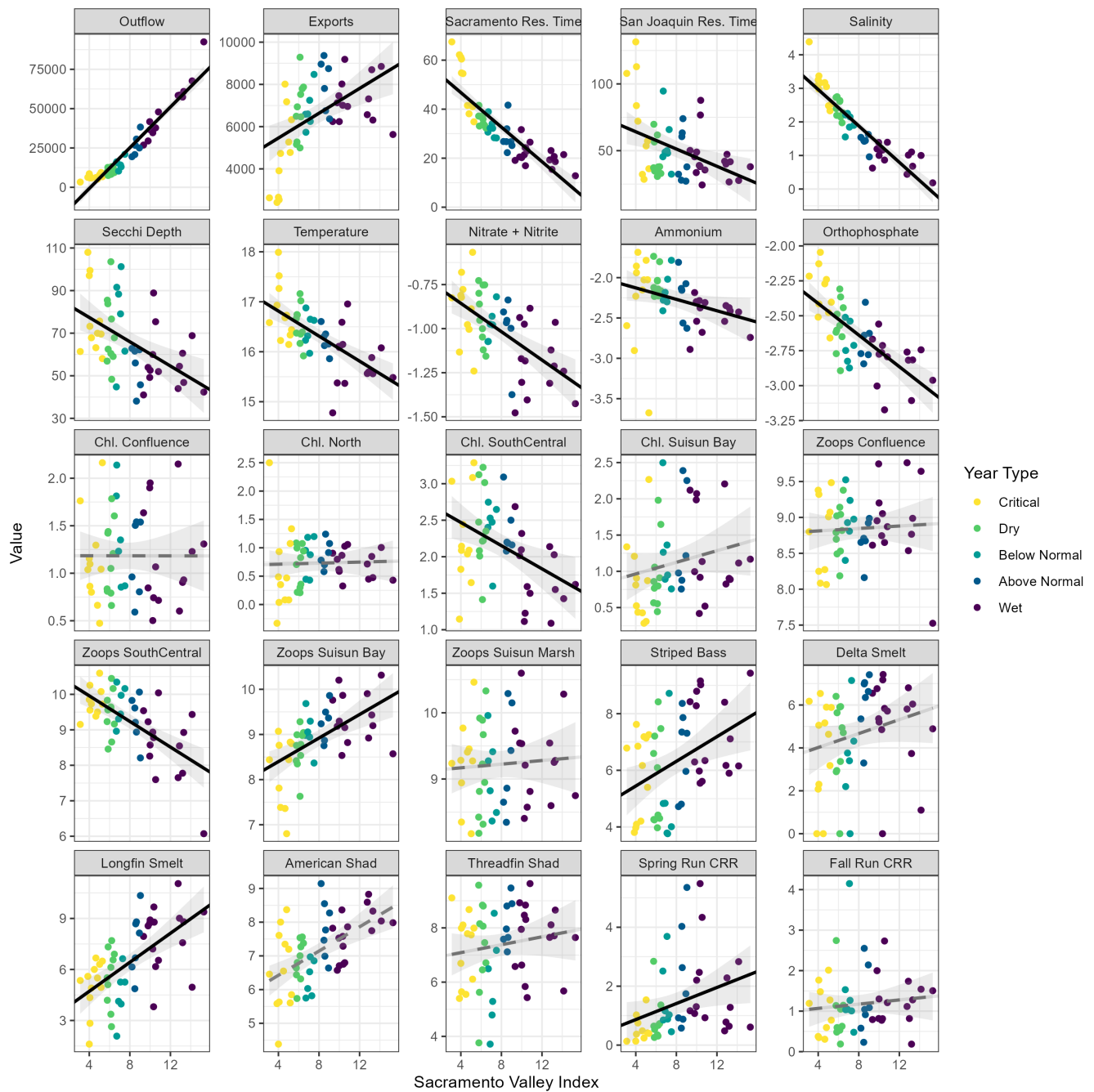
Figure 8   Linear regressions of various ecological parameters versus Sacramento Valley Index. Parameters are log-transformed where necessary to meet assumptions of normality. Significant relationships shown in *solid black*, non-significant in *dashed grey*. Units, transformations, and regression parameters are listed in Table 3.

Delta outflow was highly correlated with the Sacramento Valley Index, but the non-linear model had a better fit (Figure 9). In Critical years, the model shows that Delta outflow continues to be maintained at a minimum flow, despite the

decreased precipitation, most likely as a result of water management. Allowing Delta outflow to decrease linearly with inflows and precipitation increases the risk of salinity intrusion (Gartrell et al. 2022); therefore, water managers alter
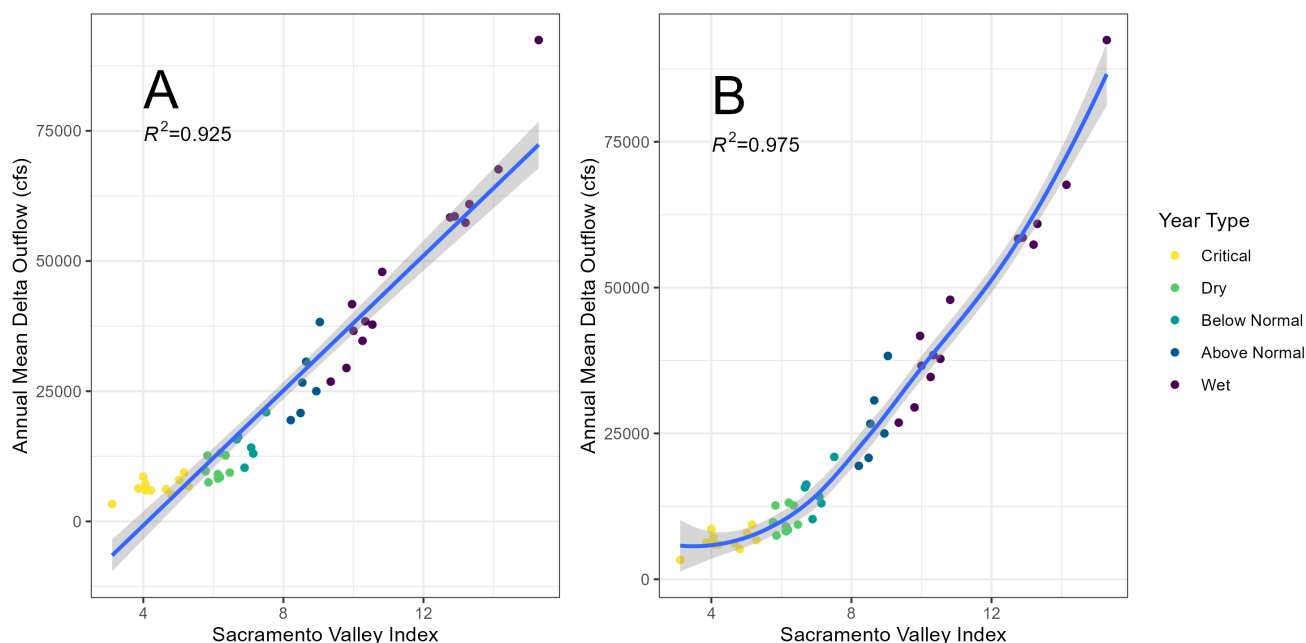
Figure 9 Annual mean net Delta outflow versus Sacramento Valley Index modeled with (**A**) a linear model and (**B**) a generalized additive model. Both models are statistically significant ($p < 0.0001$) with R^2 indicated on the graph.

reservoir release timing and export rates to maintain a minimum Delta outflow and to protect water quality (CDWR 2020; Durand et al. 2020; Ghalambor et al. 2021).

On an intra-annual basis there is a greater disconnect in this relationship. Multiple studies have described a "flattening" of the hydrograph over the course of the year, by managing lower peak flows in the spring and higher flows in the summer (Kondolf and Batalla 2005; Moyle and Mount 2007; Zimmerman et al. 2018). Water management can mitigate some drought effects (Kondolf and Batalla 2005), but it can also exacerbate some drought effects when human and environmental needs are in conflict and further reduce streamflow (Van Loon et al. 2022). Bosworth et al. (this issue) reported that peak Sacramento River inflows shifted during drought periods compared to wet periods. During wet years more inflow occurred earlier in the year as a management response to flood risk, while in drought periods a higher percentage of inflow occurred later in the season as a result of (1) peak demand occurring later in the season (Lund 2016), (2) the need to maintain cold water pools below

dams for fish survival (Anderson et al. 2022 and references therein; Hassrick et al. 2022), (3) the prioritization of reservoir recharge (Bosworth et al., this issue), and (4) the need to maintain salinity standards throughout the summer (Hutton et al. 2017).

The effect size of Drought on project exports was lower than the drought effect size for other flow parameters (Figure 6; Table 3), and the linear model of project exports versus the Sacramento Valley Index did not fit as well (Table 3; Figure 8). There was significantly less variation across water year types in project exports than in outflow. This is likely from the relatively narrow range between the minimum health and safety water-supply requirements that limit the minimum export rates and the maximum capacity of the export pumps (Gartrell et al. 2022).

Decreased Delta outflow and project exports during drought periods increased residence time and allowed salinity to move upstream, but the effect size for Drought is much more pronounced for particles released on the Sacramento River than the San Joaquin River

(Figures 5 and 6). Similarly, the linear relationship between Sacramento residence time and the Sacramento Valley Index results in a much higher R^2 than for the San Joaquin residence time model (R^2 = 0.71 versus 0.16; Figure 8). In our model, project exports were also a factor in Sacramento residence time, but water exports did not have a strong relationship with drought periods or the Sacramento Valley Index (Figure 8). CVP and SWP water exports, together with the timing of upstream reservoir releases for flood management, temperature, and salinity requirements, may contribute to the unexplained variance between the Sacramento Valley Index and Sacramento River residence time. Kimmerer and Nobriga (2008) used a particle-tracking model under many different flow scenarios and also found that residence time varies with location, and project exports had a major influence on residence time in the South Delta and along the San Joaquin river corridor. The correlation of CVP and SWP water exports and San Joaquin residence time may be the combined effects of the geographic locations of the CVP and SWP, the lower inflows of the San Joaquin, and the unimpaired flow requirements for fish passage (SWRCB 2018). The San Joaquin flows are lower than the Sacramento's, with a higher proportion of diversions along the length of the river (USEPA 2022), and a higher ratio of storage capacity to flow (Kondolf and Batalla 2005), all contributing to the different responses of residence time to drought periods between the two rivers.

Water Quality

Droughts are characterized by warmer temperatures, increased water clarity, and increased salinity (Figure 5), as also described by Bosworth et al. (this issue). These were some of the strongest effects of drought periods (Figure 6) and the relationship between Sacramento Valley Index and salinity was one of the strongest relationships (Figure 8, R^2 of 0.82). These relationships between flow and water quality have been described in many other studies in this estuary (Stern et al. 2020; Bashevkin and Mahardja 2022; Ghalambor et al. 2021) and in other systems (Baptista et al. 2010; Wetz et al. 2011; Bruesewitz et al. 2013), but in this analysis

we show that the trends are consistent over both single Dry years and multi-year droughts. There have been recent trends toward increased temperatures in the upper estuary (Bashevkin, Mahardja, et al. 2022), a long-term increase in Secchi depth (Hestir et al. 2016; Bosworth et al., this issue), and sea level rise that may increase salinity intrusion (Ghalambor et al. 2021), so some of the observed trends toward changes with drought may be the result of more frequent droughts in recent years.

Concentrations of both orthophosphate and nitrate + nitrite increased during drought periods estuary-wide (Figure 5), most likely because of decreased dilution from inflow. Nutrient loading to the upper estuary comes from agricultural runoff, wastewater treatment plants, and—potentially—groundwater, and is variable across regions, years, and seasons (Domagalski and Saleh 2015; Saleh and Domagalski 2015; 2021). Loading of nutrients may be higher during Wet years when the influx of water from snowmelt and storm runoff is higher, increasing transport of terrestrial nitrogen to the aquatic system (Saleh and Domagalski 2015). However, despite increased loading, the additional water flows will dilute nutrient concentrations. Trends in nutrient loading differ somewhat between nitrogen and phosphorus, with a greater percentage of phosphorus coming from geologic sources, whereas a greater percentage of N comes from agriculture and atmospheric deposition (Saleh and Domagalski 2021). Bosworth et al. (this issue) found similar trends, though there were also regional differences, with higher concentrations of all nutrients in the South Delta, and a significant effect on ammonium in the North Delta during drought periods that was not apparent in the estuary-wide analysis presented here.

Point sources from wastewater treatment plants in Sacramento and Stockton are more predictable and consistent sources of nutrient inputs to the estuary (Saleh and Domagalski 2015) and will be concentrated during drier years (Saleh and Domagalski 2021; Bosworth et al., this issue). Stockton and Sacramento WWTPs have upgraded

their facilities (2006 and 2021, respectively) to reduce point source nutrient (ammonium) loading into the Sacramento and San Joaquin rivers, with future reduction of nitrate + nitrite in both facilities in the next few years (Robertson–Bryan and Ascent Environmental 2019; Rinde et al. 2020; Senn et al. 2020), so previous patterns of high nutrients during droughts may shift. The trend toward higher nutrients contrasts with other systems where droughts often bring lower nutrients because of reduced runoff, as seen in coastal North Carolina (Wetz et al. 2011) and Copano Bay, Texas (Bruesewitz et al. 2013). The high density of irrigated agriculture in the watershed of the San Francisco Estuary in comparison to other estuaries (Siebert et al. 2015)—much of which continues to be irrigated with groundwater even during droughts (Langridge and Daniels 2017)—may explain this contrast.

To date there has been little research on the importance of groundwater to nutrient budgets in the estuary (but see Richardson et al. 2022). While groundwater has previously been dismissed as likely to provide a small source of organic material in the system (Jassby and Cloern 2000), other estuaries in California found groundwater to provide larger contributions of nutrients during the summer than surface water (Oberdorfer et al. 1990). Future studies should see whether groundwater contributions to nutrients in the estuary are more important than previously thought, especially since groundwater is used more frequently for irrigation during droughts (Langridge and Daniels 2017).

Chlorophyll and Zooplankton

Water-quality responses were predictable based on changes in flow, but responses further up the food web were more complex and often varied by region. Both chlorophyll and zooplankton increased in density in the South-Central Delta, while decreasing in Suisun Bay (Figure 7). The regional differences are most likely caused by the relative importance of residence time allowing biomass to increase and top-down control causing biomass to decrease (similar to responses explored by Lucas and Thompson 2012).

This paper looked at the long-term dataset; therefore, we only examined trends in chlorophyll-*a*. However, community composition of the phytoplankton that contributes to chlorophyll can have a major effect on the ecosystem. One such effect is the increasing frequency of cyanobacterial harmful algal blooms (cyanoHABs) in recent years (Lehman et al. 2013; Kudela et al. 2023). In particular, the toxigenic cyanobacteria *Microcysti*s is more common in drier years (Lehman et al. 2017; Lehman et al. 2022; Bouma–Gregson et al., this issue). Nutrients support phytoplankton growth, so when nutrients increase during drought periods, cyanoHAB formation can accelerate, outcompeting other phytoplankton species (diatoms) and causing extreme water-quality conditions, such as high pH and low dissolved oxygen (DO) (Bouma–Gregson et al., this issue). Increased cyanoHAB occurrence is a growing concern world-wide (Huisman et al. 2018; Plaas and Paerl 2021), and decreased flow, increased temperatures, and increased nutrients have been identified as drivers in many other systems as well (Wilhelm et al. 2020).

The South-Central Delta typically has some of the highest water temperatures (Mahardja et al. 2022), the highest water clarity and nutrients (Bosworth et al., this issue), and is along the San Joaquin corridor, where residence time is higher (Figure 4). Together these conditions provide ideal parameters for phytoplankton blooms. High phytoplankton uptake rates can reduce available dissolved nutrient levels in the water, but rarely to a point of nutrient limitation, except in extreme cases of large phytoplankton bloom formations (Bouma–Gregson et al., this issue). Similar blooms of phytoplankton during drought periods have been recorded previously in the estuary (Glibert et al. 2014), as well as low-inflow estuaries on the coast of Brazil (Barroso et al. 2018) and Texas (Bruesewitz et al. 2013), but the opposite effect has also been seen in other estuaries, with reduced phytoplankton productivity from reduced nutrient runoff (Wetz et al. 2011).

Decreases to chlorophyll in the Suisun Bay region are most likely tied to increased abundance and grazing by the invasive clam, *Potamocorbula*

amurensis. This invader, introduced in 1986, has been linked to the dramatic decline in both chlorophyll and zooplankton in Suisun Bay in the past (Greene et al. 2011; Kimmerer and Thompson 2014). *P. amurensis* also increases in density and spreads further upstream into the confluence during drier years (Hartman et al., Twardochleb this issue), further affecting phytoplankton and zooplankton biomass (Crauder et al. 2016). A similar response was seen even before the invasion of *P. amurensis,* when shifts in the distribution of the clam *Mya arenaria* may have reduced phytoplankton during the 1976–1977 drought (Nichols 1985). Because *P. amurensis* has such a large dampening effect on *in situ* production in Suisun Bay, much of the primary productivity and zooplankton biomass is thought to come from transport of upstream resources into the area (Kimmerer, Gross, et al. 2018) and lower flows reduce connectivity between the Delta and Suisun Bay, decreasing this subsidy (Hassrick et al. 2023).

During wetter years, the freshwater clam *Corbicula fluminea* dominates in the confluence, but has a much lower grazing rate, so it affects the phytoplankton population less (Crauder et al. 2016; Kimmerer et al. 2019; Hartman et al., this issue). In freshwater areas, *C. fluminea* is dominant, allowing chlorophyll and zooplankton to increase with increased residence time (Hartman et al., this issue). Although Suisun Marsh's salinity may be appropriate for *P. amurensis,* the clams are chiefly found in larger sloughs (Baumsteiger et al. 2017), allowing smaller dead-end sloughs with high residence times to reduce the effect of clams on the marsh ecosystem.

Shifts in salinity over the Suisun Bay will also shift the distribution of many zooplankters according to their realized salinity niche, reducing the abundance of many freshwater zooplankters in Suisun Bay, Suisun Marsh, and the confluence (Barros et al., this issue). Barros et al. (this issue) also showed that the brackish-water cyclopoid copepod *Limnoithona tetraspina* increased in abundance during droughts. However, these are much smaller than the

freshwater calanoid copepods and cladocerans, so the increased abundance has a relatively small effect on total zooplankton biomass.

Increased zooplankton abundance in the South-Central Delta region is most likely caused by the increased phytoplankton and increased residence time (Barros et al., this issue). Zooplankton responses to changes in flow are also very taxa specific, which can be masked by examining total biomass. For instance, the more brackish water species (e.g., *L. tetraspina*) move further upstream in times of low flow, which can increase total zooplankton biomass in areas such as the South-Central Delta region. In western regions, such as Suisun Bay and Suisun Marsh, low flow conditions will also decrease the biomass of less salinity-tolerant species (e.g. *Daphnia* spp. and *Pseudodiaptomus forbesi*), reducing total zooplankton biomass overall in these areas (Hassrick et al. 2023; Lee et al. 2023; Barros et al., this issue).

Fish

We examined a small number of fish for potential drought responses, but our findings suggest that there are diverse responses to drought that may align with life-history strategies (as suggested by Mims and Olden [2012]). All the pelagic fishes— age-0 Striped Bass, American Shad, Delta Smelt, Longfin Smelt, and Threadfin Shad—showed a trend toward decreased abundance during drought periods when compared to wet periods (Figure 5; Table 3), but this was only significant for Longfin Smelt and Striped Bass. Similarly, all fishes showed a trend toward decreases in abundance at lower Sacramento Valley Index values, but this was only significant for American Shad, Longfin Smelt, and Striped Bass (Figure 6; Table 3). Delta Smelt and Threadfin Shad and, which did not show significant responses, are both short-lived freshwater or semi-anadromous fishes, whereas American Shad, Longfin Smelt, and Striped Bass, are all longer-lived, fully anadromous fishes (Moyle 2002). The longer migration of fully anadromous fishes may make them more susceptible to drought since connectivity between freshwater and marine habitats is reduced, and transport time within

the Delta is increased (Michel et al. 2015; Singer et al. 2020). Researchers in other systems have also found that different life-history strategies may favor some species over others during droughts. For example, Malone et al. (2022) found that opportunistic species thrived during droughts in streams in the eastern US, while longer-lived species did better during higher-flow years. Similarly, Mims and Olden (2012) found that across the US, high flow variability (such as frequent droughts and floods) generally favors short-lived, opportunistic species. This aligns with our finding that the short-lived Threadfin Shad is not affected by drought periods, and the previous finding that the opportunistic Mississippi Silverside does well during droughts (Mahardja et al. 2016).

For those fish that *did* experience significant declines, decreased abundance may have been caused by the combination of flow, water quality, and lower trophic effects of the drought period described above. Higher water temperatures may narrow spawning windows (Brown et al. 2016), increase predation (Nobriga et al. 2021), and approach physiological limits for some species (Jeffries et al. 2016). Increased water clarity may increase susceptibility of pelagic fish to predation (Hasenbein et al. 2013; Ferrari et al. 2014). Higher salinity can limit some fishes' access to the rearing-habitat benefits of Suisun Marsh (e.g., Delta Smelt, Chinook Salmon, and Striped Bass; Colombano et al. 2020; Sommer et al. 2020), while increasing access for other species (e.g. Northern Anchovy; Cloern et al. 2017). Native pelagic fishes may not be able to take advantage of the increased zooplankton in the South-Central Delta because of higher water clarity (Hestir et al. 2016), higher summer temperatures (Bashevkin, Mahardja, et al. 2022), increased risk of entrainment (Kimmerer and Nobriga 2008; Perry et al. 2015), and increased risk of predation (Michel et al. 2020). Mahardja et al. (2021) found a similar trend, with decreases in abundance of these pelagic fishes during droughts, but recovery during successive wet years. The steep population declines seen in pelagic fishes over the last 20 to 30 years (Thomson et al. 2010; Tempel et al. 2021) may relate to droughts dominating the

past 20 years have been dominated by droughts (Figure 1), making it difficult to differentiate the effect of drought from that of long-term decline.

While salmon CRRs did not show a significant effect from drought periods during the out-migration year, there was a trend toward higher CRR during wet periods, and there was a significant trend to higher spring-run (but not fall-run) CRR with a higher Sacramento Valley Index. It was surprising that the relationship was not stronger since multiple studies have suggested lower juvenile survival during lower outflow periods because of increased migration time and increased temperatures (Hance et al. 2022). Similar results have been seen in other systems where droughts greatly decrease salmonid migration windows, survival probabilities, and habitat availability (Deitch et al. 2018; Kastl et al. 2022). The difference between responses in spring-run Chinook Salmon versus fall-run Chinook Salmon may be caused by hatchery practices designed to buffer the population from droughts by increasing production and transport of juveniles directly to the estuary or ocean, bypassing areas of high mortality (Sturrock et al. 2019).

CONCLUSIONS

The IEP Drought Synthesis Team evaluated over 40 years of data and found several important correlations between droughts and ecological metrics. Reduced freshwater flow through the upper estuary was associated with cascading changes throughout the ecosystem, which may have been caused by increasing residence time and decreasing transport. Water clarity increased, differences between regions of the estuary increased, and these changes are also associated with warmer temperatures. The resulting relatively warm, clear, slow-moving waters were correlated with changes to phytoplankton, zooplankton, and fish abundances and distributions. With an increasing frequency of droughts as predicted under climate-change scenarios (Swain et al. 2018; Persad et al. 2020), and as already seen in recent years (Swain et al. 2014), this low-outflow, warmer, clearer estuary invaded by non-native species with low

pelagic fish production is rapidly becoming the new "normal." While this may seem bleak, understanding the effects of drought is the first step in developing management and mitigation methods to mitigate drought's detrimental effects on the environment.

ACKNOWLEDGEMENTS

REFERENCES

Anderson JJ, Beer WN, Israel JA, Greene S. 2022. Targeting river operations to the critical thermal window of fish incubation: model and case study on Sacramento River winter-run Chinook salmon. River Res Appl. [accessed 2023 Sep 1];38(5):895–905. *https://doi.org/10.1002/rra.3965*

Andrew JT, Sauquet E. 2017. Climate change impacts and water management adaptation in two Mediterranean-climate watersheds: learning from the Durance and Sacramento rivers. Water. [accessed 2023 Jan 4];9(2):126. *https://doi.org/10.3390/w9020126*

Andrews SW, Gross ES, Hutton PH. 2017. Modeling salt intrusion in the San Francisco Estuary prior to anthropogenic influence. Cont Shelf Res. [accessed 2023 Jan 4];146:58–81. *https://doi.org/10.1016/j.csr.2017.07.010*

Azat J. 2021. GrandTab ver. 2023.06.26. California Central Valley Chinook Population Database Report. California Department of Fish and Wildlife. [accessed 2023 Jan 4]. Available from: *https://nrm.dfg.ca.gov/FileHandler.ashx?DocumentID=84381*

Baptista J, Martinho F, Dolbeth M, Viegas I, Cabral H, Pardal M. 2010. Effects of freshwater flow on the fish assemblage of the Mondego estuary (Portugal): comparison between drought and non-drought years. Mar Freshw Res. [accessed 2023 Sep 1];61(4):490–501. *https://doi.org/10.1071/MF09174*

Barros A, Hartman R, Bashevkin S, Burdi C. 2024. Years of drought and salt; decreasing flows determine the distribution of zooplankton resources in the estuary. San Franc Estuary Watershed Sci. *https://doi.org/10.15447/sfews.2024v22iss1art3*

Barroso HdS, Tavares TCL, Soares MdO, Garcia TM, Rozendo B, Vieira ASC, Viana PB, Pontes TM, Ferreira TJT, Pereira Filho J, et al. 2018. Intra-annual variability of phytoplankton biomass and nutrients in a tropical estuary during a severe drought. Estuar Coast Shelf Sci. [accessed 2023 Jan 4];213:283–293. *https://doi.org/10.1016/j.ecss.2018.08.023*

Bashevkin SM. 2021. deltamapr: spatial data for the Bay–Delta. GitHub. [accessed 2023 Feb 6]. Interagency Ecological Program. Available from: *https://github.com/InteragencyEcologicalProgram/deltamapr*

Bashevkin SM, Hartman R, Thomas M, Barros A, Burdi CE, Hennessy A, Tempel T, Kayfetz K. 2022. Five decades (1972–2020) of zooplankton monitoring in the upper San Francisco Estuary. PLoS ONE. [accessed 2022 May 17];17(3):e0265402. *https://doi.org/10.1371/journal.pone.0265402*

Bashevkin SM, Mahardja B. 2022. Seasonally variable relationships between surface water temperature and inflow in the upper San Francisco Estuary. Limnol Oceanogr. [accessed 2023 Jan 4];67:684–702. *https://doi.org/10.1002/lno.12027*

Bashevkin SM, Mahardja B, Brown LR. 2022. Warming in the upper San Francisco Estuary: patterns of water temperature change from five decades of data. Limnol Oceanogr. [accessed 2023 Jan 3];67(5):1065–1080. *https://doi.org/10.1002/lno.12057*

Bashevkin SM, Perry SE, Stumpner EB, Hartman R. 2023. Six decades (1959–2022) of water quality in the upper San Francisco Estuary: an integrated database of 16 discrete monitoring surveys in the Sacramento San Joaquin Delta, Suisun Bay, Suisun Marsh, and San Francisco Bay ver 7. Environmental Data Initiative. [accessed 2023 Sep 7] *https://doi.org/10.6073/pasta/8dbd29c8c22f3295 bbc5d3819fb51d00*

Baumsteiger J, Schroeter RE, O'Rear TA, Cook JD, Moyle PB. 2017. Long-term surveys show invasive overbite clams (*Potamocorbula amurensis*) are spatially limited in Suisun Marsh, California. San Franc Estuary Watershed Sci. [accessed 2023 Jan 4];15(2). *https://doi.org/10.15447/sfews.2017v15iss2art6*

Ben–Shachar MS, Makowski D, Lüdecke D, Patil I, Wiernik BM, Thériault R. 2023. Package effectsize: indices of effect size. CRAN: The Comprehensive R Archive Network (CRAN). [accessed 2023 Sep 1]. Available from: *https://easystats.github.io/effectsize/*

Bever AJ, MacWilliams ML, Herbold B, Brown LR, Feyrer FV. 2016. Linking hydrodynamic complexity to Delta Smelt (*Hypomesus transpacificus*) distribution in the San Francisco Estuary, USA. San Franc Estuary Watershed Sci. [accessed 2023 Jan 4];14(1). *https://doi.org/10.15447/sfews.2016v14iss1art3*

Bosworth DH, Bashevkin SM, Bouma–Gregson K, Hartman R, Stumpner EB. 2024. The anatomy of a drought in the upper San Francisco estuary: water quality and lower-trophic responses to multi-year droughts over a long-term record (1975–2021). San Franc Estuary and Watershed Sci. *https://doi.org/10.15447/sfews.2024v22iss1art1*

Bouma–Gregson K, Bosworth D, Flynn TM, Maguire A, Rinde J, Hartman R. 2024. Delta blue(green)s: the effect of drought and drought management actions on *Microcystis* in the Sacramento–San Joaquin Delta. San Franc Estuary Watershed Sci. *https://doi.org/10.15447/sfews.2024v22iss1art2*

Brown LR, Komoroske LM, Wagner RW, Morgan–King T, May JT, Connon RE, Fangue NA. 2016. Coupled downscaled climate models and ecophysiological metrics forecast habitat compression for an endangered estuarine fish. PLoS ONE. [accessed 2023 Jan 12];11(1):e0146724. *https://doi.org/10.1371%2Fjournal.pone.0146724*

Bruesewitz DA, Gardner WS, Mooney RF, Pollard L, Buskey EJ. 2013. Estuarine ecosystem function response to flood and drought in a shallow, semiarid estuary: nitrogen cycling and ecosystem metabolism. Limnol Oceanogr. [accessed 2023 Jan 4];58(6):2293–2309. *https://doi.org/10.4319/lo.2013.58.6.2293*

Burdi CE, Slater SB, Bippus TL, Jimenez JA. 2021. Mysid and amphipod length–weight relationships in the San Francisco Estuary. IEP Newsletter. [accessed 2024 Mar 11];40(1):15-25. Available from: *https://cadwr.app.box.com/v/ InteragencyEcologicalProgram/file/860495889310*

[CDWR] California Department of Water Resources. 2002. Dayflow: an estimate of daily average Delta Outflow. Dayflow documentation 1997 through present. California Natural Resources Agency Open Data. [accessed 2023 Jan 4]. Available from: *https://data.cnra.ca.gov/dataset/dayflow/ resource/776b90ca-673e-4b56-8cf3-ec26792708c3*

[CDWR] California Department of Water Resources. 2020. California's most significant droughts: comparing historical and recent conditions. Sacramento (CA): CDWR. [accessed 2023 Feb 6]. Available from: *https://cawaterlibrary.net/wp-content/ uploads/2017/05/CalSignficantDroughts_v10_int.pdf*

[CDWR-CCSS] California Department of Water Resources, California Cooperative Snow Surveys: Chronological reconstructed Sacramento and San Joaquin Valley Water Year Hydrologic Classification indices. 2022. Sacramento (CA): California Data Exchange Center. [accessed 2023 Jan 10]. Available from: *https://cdec.water.ca.gov/ reportapp/javareports?name=WSIHIST*

Carlson SM, Matern SA. 2000. Mysid shrimp in Suisun Marsh. IEP Newsletter. 13(4):16–20.

Cloern JE, Jassby AD, Schraga TS, Nejad E, Martin C. 2017. Ecosystem variability along the estuarine salinity gradient: examples from long-term study of San Francisco Bay. Limnol Oceanogr. [accessed 2023 Sep 1];62(S1):S272–S291. *https://doi.org/10.1002/lno.10537*

Colombano DD, Manfree AD, O'Rear TA, Durand JR, Moyle PB. 2020. Estuarine–terrestrial habitat gradients enhance nursery function for resident and transient fishes in the San Francisco Estuary. Mar Ecol Prog Ser. [accessed 2023 Sep 1];637:141–157. *https://doi.org/10.3354/meps13238*

Crauder JS, Thompson JK, Parchaso F, Anduaga RI, Pearson SA, Gehrts K, Fuller H, Wells E. 2016. Bivalve effects on the food web supporting Delta Smelt—a long-term study of bivalve recruitment, biomass, and grazing rate patterns with varying freshwater outflow. Open-File Report 2016–1005 . Reston (VA): US Geological Survey. [accessed 2023 Jan 4]. *https://doi.org/10.3133/ofr20161005*

Deitch MJ, Van Docto M, Obedzinski M, Nossaman SP, Bartshire A. 2018. Impact of multi-annual drought on streamflow and habitat in coastal California salmonid streams. Hydrol Sci J. [accessed 2023 Jan 4];63(8):1219–1235. *https://doi.org/10.1080/02626667.2018.1492722*

Dettinger M. 2011. Climate change, atmospheric rivers, and floods in California–a multimodel analysis of storm frequency and magnitude changes. J Am Water Resour Assoc. [accessed 2022 Jan 9];47(3):514–523. *https://doi.org/10.1111/j.1752-1688.2011.00546.x*

Domagalski J, Saleh D. 2015. Sources and transport of phosphorus to rivers in California and adjacent states, U.S., as determined by SPARROW modeling. J Am Water Resour Assoc. [accessed 2023 Jun 20];51(6):1463–1486. *https://doi.org/10.1111/1752-1688.12326*

Durand JR, Bombardelli F, Fleenor WE, Henneberry Y, Herman J, Jeffres C, Leinfelder–Miles M, Lund JR, Lusardi R, Manfree AD, et al. 2020. Drought and the Sacramento–San Joaquin Delta, 2012–2016: environmental review and lessons. San Franc Estuary Watershed Sci. [accessed 2023 Jan 4];18(2). *https://doi.org/10.15447/sfews.2020v18iss2art2*

Ferrari MCO, Ranåker L, Weinersmith KL, Young MJ, Sih A, Conrad JL. 2014. Effects of turbidity and an invasive waterweed on predation by introduced largemouth bass. Environ Biol Fish. [accessed 2023 Jan 12];97:79–90. *https://doi.org/10.1007/s10641-013-0125-7*

Feyrer F, Hobbs J, Sommer T. 2010. Salinity inhabited by age-0 splittail (*Pogonichthys macrolepidotus*) as determined by direct field observation and retrospective analyses with otolith chemistry. San Franc Estuary Watershed Sci. [accessed 2023 Jun 22];8(2). *https://doi.org/10.15447/sfews.2010v8iss2art2*

Feyrer F, Nobriga ML, Sommer TR. 2007. Multidecadal trends for three declining fish species: habitat patterns and mechanisms in the San Francisco Estuary, California, USA. Can J Fish Aquat Sci. [accessed 2023 Jan 3];64:723–734. *https://doi.org/10.1139/f07-048*

Gartrell G, Mount J, Hanak E. 2022. Tracking where water goes in a changing Sacramento–San Joaquin Delta. [accessed 2022 Dec 10]. San Francisco (CA): Public Policy Institute of California. Policy Brief—May 2022. Available from: *https://www.ppic.org/wp-content/uploads/policy-brief-tracking-where-water-goes-in-a-changing-sacramento-san-joaquin-delta.pdf*

Gearty AJ, Ignoffo TR, Slaughter AM, Kimmerer WJ. 2021. Growth and reproductive rates of the dominant copepod *Pseudodiaptomus forbesi* in response to environmental factors and habitat type in the northern San Francisco Estuary. Aquat Ecol. [accessed 2021 Sep 8];55:825–848. *https://doi.org/10.1007/s10452-021-09863-4*

Ghalambor CK, Gross ES, Grosholtz ED, Jeffries KM, Largier JK, McCormick SD, Sommer T, Velotta J, Whitehead A. 2021. Ecological effects of climate-driven salinity variation in the San Francisco Estuary: can we anticipate and manage the coming changes? San Franc Estuary Watershed Sci. [accessed 2023 Jan 4];19(2). *http://doi.org/10.15447/sfews.2021v19iss2art3*

Glibert PM, Dugdale R, Wilkerson FP, Parker AE, Alexander J, Antell E, Blaser S, Johnson A, Lee J, Lee T, et al. 2014. Major–but rare–spring blooms in 2014 in San Francisco Bay Delta, California, a result of the long-term drought, increased residence time, and altered nutrient loads and forms. J Exp Mar Biol Ecol. [accessed 2023 Jan 4];460:8–18. https://doi.org/10.1016/j.jembe.2014.06.001

Greene VE, Sullivan LJ, Thompson JK, Kimmerer WJ. 2011. Grazing impact of the invasive clam *Corbula amurensis* on the microplankton assemblage of the northern San Francisco Estuary. Mar Ecol Prog Ser. [accessed 2023 Jan 4];431:183–193. https://doi.org/10.3354/meps09099

Hammock BG, Lesmeister S, Flores I, Bradburd G, Hammock F, Teh S. 2015. Low food availability narrows the tolerance of the copepod *Eurytemora affinis* to salinity, but not to temperature. Estuaries Coast. [accessed 2023 Sep 1];39(1):189–200. https://doi.org/10.1007/s12237-015-9988-5

Hammock BG, Moose SP, Solis SS, Goharian E, Teh SJ. 2019. Hydrodynamic modeling coupled with long-term field data provide evidence for suppression of phytoplankton by invasive clams and freshwater exports in the San Francisco Estuary. Environ Manag. [accessed 2023 Jan 4];63:703–717. https://doi.org/10.1007/s00267-019-01159-6

Hanak E, Lund J, Fleenor W, Mount J, Moyle P, Bennett W, Gray B, Durand J, 2012. Where the wild things aren't: making the Delta a better place for native species. San Francisco (CA): Public Policy Institute of California. [accessed 2021 Sep 27]. Available from: https://www.ppic.org/publication/where-the-wild-things-arent-making-the-delta-a-better-place-for-native-species/

Hance DJ, Perry RW, Pope AC, Ammann AJ, Hassrick JL, Hansen G. 2022. From drought to deluge: spatiotemporal variation in migration routing, survival, travel time and floodplain use of an endangered migratory fish. Can J Fish Aquat Sci. 79(3):410–428. [accessed 2023 Jan 3] https://doi.org/10.1139/cjfas-2021-0042

Hartman R, Twardochleb L, Burdi C, Wells E. 2024. Amazing graze: shifts in distribution of *Maeotias* and *Potamocorbula* during droughts. San Franc Estuary Watershed Sci. https://doi.org/10.15447/sfews.2024v22iss1art4

Hasenbein M, Komoroske LM, Connon R, Geist J, Fangue NA. 2013. Turbidity and salinity affect feeding performance and physiological stress in the endangered Delta Smelt. Integr Comp Biol. [accessed 2023 Jan 12];53(4):620–634. https://doi.org/10.1093/icb/ict082

Hassrick JL, Ammann AJ, Perry RW, John SN, Daniels ME. 2022. Factors affecting spatiotemporal variation in survival of endangered winter-fun Chinook Salmon out-migrating from the Sacramento River. N Am J Fish Manag. 42(2):375–395. [accessed 2023 Jan 4] https://doi.org/10.1002/nafm.10748

Hassrick JL, Korman J, Kimmerer WJ, Gross ES, Grimaldo LF, Lee C, Schultz AA. 2023. Freshwater flow affects subsidies of a copepod (*Pseudodiaptomus forbesi*) to low-salinity food webs in the upper San Francisco Estuary. Estuaries Coast. [accessed 2023 Sep 1];46:450–462. https://doi.org/10.1007/s12237-022-01142-1

Hestir EL, Schoellhamer DH, Greenberg J, Morgan–King T, Ustin SL. 2016. The effect of submerged aquatic vegetation expansion on a declining turbidity trend in the Sacramento–San Joaquin River Delta. Estuaries Coast. [accessed 2023 Jan 4];39(4):1100–1112. https://doi.org/10.1007/s12237-015-0055-z

Huisman J, Codd GA, Paerl HW, Ibelings BW, Verspagen JMH, Visser PM. 2018. Cyanobacterial blooms. Nat Rev Microbiol. [accessed 2023 Jan 4];16(8):471–483. https://doi.org/10.1038/s41579-018-0040-1

Hutton PH, Chen L, Rath JS, Roy SB. 2019. Tidally-averaged flows in the interior Sacramento–San Joaquin River Delta: trends and change attribution. Hydrol Process. [accessed 2023 Jan 3];33(2):230–243. https://doi.org/10.1002/hyp.13320

Hutton PH, Rath JS, Roy SB. 2017. Freshwater flow to the San Francisco Bay–Delta estuary over nine decades (part 2): change attribution. Hydrol Process. [accessed 2023 Jan 4];31(14):2516–2529. https://doi.org/10.1002/hyp.11195

Jabusch T, Phil Trowbridge, Wong A, Heberger M. 2018. Assessment of nutrient status and trends in the Delta in 2001–2016: effects of drought on ambient concentrations and trends. Richmond (CA): Aquatic Science Center. SFEI Contribution No. 865. 119 p. [accessed 2023 Jan 4]. Available from: *https://www.sfei.org/documents/delta-nutrient-status-2018*

Jassby A, Cloern J. 2000. Organic matter sources and rehabilitation of the Sacramento–San Joaquin Delta (California, USA). Aquat Conserv: Mar Freshw Ecosyst. [accessed 2023 Sep 1];10(5):323–352. *https://doi.org/10.1002/1099-0755(200009/10)10:5%3C323::AID-AQC417%3E3.0.CO;2-J*

Jassby AD, Kimmerer WJ, Monismith SG, Armor C, Cloern JE, Powell TM, Schubel JR, Vendlinski TJ. 1995. Isohaline position as a habitat indicator for estuarine populations. Ecol Appl. [accessed 2023 Feb 28];5(1):272–289. *https://doi.org/10.2307/1942069*

Jeffries KM, Connon RE, Davis BE, Komoroske LM, Britton MT, Sommer T, Todgham AE, Fangue NA. 2016. Effects of high temperatures on threatened estuarine fishes during periods of extreme drought. J Exp Biol. [accessed 2023 Jan 3];219(11):1705–1716. *https://doi.org/10.1242/jeb.134528*

Kastl B, Obedzinski M, Carlson SM, Boucher WT, Grantham TE. 2022. Migration in drought: receding streams contract the seaward migration window of endangered salmon. Ecosphere. [accessed 2023 Jan 4];13(12):e4295. *https://doi.org/10.1002/ecs2.4295*

Keeley ATH, Fremier AK, Goertler PAL, Huber PR, Sturrock AM, Bashevkin SM, Barbaree BA, Grenier JL, Dilts TE, Gogol–Prokurat M, et al. 2022. Governing ecological connectivity in cross-scale dependent systems. BioScience. [accessed 2022 Feb 3];72(4):372–386. *https://doi.org/10.1093/biosci/biab140*

Kimmerer W, Gross E. 2022. Population abundance and diversion losses in a threatened estuarine pelagic fish. Estuaries Coast. [accessed 2023 Jan 3];45:2728–2745. *https://doi.org/10.1007/s12237-022-01101-w*

Kimmerer W, Wilkerson F, Downing B, Dugdale R, Gross ES, Kayfetz K, Khanna S, Parker AE, Thompson JK. 2019. Effects of drought and the emergency drought barrier on the ecosystem of the California Delta. San Franc Estuary Watershed Sci. [accessed 2023 Jan 4];17(3). *https://doi.org/10.15447/sfews.2019v17iss3art2*

Kimmerer WJ, Gross ES, Slaughter AM, Durand JR. 2018. Spatial subsidies and mortality of an estuarine copepod revealed using a box model. Estuaries Coast. [accessed 2023 Jan 3];42:218–236. *https://doi.org/10.1007/s12237-018-0436-1*

Kimmerer WJ, Ignoffo TR, Kayfetz KR, Slaughter AM. 2018. Effects of freshwater flow and phytoplankton biomass on growth, reproduction, and spatial subsidies of the estuarine copepod *Pseudodiaptomus forbesi*. Hydrobiologia. [accessed 2021 Aug 07];807(1):113–130. *https://doi.org/10.1007/s10750-017-3385-y*

Kimmerer WJ, MacWilliams ML, Gross ES. 2013. Variation of fish habitat and extent of the low-salinity zone with freshwater flow in the San Francisco Estuary. San Franc Estuary Watershed Sci. [accessed 2023 Sep 1];11(4):16. Available from: *https://escholarship.org/uc/item/3pz7x1x8*

Kimmerer WJ, Nobriga ML. 2008. Investigating particle transport and fate in the Sacramento–San Joaquin Delta using particle tracking model. San Franc Estuary Watershed Sci. [accessed 2023 Sep 1];6(1). *https://doi.org/10.15447/sfews.2008v6iss1art4*

Kimmerer WJ, Thompson JK. 2014. Phytoplankton growth balanced by clam and zooplankton grazing and net transport into the low-salinity zone of the San Francisco Estuary. Estuaries Coast. [accessed 2023 Jan 4];37:1202–1218. *https://doi.org/10.1007/s12237-013-9753-6*

Kondolf MG, Batalla RJ. 2005. Hydrological effects of dams and water diversions on rivers of Mediterranean-climate regions: examples from California. Chapter 11 In: Garcia C, Batalla RJ, editors. Developments in earth surface processes. [unknown]: Elsevier. p. 197–211.

Kudela RM, Howard MD, Monismith S, Paerl HW. 2023. Status, trends, and drivers of harmful algal blooms along the freshwater-to-marine gradient in the San Francisco Bay–Delta System. San Franc Estuary Watershed Sci. [accessed 2024 Mar 11];20(4). https://doi.org/10.15447/sfews.2023v20iss4art6

Langridge R, Daniels B. 2017. Accounting for climate change and drought in implementing sustainable groundwater management. Water Resour Manag. [accessed 2023 Sep 22];31(11):3287–3298. https://doi.org/10.1007/s11269-017-1607-8

Lee CY, Smith AG, Hassrick JL, Kalmbach AJ, Sabal MC, Cox DM, Grimaldo L, Schultz A. 2023. Flow augmentations modify an estuarine prey field. San Franc Estuary Watershed Sci. [accessed 2024 Mar 11];21(2). http://doi.org/10.15447/sfews.2023v21iss2art1

Lehman P, Marr K, Boyer G, Acuna S, Teh S. 2013. Long-term trends and causal factors associated with *Microcystis* abundance and toxicity in San Francisco Estuary and implications for climate change impacts. Hydrobiologia. [accessed 2023 Jan 4];718:141–158. https://doi.org/10.1007/s10750-013-1612-8

Lehman PW, Boyer G, Satchwell M, Waller S. 2008. The influence of environmental conditions on the seasonal variation of *Microcystis* cell density and microcystins concentration in San Francisco Estuary. Hydrobiologia. [accessed 2023 Feb 23];600(1):187–204. https://doi.org/10.1007/s10750-007-9231-x

Lehman PW, Kurobe T, Lesmeister S, Baxa D, Tung A, Teh SJ. 2017. Impacts of the 2014 severe drought on the *Microcystis* bloom in San Francisco Estuary. Harmful Algae. [accessed 2023 Jan 4];63):94–108. https://doi.org/10.1016/j.hal.2017.01.011

Lehman PW, Kurobe T, Teh SJ. 2022. Impact of extreme wet and dry years on the persistence of *Microcystis* harmful algal blooms in San Francisco Estuary. Quat Int. [accessed 2023 Jan 4];621:16–25. https://doi.org/10.1016/j.quaint.2019.12.003

Livsey DN, Downing–Kunz MA, Schoellhamer DH, Manning A. 2021. Suspended-sediment flux in the San Francisco Estuary; part II: the impact of the 2013–2016 California drought and controls on sediment flux. Estuaries Coast. [accessed 2023 Jan 4];44(4):972–990. https://doi.org/10.1007/s12237-020-00840-y

Lucas LV, Thompson JK. 2012. Changing restoration rules: exotic bivalves interact with residence time and depth to control phytoplankton productivity. Ecosphere. [accessed 2023 Jun 20];3(12):1–26. https://doi.org/10.1890/ES12-00251.1

Lund J. 2016. California's agricultural and urban water supply reliability and the Sacramento–San Joaquin Delta. San Franc Estuary Watershed Sci. [accessed 2023 Sep 22];14(3). https://doi.org/10.15447/sfews.2016v14iss3art6

Mahardja B, Bashevkin SM, Pien C, Nelson M, Davis BE, Hartman R. 2022. Escape from the heat: thermal stratification in a well-mixed estuary and implications for fish species facing a changing climate. Hydrobiologia. [accessed 2023 Jan 4];849:2895–2918. https://doi.org/10.1007/s10750-022-04886-w

Mahardja B, Conrad JL, Lusher L, Schreier B. 2016. Abundance trends, distribution, and habitat associations of the invasive Mississippi Silverside (*Menidia audens*) in the Sacramento–San Joaquin Delta, California, USA. San Franc Estuary Watershed Sci. [accessed 2023 Jan 3];14(1). http://doi.org/10.15447/sfews.2016v14iss1art2

Mahardja B, Tobias V, Khanna S, Mitchell L, Lehman P, Sommer T, Brown L, Culberson S, Conrad JL. 2021. Resistance and resilience of pelagic and littoral fishes to drought in the San Francisco Estuary. Ecol Appl. [accessed 2023 Jan 3];31(2):e02243. https://doi.org/10.1002%2Feap.2243

Malone EW, Perkin JS, Keith Gibbs W, Padgett M, Kulp M, Moore SE. 2022. High and dry in days gone by: life-history theory predicts Appalachian mountain stream fish assemblage transformation during historical drought. Ecol Freshw Fish. [accessed 2021 Dec 20];31(1):29–44. https://doi.org/10.1111/eff.12606

Michel CJ, Ammann AJ, Lindley ST, Sandstrom PT, Chapman ED, Thomas MJ, Singer GP, Klimley AP, MacFarlane RB. 2015. Chinook Salmon outmigration survival in wet and dry years in California's Sacramento River. Can J Fish Aquat Sci. [accessed 2019 May 5];72(11):1749–1759. https://doi.org/10.1139/cjfas-2014-0528

Michel CJ, Henderson MJ, Loomis CM, Smith JM, Demetras NJ, Iglesias IS, Lehman BM, Huff DD. 2020. Fish predation on a landscape scale. Ecosphere. [accessed 2023 Jun 22];11(6):e03168. https://doi.org/10.1002/ecs2.3168

Mims MC, Olden JD. 2012. Life history theory predicts fish assemblage response to hydrologic regimes. Ecology. [accessed 2022 Sep 22];93(1):35–45. https://doi.org/10.1890/11-0370.1

Moyle PB. 2002. Inland fishes of California. Berkeley (CA): University of California Press. 517 p.

Moyle PB, Manfree AD, Fiedler PL. 2013. The future of Suisun Marsh as mitigation habitat. San Franc Estuary Watershed Sci. [accessed 2023 Jan 4];11(3). https://doi.org/10.15447/sfews.2013v11iss3art10

Moyle PB, Manfree AD, Fiedler PL. 2014. Suisun Marsh: ecological history and possible futures. Berkeley (CA): University of California Press. 256 p.

Moyle PB, Mount JF. 2007. Homogenous rivers, homogenous faunas. [accessed 2023 Jan 3];104(14):5711–5712. https://doi.org/10.1073/pnas.0701457104

Nichols FH. 1985. Increased benthic grazing: an alternative explanation for low phytoplankton biomass in northern San Francisco Bay during the 1976–1977 drought. Estuar Coast Shelf Sci. [accessed 2023 Sep 20];21(3):379–388. https://doi.org/10.1016/0272-7714(85)90018-6

Nobriga ML, Michel CJ, Johnson RC, Wikert JD. 2021. Coldwater fish in a warm water world: implications for predation of salmon smolts during estuary transit. Ecol Evol. [accessed 2023 Jan 3];11(15):10381–10395. https://doi.org/10.1002/ece3.7840

Nobriga ML, Rosenfield JA. 2016. Population dynamics of an estuarine forage fish: disaggregating forces driving long-term decline of Longfin Smelt in California's San Francisco Estuary. Trans Am Fish Soc. [accessed 2023 Jan 3];145(1):44–58. https://doi.org/10.1080/00028487.2015.1100136

Oberdorfer JA, Valentino MA, Smith SV. 1990. Groundwater contribution to the nutrient budget of Tomales Bay, California. Biogeochemistry. [accessed 2023 Mar 16];10(3):199–216. https://doi.org/10.1007/BF00003144

Paerl HW, Huisman J. 2008. Blooms like it hot. Science. [accessed 2023 Feb 23];320(5872):57–58. https://doi.org/10.1126/science.1155398

Perry RW, Brandes PL, Burau JR, Sandstrom PT, Skalski JR. 2015. Effect of tides, river flow, and gate operations on entrainment of juvenile salmon into the interior Sacramento–San Joaquin River Delta. Trans Am Fish Soc. [accessed 2023 May 1];144(3):445–455. https://doi.org/10.1080/00028487.2014.1001038

Persad GG, Swain DL, Kouba C, Ortiz–Partida JP. 2020. Inter-model agreement on projected shifts in California hydroclimate characteristics critical to water management. Climatic Change. [accessed 2023 Sep 22];162(3):1493–1513. https://doi.org/10.1007/s10584-020-02882-4

Plaas HE, Paerl HW. 2021. Toxic cyanobacteria: a growing threat to water and air quality. Environ Sci Tech. [accessed 2023 Jan 4];55(1):44–64. https://doi.org/10.1021/acs.est.0c06653

R Core Team. 2022. R: a language and environment for statistical computing. 4.2.2 edition. Vienna (Austria). [accessed 2023 Feb 13]. Available from: https://www.R-project.org/

Richardson CM, Fackrell JK, Kraus TE, Young M, Paytan A. 2022. Nutrient and trace element contributions from drained islands in the Sacramento–San Joaquin Delta, California. San Franc Estuary Watershed Sci. [accessed 2024 Mar 11];20(2). https://doi.org/10.15447/sfews.2022v20iss2art5

Rinde J, Perry S, Flynn TM, Lesmeister S. 2020. Adaptive monitoring recommendations for dissolved oxygen along the Stockton Deep Water Ship Channel. Sacramento (CA): California Department of Water Resources, Division of Environmental Services. 21 p.

Robertson–Bryan I, Ascent Environmental. 2019. City of Stockton Regional Wastewater Control Facility Modifications Project final environmental impact report. State clearinghouse no. 2018092017 Stockton (CA): City of Stockton Municipal Utilities Department [accessed 2023 Jan 4]. Available from: https://www.stocktonca.gov/Documents/Services/Water,%20Sewer%20&%20Stormwater/Sewer/Regional%20Wastewater%20Control%20Facility%20Modification%20Project/RWCF_Mods_Proj_FEIR.pdf

Saleh D, Domagalski J. 2015. SPARROW modeling of nitrogen sources and transport in rivers and streams of California and adjacent states, U.S. J Am Water Resour Assoc. [accessed 2023 Jan 4];51(6):1487–1507. https://doi.org/10.1111/1752-1688.12325

Saleh D, Domagalski J. 2021. Concentrations, loads, and associated trends of nutrients entering the Sacramento–San Joaquin Delta, California. San Franc Estuary Watershed Sci. [accessed 2023 Jan 4];19(4). https://doi.org/10.15447/sfews.2021v19iss4art6

Schoellhamer DH, Wright SA, Monismith SG, Bergamaschi BA. 2016. Recent advances in understanding flow dynamics and transport of water-quality constituents in the Sacramento–San Joaquin River Delta. San Franc Estuary Watershed Sci. [accessed 2023 Jan 4];14(4). https://doi.org/10.15447/sfews.2016v14iss4art1

Senn D, Kraus T, Richey A, Bergamaschi B, Brown L, Conrad L, Francis C, Kimmerer W, Kudela R, Otten T et al. 2020. Changing nitrogen inputs to the northern San Francisco Estuary: potential ecosystem responses and opportunities for investigation. SFEI Contribution #973. Richmond (CA): San Fransisco Estuary Institute. [accessed 2023 Jan 6]. Available from: https://sciencetracker.deltacouncil.ca.gov/sites/default/files/2022-12/2020_Delta_Nutrient_Reduction_Responses.pdf

Siebert S, Kummu M, Porkka M, Döll P, Ramankutty N, Scanlon BR. 2015. A global data set of the extent of irrigated land from 1900 to 2005. Hydrol Earth Syst Sci. [accessed 2023 Sep 22];19(3):1521–1545. https://doi.org/10.5194/hess-19-1521-2015

Singer GP, Chapman ED, Ammann AJ, Klimley AP, Rypel AL, Fangue NA. 2020. Historic drought influences outmigration dynamics of juvenile fall and spring-run Chinook Salmon. Environ Biol Fishes. [accessed 2023 Jan 3];103(5):543–559. https://doi.org/10.1007/s10641-020-00975-8

Sommer T, Hartman R, Koller M, Koohafkan M, Conrad JL, MacWilliams M, Bever A, Burdi C, Beakes MP. 2020. Evaluation of a large-scale flow manipulation to the upper San Francisco Estuary: response of habitat conditions for an endangered native fish. Plos ONE. [accessed 2023 Jan 4]; 15(10):e0234673. https://doi.org/10.1371/journal.pone.0234673

Sommer T, Mejia F. 2013. A place to call home: a synthesis of Delta Smelt habitat in the upper San Francisco Estuary. San Franc Estuary Watershed Sci. [accessed 2023 Jan 3];11(2):25. https://doi.org/10.15447/sfews.2013v11iss2art4

Stern MA, Flint LE, Flint AL, Knowles N, Wright SA. 2020. The future of sediment transport and streamflow under a changing climate and the implications for long-term resilience of the San Francisco Bay–Delta. Water Resour Res. [accessed 2023 Jan 4];56(9):e2019WR026245. https://doi.org/10.1029/2019wr026245

Stine S. 1994. Extreme and persistent drought in California and Patagonia during mediaeval time. Nature. [accessed 2023 Jan 4];369(6481):546–549. https://doi.org/10.1038/369546a0

Stompe DK, Moyle PB, Oken KL, Hobbs JA, Durand JR. 2023. A spatiotemporal history of key pelagic fish species in the San Francisco Estuary, CA. Estuaries Coast. [accessed 2023 Sep 22];46(4):1067–1082. https://doi.org/10.1007/s12237-023-01189-8

Sturrock AM, Satterthaite WH, Cervantes–Yoshida KM, Huber ER, Sturrock HJW, Nusslé S, Carlson SM. 2019. Eight decades of hatchery salmon releases in the California Central Valley: factors influencing straying and resilience. Fisheries. [accessed 2023 Feb 28];44(9):433–444. https://doi.org/10.1002/fsh.10267

Swain DL, Langenbrunner B, Neelin JD, Hall A. 2018. Increasing precipitation volatility in twenty-first-century California. Nat Clim Change. [accessed 2023 Jan 4];8(5):427–433. https://doi.org/10.1038/s41558-018-0140-y

Swain DL, Tsiang M, Haugen M, Singh D, Charland A, Rajaratnam B, Diffenbaugh NS. 2014. The extraordinary California drought of 2013/2014: character, context, and the role of climate change. Bull Am Met Soc. 95(9):S3–S7. [accessed 2023 Sep 22]. Available from: *https://www.proquest.com/openview/437b06df38d374695901882dfac98766/1?pq-origsite=gscholar{&}cbl=31345*

[SWRCB] State Water Resources Control Board. 2018. Water Quality Control Plan for the San Francisco Bay/Sacramento–San Joaquin Delta Estuary. Sacramento (CA): SWRCB. Resolution no. 2018-0059. [accessed 2023 Feb 23]. 63 p. Available from: *https://www.waterboards.ca.gov/plans_policies/docs/2018wqcp.pdf*

Tempel TL, Malinich TD, Burns J, Barros A, Burdi CE, Hobbs JA. 2021. The value of long-term monitoring of the San Francisco Estuary for Delta Smelt and Longfin Smelt. California Fish and Wildlife Special CESA Issue. [accessed 2024 Mar 11];148–171. *https://doi.org/10.51492/cfwj.cesasi.7*

Thomson JR, Kimmerer WJ, Brown LR, Newman KB, Mac Nally R, Bennett WA, Feyrer F, Fleishman E. 2010. Bayesian change point analysis of abundance trends for pelagic fishes in the upper San Francisco Estuary. Ecol Appl. 20(5):1431–1448. [accessed 2023 Jan 15] *https://doi.org/10.1890/09-0998.1*

[USEPA] US Environmental Protection Agency. San Francisco Bay Delta: about the watershed. 2022. [accessed 2022 Dec 28]. Available from: *https://www.epa.gov/sfbay-delta/about-watershed*

Van Loon AF, Rangecroft S, Coxon G, Werner M, Wanders N, Di Baldassarre G, Tijdeman E, Bosman M, Gleeson T, Nauditt A, et al. 2022. Streamflow droughts aggravated by human activities despite management. Environ Res Lett. [accessed 2023 Mar 16];17(4):044059. *https://doi.org/10.1088/1748-9326/ac5def*

Vroom J, van der Wegen M, Martyr–Koller R, Lucas L. 2017. What determines water temperature dynamics in the San Francisco Bay–Delta System? Water Resour Res. [accessed 2023 Jan 4];53(11):9901–9921. *https://doi.org/10.1002/2016WR020062*

Weston DP, Chen D, Lydy MJ. 2015. Stormwater-related transport of the insecticides bifenthrin, fipronil, imidacloprid, and chlorpyrifos into a tidal wetland, San Francisco Bay, California. Sci Total Environ. [accessed 2024 Mar 11];527–528:18–25. *https://doi.org/10.1016/j.scitotenv.2015.04.095*

Wetz MS, Hutchinson EA, Lunetta RS, Paerl HW, Christopher Taylor J. 2011. Severe droughts reduce estuarine primary productivity with cascading effects on higher trophic levels. Limnol Oceanogr. [accessed 2023 Jan 4];56(2):627–638. *https://doi.org/10.4319/lo.2011.56.2.0627*

White J. 2022. Fall Midwater Trawl Survey end of season report: 2021. [accessed 2023 Jan 4]. Stoctkon (CA): California Department of Fish and Wildlife. 37. Available from: *https://nrm.dfg.ca.gov/FileHandler.ashx?DocumentID=199043*

Wilhelm SW, Bullerjahn GS, McKay RML, Moran MA. 2020. The complicated and confusing ecology of *Microcystis* blooms. mBio. [accessed 2023 Jan 4];11(3):e00529–00520. *https://doi.org/10.1128/mBio.00529-20*

Wood S. 2017. Generalized additive models: an introduction with R. 2nd ed. (Boca Raton): Chapman and Hall/CRC. 496 p.

Yanagitsuru YR, Main MA, Lewis LS, Hobbs JA, Hung T–C, Connon RE, Fangue NA. 2021. Effects of temperature on hatching and growth performance of embryos and yolk-sac larvae of a threatened estuarine fish: Longfin Smelt (*Spirinchus thaleichthys*). Aquaculture. [accessed 2024 Mar 11];537:736502. *https://doi.org/10.1016/j.aquaculture.2021.736502*

Zierdt Smith EL, Shrader KH, Thompson JK, Parchaso F, Gehrts K, Wells E. 2023. Bivalve effects on the food web supporting delta smelt—a spatially intensive study of bivalve recruitment, biomass, and grazing rate patterns with varying freshwater outflow in 2019. Report No. 2022–1102. [accessed 2024 Mar 11]. Reston (VA): US Geological Survey. Available from: *http://pubs.er.usgs.gov/publication/ofr20221102*

Zimmerman JKH, Carlisle DM, May JT, Klausmeyer KR, Grantham TE, Brown LR, Howard JK. 2018. Patterns and magnitude of flow alteration in California, USA. Freshw Biol. [accessed 2023 Jan 1];63(8):859–873. *https://doi.org/10.1111/fwb.13058*