UC Davis

San Francisco Estuary and Watershed Science

Title

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)

Permalink

https://escholarship.org/uc/item/1h7375k3

Journal

San Francisco Estuary and Watershed Science, 22(1)

Authors

Bosworth, David H.
Bashevkin, Samuel M.
Bouma—Gregson, Keith
et al.

Publication Date

2024

DOI

10.15447/sfews.2024v22iss1art1

Supplemental Material

https://escholarship.org/uc/item/1h7375k3#supplemental

Copyright Information

Copyright 2024 by the author(s). This work is made available under the terms of a Creative Commons Attribution License, available at https://creativecommons.org/licenses/by/4.0/

Peer reviewed



RESEARCH

The Anatomy of a Drought in the Upper San Francisco Estuary: Water Quality and Lower-Trophic Responses to Multi-Year Droughts

David H. Bosworth^{1*}, Samuel M. Bashevkin^{2,3}, Keith Bouma-Gregson⁴, Rosemary Hartman¹, Elizabeth B. Stumpner¹

ABSTRACT

Multi-year droughts are ever-present and transformational features of California's Mediterranean climate and can fundamentally affect the water quality and the ecosystem responses of the San Francisco Estuary (estuary) and the Sacramento-San Joaquin Delta (Delta). This study assessed data collected by long-term monitoring programs over the past 46 water years (1975–2021) to evaluate how water quality in the estuary changes during multi-year droughts. Data were aggregated by region (South-Central Delta, North Delta, confluence, Suisun Bay, and Suisun Marsh) and season, then differences between multi-year drought periods, multi-year wet periods, and neutral periods were

SFEWS Volume 22 | Issue 1 | Article 1

https://doi.org/10.15447/sfews.2024v22iss1art1

- * Corresponding author: david.bosworth@water.ca.gov
- 1 California Department of Water Resources West Sacramento, CA 95691 USA
- 2 Delta Stewardship Council Delta Science Program Sacramento, CA 95814 USA
- 3 California State Water Resources Control Board Sacramento, CA 95814 USA
- 4 US Geological Survey California Water Science Center Sacramento, CA 95819 USA

compared using generalized linear models. We found that multi-year drought periods altered multiple physical and chemical parameters in the estuary, increasing water temperature, salinity, water clarity, and nutrient levels. This trend was consistent across regions and seasons, with few exceptions. Increases in these parameters during drought periods were likely caused by reduced Delta inflows that intensified in each successive dry year because of reduced precipitation and managed estuarine inflows and outflows. Drought periods did not substantially affect tidal velocities within the estuary, which remained mostly consistent across wet and drought periods. Trends in chlorophyll concentrations during drought periods were more nuanced with higher concentrations occurring in the South-Central Delta region and during the winter and spring. Together, these results characterized drought in the estuary as warm, clear, high in nutrients, with patchy phytoplankton blooms (as indexed by chlorophyll), all of which have implications for higher trophic levels. Considering that droughts are expected to increase in frequency and intensity in California with climate change, understanding the effects of multi-year droughts on the water quality conditions of the estuary can help inform water management decisions.

KEYWORDS

water quality, nutrient, chlorophyll, drought, inflow, outflow, estuary

INTRODUCTION

The Mediterranean climate in California is characterized by hot, dry summers and cool, wet winters. Typically, there is little to no precipitation for approximately six months (April–September) out of the year in the central and southern regions of the state. California also experiences high inter-annual variability in precipitation, with rainfall ranging from a historic low of 23.8 cm in 1924 to a high of 105.8 cm in 2017, usually depending on just a few massive storms each year (Dettinger 2011). This high variability leads to floods and multi-year droughts that result in large year-to-year changes in the aquatic community (Nichols et al. 1990). There are various definitions for "drought," including meteorological droughts (low precipitation), hydrological droughts (low streamflows), agricultural droughts (lack of water for irrigation), and socioeconomic droughts (lack of water for human uses) (CDWR 2020). For this study, we define droughts in California as multiple years of below average precipitation and a resulting water supply shortage.

The effects of reduced flow on water quality and the ecosystem of the San Francisco Estuary (hereafter "estuary") including the Sacramento-San Joaquin Delta (hereafter "Delta") are well studied, but there has been more emphasis on inflow to or outflow from the estuary and the Delta on the annual time scale rather than the effect of multi-year droughts. Previous studies describing multi-year droughts in the estuary have most frequently focused on (1) the human uses and management impacts of prolonged droughts (Mount et al. 2017; Lund et al. 2018; Durand et al. 2020), (2) the impact of reduced precipitation and flow on the environment (Kimmerer et al. 2019; Mahardja et al. 2021), or (3) relationships between flow and fishes (Kimmerer 2002b; Sommer et al. 2004; Goertler et al. 2021). However, the drivers of these flow-abundance relationships are not always clear. Mahardja et al. (2021) found that many pelagic species have low resistance to drought (with steep declines during drought periods) but may recover with the onset of wetter conditions, whereas littoral fishes can more easily maintain their populations through droughts. Most non-native fishes were also more resilient to droughts than native fishes, with Mississippi silversides increasing during droughts (Mahardja et al. 2016).

Understanding the fundamental changes to water quality that occur during a drought can improve understanding of how the whole ecosystem responds to drought. Parameters such as flow, velocity, temperature, water clarity, and salinity directly influence the spatial distribution of fish assemblages but also affect phytoplankton distributions and abundances (which are frequently measured by chlorophyll-a [hereafter "chlorophyll"] concentration). Decreases in flow result in increased residence time, which may lead to increases in phytoplankton biomass (Lucas et al. 2009; Glibert et al. 2014). Because phytoplankton help form the base of the food web of the estuary and can also form harmful algal blooms (Lehman et al. 2022), the response of phytoplankton to drought is consequential for food web production and public health. Phytoplankton growth rates depend on temperature, light, nutrient availability, and predation (Jassby et al. 2002). In the estuary, these four variables are influenced by water flows through the system, which are determined by inter-annual precipitation and water management decisions, such as reservoir releases and diversions (Hutton et al. 2017b). Thus, the interplay between management decisions and hydrology have direct and indirect effects on foundational physical and water quality parameters (inflows, water velocity, temperature, salinity, light availability, nutrients, and chlorophyll) that influence how the higher food web is reshaped during droughts.

Research on the water quality foundations of the estuary during droughts has found varying, nuanced relationships between flow and key environmental parameters. Water temperatures increase during periods of low inflow, though the pattern varies by region and season and the causality of the relationship is unclear (Bashevkin and Mahardja 2022). Lower flows result in lower suspended sediment concentration and a resulting increase in water clarity (Livsey et al. 2021). Jabusch et al. (2018) found dry years had increased nitrate, dissolved inorganic nitrogen, and ortho-phosphate concentrations over wet years in the estuary during the 2012–2016 drought. While concentrations of nutrients may be highest during dry years, loadings of nutrients are often higher during wet years (Kimmerer 2002a; Novick et al. 2015).

Chlorophyll, an index of phytoplankton biomass, has a complex regional and seasonal response to interannual hydrologic variation in the estuary. Analyzing data from 1970–1993, Lehman (1996) found lower chlorophyll during dry years in the southern Delta, but higher chlorophyll in the northern Delta, while Arthur and Ball (1979) observed an increase in chlorophyll in the southern Delta but a decrease in the confluence and Suisun Bay during the 1977 drought. During the more recent drought of 2012-2016, Jabusch et al. (2018) found high chlorophyll values in the south Delta, and Glibert et al. (2014) observed an increase in chlorophyll in the northern Delta and Suisun Bay during the spring of 2014. Looking at the relationship between chlorophyll and flow, Jassby (2008) found a negative relationship between the two variables in the western Delta during the spring and summer of 1996-2005, but Kimmerer (2002a) did not find a relationship between chlorophyll and the location of the bottom 2 PSU (practical salinity units) isohaline, which is closely correlated with Delta outflow. A more holistic approach using data across longer time periods could resolve some of these differences, fill in some gaps, and detail how these interactions may have changed across the decades.

Three years during the most recent California drought (2020–2022) constitute the driest 3-year period on record (CDWR 2022c). Given that climate extremes like drought and flooding are expected to increase in frequency with climate change (Swain et al. 2018), there is a need to measure the influence that climate extremes have

on ecosystem processes in the estuary. This study represents an effort to synthesize and analyze data across the long-term record to describe how water quality in the estuary changed during droughts over a 46-year record (1975–2021, Figure 1) and how changes to those water quality parameters may have affected the rest of the ecosystem. Specifically, our research question is: how have multi-year droughts affected water flow (inflow, outflow, and velocity), water quality (temperature, Secchi depth, and salinity), dissolved inorganic nutrients (ammonium, nitrate + nitrite, and ortho-phosphate), and chlorophyll in the estuary both seasonally and regionally?

We hypothesize droughts will cause:

- Inflow and outflow to shift seasonally, with proportionally more flow in the summer and fall than winter and spring;
- Decreases in net water velocities (particularly during the winter and spring) and no change in tidal velocities;
- Increases in temperature, Secchi depth, and salinity;
- Increases in dissolved inorganic nutrient concentrations; and
- Increases in chlorophyll concentrations in some regions of the estuary but not others.

This paper is one of a series of papers produced by the Interagency Ecological Program Drought Synthesis Team. The team was formed in 2021 as part of several actions responding to the extremely dry water year, with a goal of understanding the ecological response to unprecedented dry conditions. The team analyzed effects of drought on a broad suite of environmental parameters including hydrology, water quality, phytoplankton, invertebrates, and fishes. In this series of papers, the authors define "drought" as two or more consecutive years with a Sacramento Valley Water Year Hydrologic Index classification of "Below Normal," "Dry," or "Critically Dry," similar to Mahardja et al. (2021). Each paper in this series can stand alone,

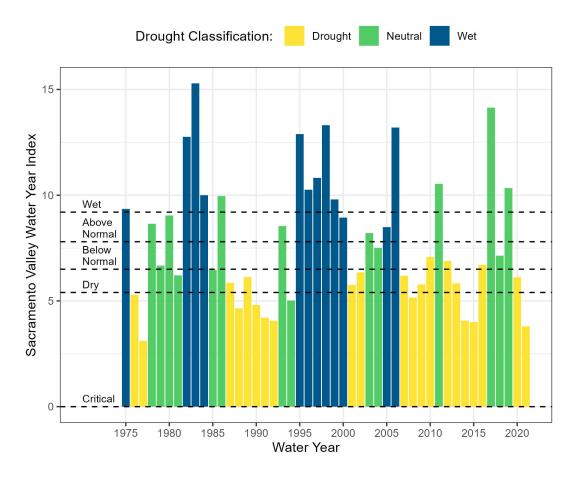


Figure 1 Sacramento Valley Water Year Hydrologic Index and drought classifications for all years used in this analysis, water years 1975–2021. Source: CDWR 2022a.

but many of the papers refer to each other and provide complementary information. (See in this issue: Barros et al.; Bouma-Gregson et al.; Hartman, Stumpner, et al.; and Hartman, Twardochleb, et al.).

METHODS

Study Area

Our study area consists of the Delta, Suisun Bay, and Suisun Marsh which altogether we define as the upper San Francisco Estuary (upper estuary). The tidal freshwater Delta is the large network of leveed channels and open water habitat located at the nexus of the Sacramento, San Joaquin, Cosumnes, and Mokelumne Rivers east of San Francisco Bay in California (Figure 2). Suisun Bay is the large embayment directly west and downstream of the Delta and is the transition zone between the freshwater Delta and the

saline San Francisco Bay. Suisun Marsh, a large brackish marsh complex, is located directly north of Suisun Bay. We used the 'deltamapr' R package (Bashevkin et al. 2021) to divide the upper estuary into five regions for analysis: the North Delta, South-Central Delta, confluence, Suisun Bay, and Suisun Marsh regions (Figure 2).

Data Sources and Processing

Throughout this paper we used various definitions for "year." In addition to traditional calendar years, we used "water years" and "adjusted water years." A "water year" is defined as the period from October 1 of the previous calendar year through September 30 of the current calendar year. We used water years in the analyses for the Delta inflow, outflow, and velocity parameters because the water management decisions represented in those results are more closely tied to the water year. For the remaining parameters

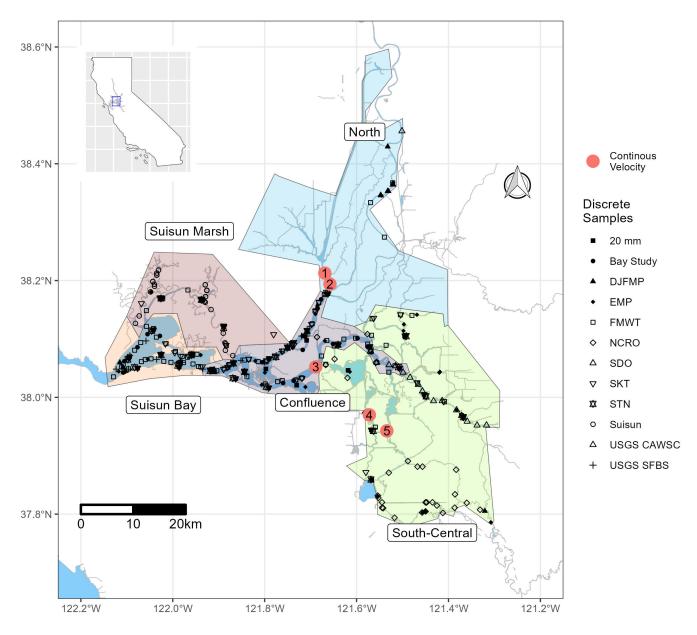


Figure 2 Map of Sampling Locations and regions used in the analysis. Continuous velocity stations: 1 = Cache Slough at Ryer Island (USGS station 11455350); 2 = Cache Slough above Ryer Island Ferry near Rio Vista, California (USGS station 11455385); 3 = San Joaquin River at Jersey Point, California (USGS station 11337190); 4 = Old River at Bacon Island, California (USGS station 1131405); 5 = Middle River at Middle River, California (USGS station 11312676). See Table 1 for details regarding the discrete sampling surveys. Base maps are from the 'deltamapr' (Bashevkin et al. 2021) and 'tigris' (Walker and Rudis 2023) R packages.

(water quality, dissolved inorganic nutrients, and chlorophyll), we used an "adjusted water year," which we defined as December 1 of the previous calendar year through November 30 of the current calendar year. This allowed for the entire "fall" season, which we defined as September–November, to be included in the same adjusted

water year in our analyses of these parameters and accounted for the lag in ecological responses to the start of the new water year.

Hydrology Data

We acquired Delta inflow and outflow data for water years 1975–2021 from CDWR's Dayflow

model (CDWR 2022b). This model uses measured instantaneous flow and export data from stations throughout the Delta to calculate daily average Delta inflow and export values. These values along with estimates of precipitation inputs and within-Delta water use are then used to calculate a daily average net Delta Outflow index.

Instantaneous water velocity data collected at five US Geological Survey (USGS) stream gages (Figure 2) in the Delta were obtained from the USGS National Water Information System (USGS 2023) using the 'dataRetrieval' R package (DeCicco et al. 2022). The five water velocity stations used in this study are: Cache Slough at Ryer Island (USGS station number 11455350), Cache Slough above Ryer Island Ferry near Rio Vista, California (11455385), San Joaquin River at Jersey Point, California (11337190), Middle River at Middle River, California (11312676), and Old River at Bacon Island, California (11313405). The Cache Slough at Ryer Island station (11455350) was discontinued in April 2019 and was replaced by Cache Slough above Ryer Island Ferry near Rio Vista, California (11455385). Data for these two stations located on Cache Slough were combined to represent Cache Slough above its confluence with the Sacramento River. We acquired water velocity data for water years 2008-2021 as defined by the periods of record of the five USGS stream gages.

The instantaneous water velocity data, collected at 15-minute intervals, were processed through a low-pass filter to remove tidal-period variation and calculate net velocity (Godin 1972). Before applying the filter, we imputed values for gaps up to 2 hours in the instantaneous data using linear interpolation with the 'imputeTS' R package (Moritz and Bartz-Beielstein 2017). The difference of the instantaneous velocity and net velocity resulted in the tidal velocity. We aggregated the net velocity data into weekly means, whereas tidal velocity was grouped into weekly minimum, maximum, and maximum absolute values.

Water Quality, Nutrient, and Chlorophyll Data

We compiled the water quality (water temperature, salinity, and Secchi depth), dissolved inorganic nutrient (dissolved ammonium, dissolved nitrate + nitrite, and dissolved orthophosphate), and chlorophyll-a (or chlorophyll) data from the integrated discrete water quality dataset published on the Environmental Data Initiative repository (Bashevkin et al. 2023). This dataset contains water quality, nutrient, and chlorophyll data collected by 16 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 adjusted water years 1975-2021 within our study area in the upper estuary (Figure 2). For more details about which surveys we used for each water quality, nutrient, and chlorophyll parameter, refer to Table 1. All water temperature and salinity measurements were typically collected within a depth of 1 m, and the nutrient and chlorophyll samples were collected at various depths less than 5m from the surface. For more information on data collection methods, refer to the data publication on the Environmental Data Initiative repository (Bashevkin et al. 2023).

Because some surveys collected more than one sample per day at a station, we filtered the water quality, nutrient, and chlorophyll samples and kept only one sample per station and day to ensure each sample had equal weight. The Suisun Marsh region was excluded from the nutrient and chlorophyll analyses because of inconsistent long-term sampling. For more information about the processing methods used for the water quality, nutrient, and chlorophyll data, refer to Appendix A.

To prepare the discrete water quality, dissolved inorganic nutrient, and chlorophyll data for analysis, we aggregated the dataset for each parameter as seasonal-regional averages. Seasons were defined as follows: winter (December of the previous calendar year, and January–February), spring (March–May), summer (June–August), and fall (September–November). To aggregate the data, we calculated monthly averages for each region, which we then used to calculate seasonal-regional averages for each adjusted water year. Before aggregating the nutrient and chlorophyll data, we substituted the values below

Table 1 Surveys used for each water quality, nutrient, and chlorophyll parameter and their periods of record

Survey	Abbreviation	Operator ^a	Parameters collected	Period of record (adjusted water years)
20-mm Survey	20 mm	CDFW	salinity, Secchi depth, water temperature	1995 – 2021
Bay Study	Bay Study	CDFW	salinity, Secchi depth, water temperature	1980 – 2021
Fall Midwater Trawl	FMWT	CDFW	salinity, Secchi depth, water temperature	1975 – 2021
Spring Kodiak Trawl	SKT	CDFW	salinity, Secchi depth, water temperature	2002 - 2021
Summer Townet Survey	STN	CDFW	salinity, Secchi depth, water temperature	1975 – 2021
Delta Juvenile Fish Monitoring Program	DJFMP	USFWS	Secchi depth, water temperature	1976 – 2021
Environmental Monitoring Program	EMP	CDWR	chlorophyll, nitrate + nitrite, orthophosphate, salinity, Secchi depth, water temperature	1975 – 2021
Program			ammonium	1979 – 2021
North Central Region Office monitoring program	NCRO	CDWR	chlorophyll, salinity, water temperature	1999 – 2021
			ammonium	2001 - 2021
			nitrate + nitrite, orthophosphate	2014 - 2021
Stockton Dissolved Oxygen monitoring	SDO	CDWR	water temperature	1997 – 2021
			Secchi depth	2001 – 2021
			salinity	2003 - 2021
Suisun Marsh Fish Study ^b	Suisun	UCD	salinity, water temperature	1979 – 2021
		UCD	Secchi depth	1980 – 2021
Sacramento River at Freeport, California (11447650)	USGS CAWSC	USGS ^c	salinity, water temperature	1975 – 2021
			ammonium, nitrate + nitrite	1979 – 2021
			orthophosphate	1981 – 2021
San Francisco Bay Water Quality Program	USGS SFBS	USGS ^c	ammonium, nitrate + nitrite, orthophosphate, salinity, water temperature	1975 – 2021
i rogiani			chlorophyll	1977 – 2021

a. CDFW: California Department of Fish and Wildlife; USFWS: US Fish and Wildlife Service; CDWR: California Department of Water Resources; UCD: University of California Davis; USGS: US Geological Survey.

the laboratory reporting limit (RL) with simulated values between zero and the RL based on a uniform distribution. We ran one simulation for each parameter and set a seed prior to running the simulation to ensure reproducibility. Overall, 6.8% of the ammonium, 1.4% of the nitrate + nitrite, 0.7% of the ortho-phosphate, and 0.2% of the chlorophyll values were below the RL and required replacement with simulated values. More information about reporting limits including the values used in our dataset is available in Appendix A.

ANALYSIS METHODS

Drought Classification

To assess the effects of drought on water quality, dissolved inorganic nutrient, chlorophyll, and flow parameters, we classified each water year and adjusted water year as one of three drought classifications (drought, neutral, and wet periods) using CDWR's Sacramento Valley Water Year Hydrologic Index classifications (CDWR 2022a) (Figure 1). "Drought periods" were defined as two or more years in a row with a Sacramento Valley Water Year Hydrologic Index classification of "Below Normal," "Dry," or "Critical," and "wet periods" were defined as two or more years in a row with a hydrologic index classification of "Wet" or "Above Normal." "Neutral periods"

b. We only included sampling locations within the larger sloughs (Montezuma Slough, Suisun Slough, and Nurse Slough) from the Suisun Marsh study.

c. USGS data from National Water Information System (USGS 2023).

comprised years that may be classified as Wet or Dry but were not comprised of a series of multiple Wet or Dry years (Figure 1). Velocity data were evaluated by the Sacramento Valley Water Year Hydrologic Index classifications because there were no consecutive Wet years within the short-term record during which velocity data were available (water years 2008–2021).

In hydrologically modified systems such as this estuary, there is a key human-controlled link between watershed supply and realized inflows. Inflows to the estuary are highly controlled by upstream dams and water diversions (Kimmerer 2004; Brown and Bauer 2010). Water is stored above these dams in reservoirs and released over time depending on the season and year type. While precipitation-based drought indices, including the Sacramento Valley Water Year Hydrologic Index, relate to the amount of water available to reservoirs, the final determinant of inflows to the estuary are the management decisions dictating dam releases as well as water diversions and exports downstream of the dams. Therefore, any estimated effects of precipitation-based drought indices in the estuary are a combination of the effect of drought/wet period management as applied to the drought/wet period.

Inflow and Outflow Analysis

To assess the effect of water management decisions on actual inflow into the upper estuary, the cumulative proportional inflow and outflow were calculated for each water year as the proportion of the water year total that had arrived by each day of the water year. After classifying each water year as one of three drought classifications (drought, neutral, and wet periods), we further assigned each water year a period-year according to the successive year of a drought period, neutral period, or wet period. For example, the second year of a drought, neutral, or wet period would be categorized with a periodyear value of 2, while the first year of a drought, neutral, or wet period would be categorized with a period-year value of 1. Because there were few periods greater than 3 years in length, all periodyears of 3 or greater were combined into one

category (3+). The maximum number of periodyears was 6 (drought in 1992 and wet in 2000; Figure 1). The cumulative inflows and outflows for each drought classification and periodyear category were then visualized within each water year to examine how water management decisions altered seasonal inflow and outflow patterns through successive years of each drought classification.

Water Quality, Nutrient, and Chlorophyll Analysis

Each water quality, dissolved inorganic nutrient, and chlorophyll variable was analyzed with a linear model designed to evaluate the drought classification and how that impact varies seasonally and regionally. Models were fit with fixed categorical predictors (i.e., ANOVAs) for drought classification, season, and region, as well as all two-way interactions.

For some variables, additional predictors were included to account for other factors that could influence the result. Secchi depth had an overall increasing pattern over time (Figure A1) with variable trends by season and region, so we accounted for this with an additional effect of a three-way interaction between numerical adjusted water year, season, and region. Chlorophyll concentrations highly depended on whether data were collected before or after the 1987 invasion of the clam, Potamocorbula amurensis, which has been identified as the cause of a regime shift in the estuary in previous studies (Kimmerer 2002b). Therefore, we included a categorical predictor for "regime" and the interaction of regime and region, with all data before 1987 categorized as "pre-clam" and data after 1987 categorized as "post-clam." Changes to waste-water treatment plants (WWTP) have controlled the loading of ammonium in the system, in particular the Stockton Regional Wastewater Control Facility in the south Delta and the Sacramento Regional Wastewater Treatment Plant in the north Delta (Saleh and Domagalski 2021). The Stockton Wastewater Control Facility was upgraded to tertiary treatment in 2006 (Rinde et al. 2020), and the Sacramento Regional WWTP was upgraded in 2021, both greatly reducing ammonium loading. Therefore, for the ammonium analysis, we

restricted the dataset to data prior to 2021 and included a categorical "treatment plant upgrade" term for the Stockton upgrade in 2006 and the interaction of treatment plant upgrade with region in the model. All data prior to 2006 were classified as "before upgrade" and data 2006–2020 were "after upgrade."

Model assumptions were checked by inspecting residual histograms, plots of the residuals versus model predictions, and plots of the observed versus model-predicted data. When needed to satisfy the normality assumption, response variables were log transformed (this applied to salinity, Secchi depth, nitrate + nitrite, ammonium, ortho-phosphate, and chlorophyll).

To evaluate the effects of drought classification on each focal variable, we calculated the partial R^2 as:

$$\frac{SS_{DroughtClassification}}{SS_{DroughtClassification} + SS_{residuals}},$$
 Eq1

where SS = sum of squares and $SS_{DroughtClassification}$ represented the sum of the main effect and all interactions of the drought classification factor. We also conducted Tukey post-hoc tests with the 'emmeans' R package (Lenth et al. 2022) to evaluate the region- and season-specific effects of each drought classification. Type III sum of squares were used to assess significance of ANOVA model terms.

R code used for retrieval, preparation, and analysis of the hydrology, water quality, nutrient, and chlorophyll data used in this study are available in the WQ-LT-Publication GitHub repository archived on Zenodo (Bosworth et al. 2024).

RESULTS

Delta Inflow and Outflow

Delta inflow changed in response to water management throughout successive years of drought and wet periods. As droughts progressed, reservoir managers prioritized storage earlier in the water year. This was most clear for the third or later year of a drought period when inflow was lower during the beginning of the water year until it catches up with the other period-years in April (Figure 3). The cumulative proportional inflow curve was also more linear during drought periods than neutral or wet periods, indicating that inflow was more consistent throughout the year. Neutral periods did not have consistent patterns across period-years. As wet periods progressed, more water was released from reservoirs earlier in the water year. Wet periods had the strongest seasonal pattern to inflow, and this pattern became stronger with each successive year. More water was released earlier in the water year and less water released later in the water year for wet periods compared to drought and neutral periods (Figure 3).

Delta outflow showed similar patterns as inflow except for a less pronounced difference in drought periods with less consistent separation among period-year classifications (Figure A2). Neutral periods had greater variability in outflow patterns among water years compared to inflow, while wet periods had almost identical outflow patterns as inflow.

Net and Tidal Velocity

While the relationship between Delta outflow and velocity was nuanced across seasons, there were generally higher net positive velocities, indicative of seaward flow, during high flow events in Wet years (Figure 4A). The maximum absolute tidal velocity was greatest at the Cache Slough (USGS station numbers 11455350 and 11455385) and San Joaquin River at Jersey Point (11337190) stations farther from the export pumps in the South Delta (Figure 4B). The maximum absolute tidal velocity did not appreciably change across Sacramento Valley Water Year Hydrologic Index classifications (Critical, Dry, Below Normal, and Wet) at all stations except during periods of high outflow that occurred during seasons with high precipitation (winter and spring) during Wet years. See Appendix A for further exploration of outflow, net velocity, and tidal velocity (Figures A3 and A4).

Water Temperature

Water temperature was significantly affected (p < 0.001) by all predictor variables except

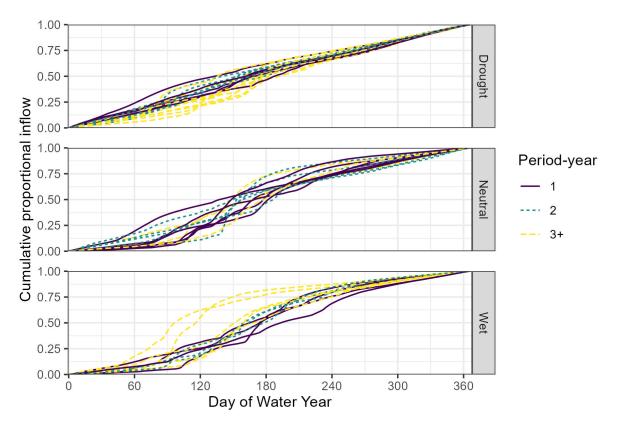


Figure 3 Seasonal patterns of cumulative proportional inflow throughout successive water years (period-year) of drought, neutral, and wet periods. Separate lines are plotted for each water year. The first water year of a drought, neutral, or wet period was categorized with a period-year value of 1, while the second water year of a drought, neutral, or wet period was categorized with a period-year value of 2. Because there were few periods greater than 3 years in length, all period-years of 3 or greater were combined into one category (3+).

region (p = 0.07305, Table 2). The partial R^2 for the drought classification variable was 0.15. Regionally, the effect of drought classification increased from west (downstream) to east (upstream). The Tukey post-hoc test indicated no significant differences in temperature among drought classifications in the Suisun Marsh region, higher temperatures in drought periods than in wet periods in the Suisun Bay (0.4 °C difference between mean predictions, p = 0.0054) and confluence (0.5 °C difference, p < 0.001) regions, and higher temperatures in drought periods than in neutral and wet periods in the South-Central Delta (0.9 °C difference between wet and drought periods, p < 0.001) and North Delta $(1.4 \,^{\circ}\text{C}, p < 0.001)$ regions (Figure 5). Seasonally, there were no significant differences among drought classifications in the winter (p > 0.05), significantly higher temperatures in drought periods than neutral and wet periods in the

spring (1.5 °C between wet and drought periods, p < 0.001) and fall (1 °C difference, p < 0.001), and significantly higher temperatures in drought periods than in wet periods in the summer (0.5 °C difference, p < 0.001) (Figure 6).

Salinity

Salinity was significantly affected (p<0.001) by all predictor variables (Table 2). The partial R^2 for the drought classification variable was 0.27. Regionally, the effect of drought classification increased from east (upstream) to west (downstream), which we expected because salinity variability follows the same pattern. The Tukey post-hoc test indicated significantly higher salinities in drought periods than neutral and wet periods in the Suisun Marsh (3.5 PSU difference between wet and drought periods, p<0.001), Suisun Bay (6.4 PSU difference, p<0.001), confluence (1.0 PSU difference, p<0.001), and

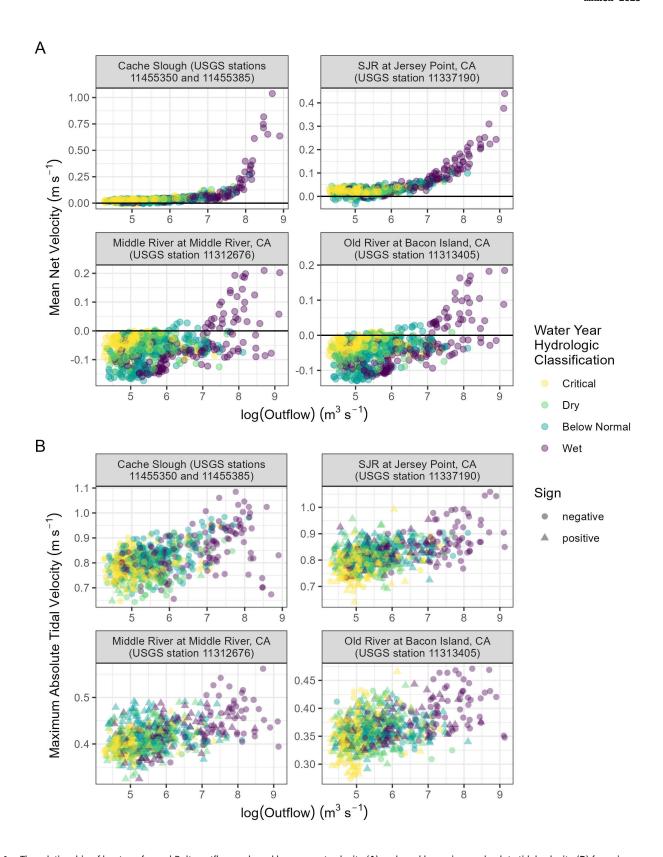


Figure 4 The relationship of log-transformed Delta outflow and weekly mean net velocity (**A**) and weekly maximum absolute tidal velocity (**B**) for unique US Geological Survey stream gages. *Color* corresponds to the Sacramento Valley Water Year Hydrologic Classification and the *sign* indicates negative (landward) and positive (seaward) direction.

Table 2 Summary ANOVA outputs for the water temperature, salinity, and Secchi depth models. Interactions are specified with a ":" between interacting variables.

Model	Parameter	Sum Sq	Df	F value	Pr(>F)
Temperature	(Intercept)	3034	1	4799	< 0.001
Temperature	Drought	10.61	2	8.389	< 0.001
Temperature	Season	2583	3	1362	< 0.001
Temperature	Region	5.432	4	2.148	0.07305
Temperature	Drought:Season	60.77	6	16.02	< 0.001
Temperature	Drought:Region	31.80	8	6.288	< 0.001
Temperature	Season:Region	178.0	12	23.47	< 0.001
Temperature	Residuals	569.0	900		
Salinity	(Intercept)	61.12	1	238.5	< 0.001
Salinity	Drought	30.41	2	59.34	< 0.001
Salinity	Season	24.91	3	32.40	< 0.001
Salinity	Region	536.1	4	523.0	< 0.001
Salinity	Drought:Season	8.414	6	5.473	< 0.001
Salinity	Drought:Region	46.45	8	22.66	< 0.001
Salinity	Season:Region	45.49	12	14.79	< 0.001
Salinity	Residuals	230.6	900		
Secchi depth	(Intercept)	0.001320	1	0.02856	0.8658
Secchi depth	Drought	3.551	2	38.42	< 0.001
Secchi depth	Season	0.1706	3	1.231	0.2973
Secchi depth	Region	0.8432	4	4.561	0.001192
Secchi depth	YearAdj	0.01543	1	0.3338	0.5636
Secchi depth	Drought:Season	1.001	6	3.611	0.001523
Secchi depth	Drought:Region	1.272	8	3.440	< 0.001
Secchi depth	Season:Region	1.207	12	2.176	0.01119
Secchi depth	Season:YearAdj	0.1628	3	1.174	0.3185
Secchi depth	Region:YearAdj	0.8953	4	4.844	< 0.001
Secchi depth	Season:Region:YearAdj	1.213	12	2.187	0.01072
Secchi depth	Residuals	40.20	870		

South-Central Delta (0.12 PSU difference, p < 0.001) regions. Salinities were not significantly different (p > 0.05) among drought classifications in the North Delta region (Figure 5). Seasonally, differences were similar in magnitude yearround, and salinities were higher in drought periods than neutral and wet periods in all seasons (winter = 0.62 PSU difference between wet and drought periods, spring = 0.51 PSU difference, summer = 0.69 PSU difference, fall = 0.75 PSU difference, p < 0.001) (Figure 6).

Secchi Depth

Secchi depth was significantly affected (p<0.05) by all predictor variables except season (p = 0.2973), adjusted water year (p = 0.5636), and the interaction term for season and adjusted water year (p = 0.3185, Table 2). The partial R² for the drought Classification variable was 0.13. Regionally, the Tukey post-hoc test indicated significantly higher Secchi depths in drought periods than wet periods in the confluence region (6 cm difference, p = 0.026), and higher Secchi depths in drought periods than neutral and wet periods in the Suisun Marsh (9 cm difference

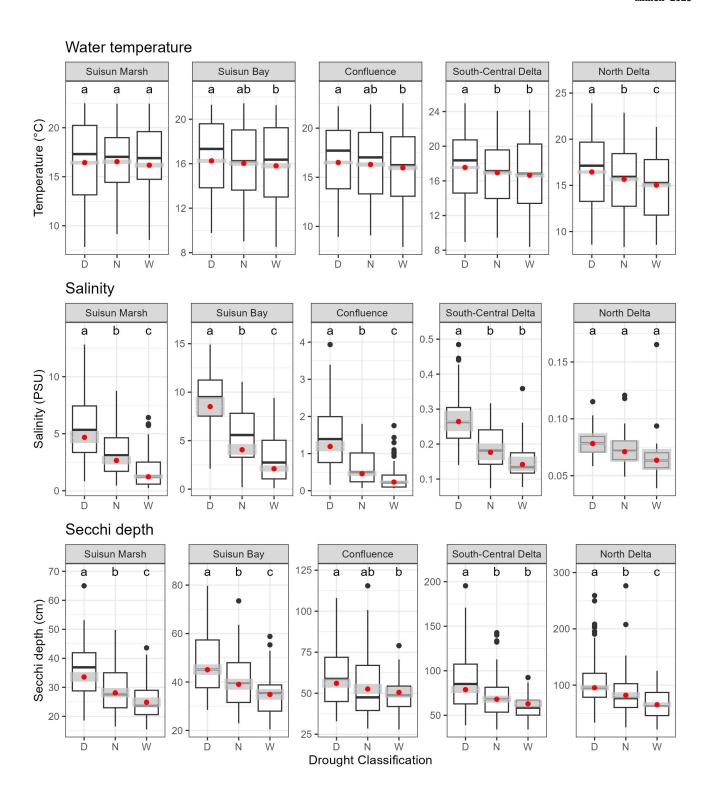


Figure 5 Observed values (*boxplots*) and model results (model means as *red points* ±95% confidence intervals as *gray boxes*) for the drought classification comparisons (drought period [D], neutral [N], and wet period [W]) by region for the water quality parameters. Different letters above *boxplots* identify statistically significant (p < 0.05) differences from a Tukey post-hoc test.

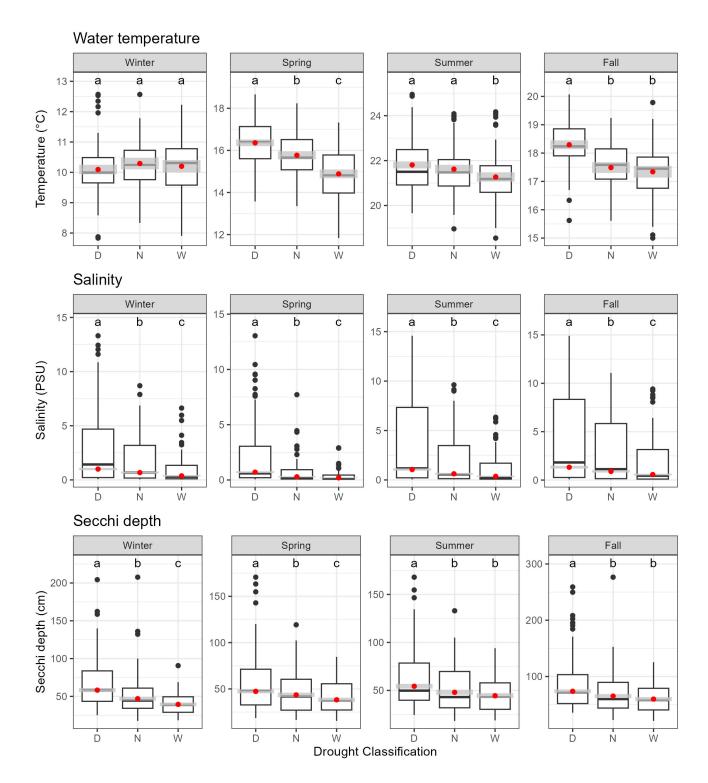


Figure 6 Observed values (*boxplots*) and model results (model means as *red points* ±95% confidence intervals as *gray boxes*) for the drought classification comparisons (drought period [D], neutral period [N], and wet period [W]) by season for the water quality parameters. Different letters above *boxplots* identify statistically significant (p < 0.05) differences from a Tukey post-hoc test.

between wet and drought periods, p < 0.001), Suisun Bay (10 cm difference, p < 0.001), South-Central Delta (16 cm difference, p < 0.001), and North Delta (30 cm difference, p < 0.001) (Figure 5). Seasonally, Secchi depths were significantly higher in drought periods than neutral and wet periods in all seasons (winter = 19 cm difference between wet and drought periods, spring = 9 cm difference, summer = 10 cm, fall = 14 cm difference, p < 0.001) (Figure 6).

Dissolved Ammonium

Dissolved ammonium concentrations were significantly affected by all predictor variables (p < 0.05; Table 3). Importantly, there were significant interactions between drought classification and both region and season, with a partial R^2 for the drought classification variable of 0.16. Ammonium concentrations were significantly higher during drought periods than wet periods in the North Delta (0.11 mg L^{-1} difference, p < 0.001), confluence (0.016 mg L⁻¹ difference, p = 0.028), and Suisun Bay (0.015 mg L⁻¹ difference, p = 0.025) regions, while concentrations were not significantly different (p>0.05) among drought classifications in the South-Central Delta region (Figure 7). Ammonium concentrations were significantly higher in drought periods than wet periods in winter $(0.060 \text{ mg L}^{-1} \text{ difference}, p < 0.001)$ and in spring $(0.052 \text{ mg L}^{-1} \text{ difference}, p < 0.001)$ but were not significantly different (p > 0.05) among drought classifications in summer or fall (Figure 8).

Ammonium concentrations before and after the 2006 Stockton Treatment Plant upgrade were significantly different (p<0.001; Table 3). Ammonium concentrations significantly decreased in the South-Central Delta (decrease of 0.060 mg L⁻¹, p<0.001) and North Delta (0.039 mg L⁻¹, p<0.001) regions, while concentrations significantly increased in the confluence (0.021 mg L⁻¹, p<0.001) and Suisun Bay (0.012 mg L⁻¹, p = 0.017) regions.

Dissolved Nitrate + Nitrite

Nitrate + nitrite concentrations were significantly affected by all predictor variables (p<0.05; Table 3), with a partial R^2 for the drought

classification variable of 0.10. Nitrate + nitrite concentrations were significantly higher during drought periods than wet periods in the confluence (0.12 mg L⁻¹ difference, p < 0.001) and Suisun Bay (0.13 mg L^{-1} difference, p < 0.001) regions, while concentrations were not significantly different (p > 0.05) between drought and wet periods in the South-Central Delta region (Figure 7). Additionally, nitrate + nitrite concentrations were not significantly different (p > 0.05) among drought classifications in the North Delta region. Seasonally, nitrate + nitrite concentrations were significantly higher during drought periods than wet periods in fall (0.068 mg L^{-1} difference, p < 0.001), spring (0.12 mg L⁻¹ difference, p < 0.001), and summer (0.051 mg L^{-1} difference, p < 0.001), but concentrations were not significantly different (p>0.05) among drought classifications in winter (Figure 8).

Dissolved Ortho-phosphate

Ortho-phosphate concentrations were significantly affected by all predictor variables (p<0.05; Table 3). The partial R^2 for the drought classification variable was 0.065. All regions had higher ortho-phosphate concentrations during drought periods than wet periods by approximately 0.02 mg L⁻¹ (p<0.001; Figure 7). Ortho-phosphate concentrations were also significantly higher during drought periods than wet periods for all seasons, with differences ranging from 0.017 mg L⁻¹ in the winter (p<0.001) to 0.028 mg L⁻¹ in the fall (p<0.001) (Figure 8).

Chlorophyll

Chlorophyll was significantly affected (p<0.001) by all predictor variables except the main effect of drought classification (p = 0.1059, Table 3). However, interactions were significant between drought classification and region (p<0.001) and between drought classification and season (p<0.001). The partial R^2 for the drought classification variable was 0.090. Chlorophyll concentrations were significantly higher during drought periods than wet periods only in the confluence and South-Central Delta regions (p = 0.028 and p<0.001, respectively) (Figure 7). The effects of drought classification were

 Table 3
 Summary ANOVA outputs for the nutrient and chlorophyll models

Model	Parameter	Sum Sq	Df	F value	Pr(>F)
Ammonium	(Intercept)	74.97	1	502.8	< 0.001
Ammonium	Drought	1.779	2	5.968	0.002700
Ammonium	Region	1.656	3	3.702	0.01160
Ammonium	Season	23.03	3	51.48	< 0.001
Ammonium	StocktonUpgrade	0.8526	1	5.719	0.01706
Ammonium	Drought:Region	9.670	6	10.81	< 0.001
Ammonium	Drought:Season	7.447	6	8.325	< 0.001
Ammonium	Region:Season	46.16	9	34.40	< 0.001
Ammonium	Region:StocktonUpgrade	22.85	3	51.09	< 0.001
Ammonium	Residuals	98.55	661		
Nitrate + Nitrite	(Intercept)	16.83	1	196.2	< 0.001
Nitrate + Nitrite	Drought	1.099	2	6.409	0.001742
Nitrate + Nitrite	Region	40.84	3	158.7	< 0.001
Nitrate + Nitrite	Season	1.315	3	5.112	0.001665
Nitrate + Nitrite	Drought:Region	3.374	6	6.557	< 0.001
Nitrate + Nitrite	Drought:Season	2.380	6	4.626	< 0.001
Nitrate + Nitrite	Region:Season	6.875	9	8.906	< 0.001
Nitrate + Nitrite	Residuals	61.58	718		
Ortho-phosphate	(Intercept)	195.7	1	2101.	< 0.001
Ortho-phosphate	Drought	1.298	2	6.968	0.001007
Ortho-phosphate	Region	11.07	3	39.60	< 0.001
Ortho-phosphate	Season	2.329	3	8.333	< 0.001
Ortho-phosphate	Drought:Region	1.814	6	3.246	0.003731
Ortho-phosphate	Drought:Season	1.550	6	2.773	0.01132
Ortho-phosphate	Region:Season	7.531	9	8.983	< 0.001
Ortho-phosphate	Residuals	67.07	720		
Chlorophyll	(Intercept)	2.067	1	8.185	0.004347
Chlorophyll	Drought	1.138	2	2.252	0.1059
Chlorophyll	Region	34.55	3	45.60	< 0.001
Chlorophyll	Season	13.18	3	17.39	< 0.001
Chlorophyll	Regime	30.42	1	120.4	< 0.001
Chlorophyll	Drought:Region	9.933	6	6.555	< 0.001
Chlorophyll	Drought:Season	6.877	6	4.538	< 0.001
Chlorophyll	Region:Season	30.34	9	13.35	< 0.001
Chlorophyll	Region:Regime	10.46	3	13.81	< 0.001
Chlorophyll	Residuals	181.1	717		

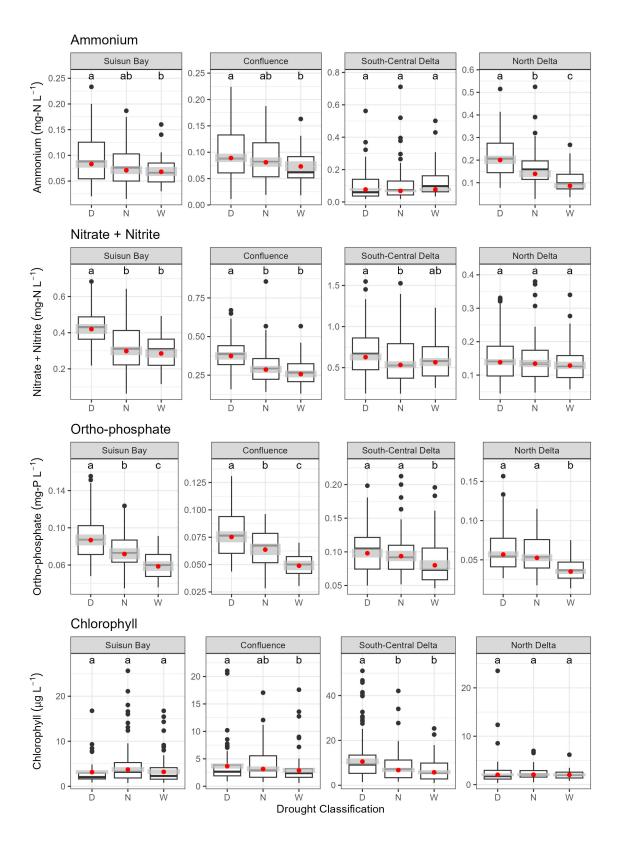


Figure 7 Observed values (boxplots) and model results (model means as $red\ points\ \pm 95\%$ confidence intervals as $gray\ boxes$) for the drought classification comparisons (drought period [D], neutral period [N], and wet period [W]) by region for the nutrient and chlorophyll parameters. Different letters above boxplots identify statistically significant (p < 0.05) differences from a Tukey post-hoc test.

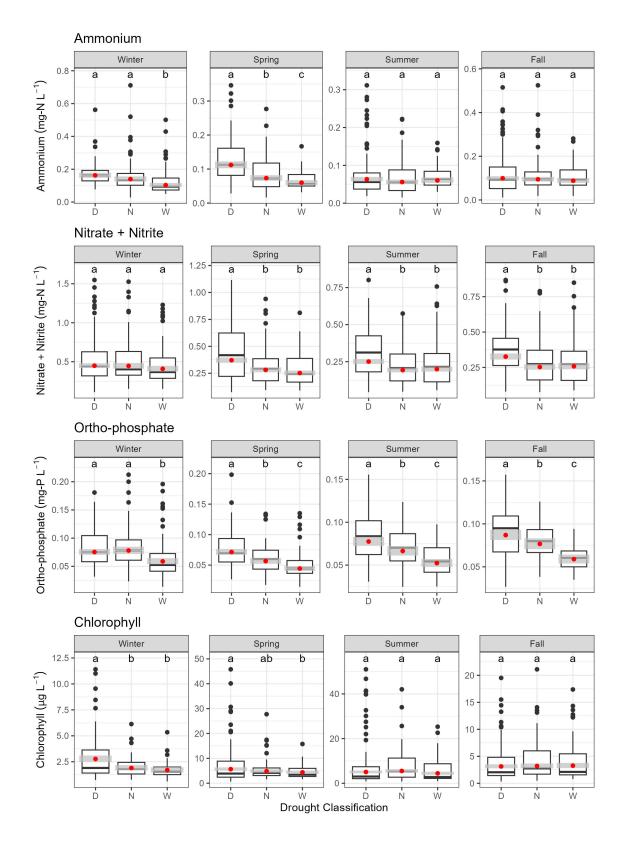


Figure 8 Observed values (*boxplots*) and model results (model means as *red points* ±95% confidence intervals as *gray boxes*) for the drought classification comparisons (drought period [D], neutral period [N], and wet period [W]) by season for the nutrient and chlorophyll parameters. Different letters above boxplots identify statistically significant (p < 0.05) differences from a Tukey post-hoc test.

greatest in the South-Central Delta region, with chlorophyll concentrations that were 4.8 μ g L⁻¹ higher during drought periods compared to wet periods (Figure 7). In the confluence region, chlorophyll concentrations were 0.77 μ g L⁻¹ higher during drought periods compared to wet periods. Comparing drought and wet periods across seasons, chlorophyll concentrations were significantly higher in winter (1.1 μ g L⁻¹ difference, p<0.001) and spring (1.3 μ g L⁻¹ difference, p=0.012) seasons during drought periods (Figure 8). Drought, wet, and neutral periods were not significantly different (p>0.05) in the North Delta or Suisun Bay regions nor during fall and summer seasons.

Chlorophyll concentrations were significantly higher before the invasion of *P. amurensis* across the upper estuary (p<0.001; Table 3) with effects that varied by region. The decrease in chlorophyll concentrations after the invasion of *P. amurensis* was smaller in the North Delta region (0.48 µg L⁻¹ difference, p = 0.0060) than in the Suisun Bay (3.3 µg L⁻¹ difference, p<0.001), confluence (2.3 µg L⁻¹ difference, p<0.001) and South-Central Delta (2.8 µg L⁻¹ difference, p<0.001) regions.

DISCUSSION

Throughout the period studied (adjusted water years 1975-2021), water temperature, salinity, water clarity, and dissolved inorganic nutrient concentrations were higher in the upper estuary during droughts. This trend was consistent across regions and seasons with few exceptions. Increases in these physical and chemical parameters during drought periods are likely caused by reduced Delta inflows because of both reduced precipitation and altered reservoir releases during droughts. While Delta inflows and outflows are strongly influenced by drought periods, tidal velocities within the upper estuary remained mostly consistent across Sacramento Valley Water Year Hydrologic Index classifications. Trends in chlorophyll concentrations during drought periods were more nuanced, with higher concentrations occurring in the South-Central Delta region and during winter and spring seasons. Together,

these results show that during drought periods, aquatic habitat in the upper estuary is warmer, clearer, and higher in nutrients, leading to patchy increases in chlorophyll. All these conditions have implications for higher trophic levels.

Patterns in Flow

The historical trends of freshwater inflow, and the resulting Delta outflow exhibiting inter- and intraannual variability have been well documented (Enright and Culberson 2009; Monismith 2016; Hutton et al. 2017a, 2017b and references therein). Delta outflow is regulated by the California State Water Resources Control Board (SWRCB) to meet water quality objectives and by the biological opinions and incidental take permits for the operation of the state and federal water projects to protect endangered fishes (USFWS 2019; SWRCB 2000; CDFW 2020). Water management activities that control freshwater outflow are intended to maintain salinity standards for beneficial uses, but these standards have been relaxed during prolonged drought periods (Durand et al. 2020). The effect of water management activities can be seen in our inflow (Figure 3) and outflow (Figure A2) analyses. As multi-year drought periods progress, increasingly more water is stored earlier in the year as reservoir refill is prioritized. During multi-year wet periods, the reverse pattern is seen in which increasingly more water is released earlier in the year, so that full reservoirs can be emptied enough to be useful for flood control.

Our comparisons of velocity to Delta outflow demonstrate that mean net velocity increased considerably during periods of elevated outflow, but tidal velocity, explored using the maximum absolute value, remained relatively constant during drier years in the short-term record (Figure 4). Only during periods of high outflow in Wet years did maximum absolute tidal velocity noticeably vary with Delta outflow (Figure 4), and the difference between the maximum and minimum outflow were usually less than 0.3 m s⁻¹. Delta Smelt (*Hypomesus transpacificus*) prefer lower current speeds, generally less than 1 m s⁻¹; however, this relationship is relatively weak (Bever et al. 2016), so a change of 0.3 m s⁻¹

may not impact Delta Smelt when other habitat conditions are favorable. Flow patterns in the Delta are complex (Moftakhari et al. 2013), and tidal cycles have periods from hours to years (Hoitink and Jay 2016). While we used a weekly time step to summarize the velocity data, using different time scales to further explore effects of drought on velocity may be informative. For example, water velocity across flood-ebb and spring-neap scales may be more relevant to fish entrainment and migration (Bennett and Burau 2015; Perry et al. 2015; Romine et al. 2021).

Water Temperature and Salinity

Water temperatures were significantly higher during drought periods than wet periods in all regions except the Suisun Marsh region (Figure 5) and in all seasons except winter (Figure 6). Temperatures were as much as 1.5 °C higher during droughts in some regions and seasons, which may push temperatures above physiological limits for some species. In particular, Delta Smelt experience behavioral changes and lower growth and survival with water temperatures above 22 °C (Davis et al. 2022), and summer temperatures surpassed 22 °C more frequently during droughts (Figure 6). While water temperatures are strongly influenced by atmospheric conditions, including air temperature (van Vliet et al. 2011; Vroom et al. 2017; Wagner et al. 2011), prior studies have also demonstrated a significant negative relationship between inflows and water temperature in the Delta (Nobriga et al. 2021; Bashevkin and Mahardja 2022). This negative relationship, where reduced inflow was correlated with higher water temperatures, was strongest in the eastern and northern Delta during the spring and fall months (Bashevkin and Mahardja 2022). The results of our water temperature analysis showed similar spatial and temporal patterns with significantly higher water temperatures during drought periods than wet periods in the South-Central Delta and North Delta regions and during the spring and fall. However, the extent to which inflow causally drives changes in water temperature have not yet been quantified (Bashevkin and Mahardja 2022).

Salinities were significantly higher during drought periods compared to wet periods in

all but the North region (Figure 5) and in all seasons (Figure 6). This result was expected because less freshwater inflow was available to displace seawater from the upper estuary during drought periods. The effect of drought periods was strongest in the westernmost regions (as much as 6 PSU in Suisun Bay and Suisun Marsh), which was also expected because these are the most seaward regions and are more subject to salinity increases. Salinity increases of 6 PSU could completely shift phytoplankton and zooplankton communities in Suisun Bay (Cloern and Jassby 2012), limit Delta Smelt habitat (Bever et al. 2016), reduce nesting habitat for birds in Suisun Marsh (Schacter et al. 2021), and could increase the upstream distribution of invasive clams and jellyfish (Hartman et al., this issue). Increasing salinity is one of the most immediately noticeable effects of reduced outflow, and combating increases in salinity will be one of the most challenging aspects of adapting to increased frequencies of droughts (Ghalambor et al. 2021).

Secchi Depth

Water clarity (as indexed by Secchi depth) was significantly higher during drought periods compared to wet periods in all regions and seasons, with increases of up to 16 cm (Figures 5 and 6). Similar increases in Secchi depth are expected to increase zooplankton vertical migration (Kimmerer et al. 2002), increase predation pressure on pelagic fishes (Ferrari et al. 2014), and increase Delta Smelt stress and food limitation (Hasenbein et al. 2016). Secchi depth is driven primarily by sediment loading, vegetation, and re-suspension of sediment from the riverbed (through tidal action and wind-wave resuspension). During years with lower inflow, including drought periods, less sediment is transported to the Delta (Stern et al. 2020; Livsey et al. 2021), with most of the sediment transport occurring during episodic, large storms during the winter and early spring (Schoellhamer 2002). The changes to sediment loads caused by these climatic events are also impacted by changes to water management, including operation of dams and diversions (Schoellhamer et al. 2012), which also change during droughts (Figure 3) (Durand et al. 2020). The increasing Secchi depth over the

past 40 years has been tied to decreased sediment loading combined with increased aquatic vegetation (Hestir et al. 2016; Schoellhamer 2011). Based on the lack of changes to tidal velocity during droughts, resuspension from water currents within the Delta is not likely to change during droughts, so changes to water clarity during drought periods are most likely driven by changes in sediment loading.

Nutrients

All the dissolved inorganic nutrients analyzed tended to have higher concentrations during drought years, but this varied seasonally and regionally (Figures 7 and 8). Ortho-phosphate concentrations were significantly higher during drought periods than wet periods across all seasons and regions; however, nitrate + nitrite and ammonium concentrations in drought and wet periods were not consistently different across regions and seasons, which indicates different drivers may be controlling the relationships for these nutrients. A similar trend was observed by Glibert (2010), who saw greater fluctuations of ammonium with changes in flow in Suisun Bay than in the lower San Joaquin River. The reverse trend, where nutrients decreased during periods of drought, has been observed in other estuaries including the Mission River estuary in Texas (Wetz et al. 2011; Bruesewitz et al. 2017) and the Neuse River estuary in North Carolina (Wetz et al. 2011). Nutrients decreased during droughts in these other estuaries in response to reduced storm flows and decreased runoff.

Concentrations of dissolved nutrients in the Delta are generally driven by three main processes – inputs from runoff and point sources, dilution from precipitation/inflow, and use/transformation by primary producers or bacteria (Novick et al. 2015). The decreased inflow and runoff during droughts result in decreased loading of nutrients from riverine sources, particularly agriculture, which contributes approximately 47% of total nitrogen and 65% of total phosphorus in the Delta (Saleh and Domagalski 2015), but decreased inflow also decreases dilution of nutrients (Dahm et al. 2016). Wastewater treatment plants provide a steadier supply of nutrients that occur at

roughly constant rates during all flow conditions (Glibert 2010; Dahm et al. 2016) and may provide as much as 25% of the total nitrogen and 20% of total phosphorus load to the Delta (Domagalski and Saleh 2015; Saleh and Domagalski 2015). While loadings increase with increased flow, concentrations may decrease due to dilution, and steady inputs from wastewater treatment plants during droughts may lead to higher concentrations in the water column, particularly when phytoplankton biomass is low. A similar pattern was found in the Aransas River estuary in Texas, where wastewater treatment plants provide high inputs of nutrients even in periods of low flow (Bruesewitz et al. 2017).

Uptake and transformation of nutrients by primary producers can significantly decrease concentrations in the water column. While nutrients are not usually limiting to phytoplankton production in the upper estuary (Jassby et al. 2002), large phytoplankton blooms can reduce concentrations of nitrogen to levels where they become limiting (Bouma-Gregson et al., this issue). During drought periods in the South-Central Delta region, ammonium and nitrate + nitrite did not increase, but chlorophyll concentrations increased. Increased rates of nitrogen consumption by phytoplankton growth during droughts may lead to lower steady-state concentrations of nitrate + nitrite despite more concentrated nutrient inputs into the system.

In our study area, the North Delta region demonstrated the most variability in the effects of drought classification on ammonium and nitrate + nitrite concentrations. Ammonium concentrations were significantly higher during drought periods than wet periods in the North Delta region, but nitrate + nitrite concentrations were not significantly different between drought and wet periods (Figure 7). Droughts affected the dominant form of nitrogen in this region considering nitrogen has been loaded primarily as ammonium into the Sacramento River from the Sacramento Regional WWTP (Kraus et al. 2017). In contrast, nitrogen has been loaded mostly as nitrate from the Stockton WWTP in the South-Central Delta region since its upgrade in 2006

(Rinde et al. 2020; Saleh and Domagalski 2021), but nitrate + nitrite concentrations were not significantly different between drought and wet periods in the South-Central Delta region. Longer residence times in the South-Central Delta region during dry years may have resulted in increased biological uptake, or relatively lower flows along the San Joaquin River (when compared to the Sacramento River) may have led to lower dilution of nutrients in wet years. In 2023, the Sacramento EchoWater Resource Recovery WWTP finished its upgrade, and the Stockton WWTP is in the process of upgrading its treatment processes as well. These WWTP upgrades will greatly reduce nitrogen loading of both ammonium and nitrate + nitrite to the Delta (Robertson-Bryan Inc. and Ascent Environmental Inc. 2019; Senn et al. 2020).

Chlorophyll

The results showed a seasonal influence of drought periods on chlorophyll concentrations, particularly in winter and spring seasons (Figure 8). Increased water clarity and longer residence time in the upper estuary during drier springs and winters may have caused higher chlorophyll accrual, particularly in cases where nutrients are plentiful (Lucas and Thompson 2012; Glibert et al. 2014; Hammock et al. 2019). Although the modeled mean chlorophyll concentrations were similar in drought and wet periods in spring, the maximum concentration was approximately 3-fold lower in wet periods compared to drought periods (Figure 8). Therefore, during spring in some drought periods, multiple environmental conditions may have aligned and resulted in greater phytoplankton abundance than occurred during wet periods. The strong negative relationship during spring between Delta inflow/ outflow and chlorophyll was observed previously (Arthur and Ball 1979; Lehman 1992; Jassby 2008).

In winter, a negative relationship between flows and chlorophyll also occurred, but the lower irradiance levels and cooler temperatures likely limited chlorophyll concentrations from reaching the same absolute concentrations as in spring, although the relative differences were similar in magnitude (Figure 8). By summer, drought classification had less of a direct effect on

chlorophyll concentrations. Although summer water temperatures increased during drought periods (0.5 °C) this increase may have minimally affected chlorophyll values given the already high summer water temperatures even in wet periods. These results contrast with other estuaries, where decreased nutrient import during droughts led to decreased chlorophyll (Bruesewitz et al. 2017; Wetz et al. 2011), though longer residence times during droughts have been shown to increase chlorophyll in other estuaries, including the Baffin Bay estuary in Texas (Cira et al. 2021).

Drought classification affected chlorophyll most strongly in the South-Central Delta region, where concentrations were higher during drought periods than wet and neutral periods (Figure 7). The South-Central Delta region had the highest chlorophyll concentrations of the four Delta regions (Figure 7) and has also experienced widespread blooms of toxic cyanobacteria since first being documented in 1999, particularly during dry years (Hayes and Waller 1999; Lehman et al. 2005). The shallow channels, longer residence time, and ample nutrients in the South-Central Delta region offer favorable conditions for phytoplankton growth. Flow is heavily modified in this region, and the amount of water exported from the Delta during summer controls net flow direction and residence time. If export pumping is reduced during droughts, the water residence time increases in the South-Central Delta region (Hammock et al. 2019), which gives phytoplankton more time to accrue biomass. This area is also higher in nutrients (Figure 7), which come from the numerous WWTPs, island drains, agricultural and urban runoff, and regeneration from sediments (Dahm et al. 2016). The abundance of cyanobacteria in this region has also been associated with droughts (Lehman et al. 2017, 2018, 2022).

Drought classification had a modest effect on chlorophyll concentrations in the confluence and no significant effect in Suisun Bay (Figure 7). In these two regions, the influence of tidal mixing and benthic grazers exert a strong control on chlorophyll concentrations (Cloern et al. 1983; Kimmerer and Thompson 2014; Nichols 1985), and values were often highest when the location of the turbidity maximum (and water clarity minimum) coincided with Suisun Bay and shallow channels (Cloern et al. 1983). While the mean chlorophyll concentration in Suisun Bay was not different among the drought classifications, the highest outliers and 75th percentile occurred in neutral periods. Beck et al. (2018) found that chlorophyll concentrations were higher in Suisun Bay when flows were higher, so the highest values in neutral periods may have been during years with higher flows. In addition, abundance and grazing rates of *P. amurensis* increased during dry years, potentially contributing to lower chlorophyll in Suisun Bay during droughts (Hartman et al. This Issue B). The complex interactions between grazers, tides, and flow management weaken the relationship between chlorophyll and water flow in the confluence and Suisun Bay (Lehman 1992).

Food Web Implications

The changes we observed in water quality and nutrients during drought periods may cascade up the food web to invertebrates and fishes. Many organisms in the estuary have strong relationships with freshwater inflow (Kimmerer 2002b), but the mechanisms behind those relationships are not always clear. In this study, we show how the environment experienced by organisms in the upper estuary changes significantly, which may help identify drivers of changes at higher trophic levels. For example, zooplankton abundance increased in the South-Central Delta region during droughts (Barros et al, this issue; Hartman et al., this issue), which mirrored the increase in chlorophyll concentrations in this region (Figure 7). Zooplankton could have taken advantage of the increased food supply made available by increased phytoplankton (Orsi and Mecum 1986; Owens et al. 2019); however, there is not always a direct relationship between zooplankton growth rates and chlorophyll concentrations because the taxa of phytoplankton that contribute to chlorophyll concentrations are not all equally available or preferred food sources for zooplankton (Jungbluth et al. 2021).

We found an increase in chlorophyll in the South-Central Delta region during drought periods but did not analyze the type of phytoplankton seen during droughts due to limitations in long-term phytoplankton monitoring data in the upper estuary. However, other research has found a higher incidence of harmful algal blooms during dry years, particularly from cyanobacteria in the genus Microcystis (Bouma-Gregson et al. this issue; Hartman et al. 2022; Lehman et al. 2022). Increases in nutrient concentrations, temperature, and water clarity, and decreases in flow are all implicated in causing *Microcystis* blooms (Lehman et al. 2013; Berg and Sutula 2015; Hartman et al. 2022; Lehman et al. 2022) and are all characteristic of drought conditions described in this study. While ortho-phosphate concentrations increased during drought periods, ammonium and nitrate + nitrite concentrations were not affected by drought periods in the South-Central Delta region, where Microcystis blooms have been seen most frequently (Figure 7). Increased amounts of nitrogen consumption by Microcystis during droughts may have resulted in lower concentrations of nitrogen in the South-Central Delta region. The use of nitrogen forms by cyanobacteria may be more complex than our current knowledge, but understanding how nutrients fuel the growth of Microcystis and other potentially harmful cyanobacterial species in the South-Central Delta region will have important food-web and human-health implications (Kudela et al. 2023).

Trends in chlorophyll concentrations provide only a partial understanding of food web impacts from phytoplankton because not all chlorophyll-containing organisms play the same role in the food web. Cryptophytes and diatoms produce polyunsaturated fatty acids that can influence zooplankton and invertebrate growth and fitness (Müller-Navarra et al. 2000; Ruess and Müller-Navarra 2019; Thomas et al. 2022). Cyanobacteria, in contrast, contain minimal long-chain omega-3 polyunsaturated fatty acids, do not produce sterols, and are an inefficient source of vitamin B12 (Ruess and Müller-Navarra 2019). Zooplankton growing in cyanobacterial blooms have been found to be sterol limited (Peltomaa et al. 2017). Additionally, some

phytoplankton have considerable defenses against grazing, which limits their energetic contribution to the food web. For example, a 2016 bloom of the filamentous diatom, Aulacoseira granulata, in the Delta did not result in higher population size or fecundity for the copepod Pseudodiaptomus forbesi (Jungbluth et al. 2021). The large cell size, thick silica cell wall, and filamentous morphology of A. granulata may have hindered consumption by P. forbesi (Lürling 2021; Ryderheim et al. 2022). While a full analysis of phytoplankton community composition was outside the scope of this paper, the analysis performed by Lehman (1996) found more cryptophytes and cyanobacteria during critically dry years. The impact of water quality parameters on the food web will be largely mediated by changes to the phytoplankton community composition, which is shaped by bottom up (water quality) and top-down (grazing) factors.

Many pelagic fishes decline during droughts (Mahardja et al. 2021; Nelson et al., unpublished draft, see "Notes"), and their decline may be influenced by many of the water quality variables we evaluated. Clearer water can reduce feeding efficiency (Hasenbein et al. 2013) and make pelagic fishes more vulnerable to predators (Ferrari et al. 2014). Higher temperatures increase the metabolic demands of pelagic fishes and can also increase their susceptibility to predation (Davis et al. 2019; Nobriga et al. 2021). Reduced flows may slow movement of outmigrating juvenile salmon or cause them to become entrained in water project intakes (Romine et al. 2021). Changes to nutrient and chlorophyll concentrations are less likely to directly affect fishes; however, if chlorophyll concentrations increase in the form of harmful algal blooms, fish survival may be reduced through toxicity, reduced oxygen, or increased pH (Acuna et al. 2012; Kurobe et al. 2018; Bouma-Gregson et al., this issue).

The interannual changes in water quality conditions could also lead to spatial or temporal mismatches between the life histories and traits of higher organisms and their optimal abiotic conditions. For example, Delta Smelt typically rear in the low salinity zone (0.5-6 PSU) during the fall (Sommer and Mejia 2013). However, in drought years, the region of optimal salinity is in the narrow, channelized Sacramento and San Joaquin Rivers. In wet years, the region of optimum salinity is in the comparably more hospitable shallow shoals and wetlands of Suisun Bay and Marsh where temperatures, turbidity, and phytoplankton production are more suitable (Sommer and Mejia 2013; FLOAT-MAST 2021). Similarly, lower flows and higher temperatures during droughts may mean that out-migrating juvenile salmonids do not reach the Delta until temperatures are too warm for survival (Nobriga et al. 2021).

Future droughts will be more frequent and severe (Swain et al. 2018), so the already fragile food web may have difficulty coping with the changes to water quality we found by analyzing past droughts. Furthermore, sea level rise will cause landward salinities to increase (Ghalambor et al. 2021), and climate change will further increase temperatures (Dettinger et al. 2016; Pierce et al. 2018). With the exception of ammonium, the impacts of drought described in this paper will help predict conditions in the future, but we can expect many of the patterns described here to be magnified and the impact intensified.

CONCLUSIONS

Drought is an ever-present and transformational feature of California's Mediterranean climate. Looking at 46 years of data collected in the San Francisco Estuary, we found that droughts affected multiple physical and chemical parameters in the upper estuary. Extended periods of belowaverage precipitation decreased water supply and resulted in reduced Delta inflow that intensified in each successive dry year. Reduced inflow during drought periods affected the upper estuary by making it warmer, saltier, and clearer, with higher nutrient concentrations and patchy increases in chlorophyll when compared to wet and neutral periods. These impacts of drought on water quality, nutrients, and chlorophyll can, in turn, affect the higher trophic levels within the upper estuary. While most of the water quality and lower

trophic level responses to drought periods found by our study were expected, our work reaffirms the existence of these trends across almost a half century spanning numerous multi-year droughts. Climate extremes, like drought and flooding, are expected to increase in frequency and intensity in California with climate change (Swain et al. 2018). Therefore, understanding how droughts influence the water quality conditions of the upper estuary can help inform water management decisions in the upper estuary, both currently and in the future.

ACKNOWLEDGMENTS

We would like to thank Sarah Perry (California Department of Water Resources [CDWR]) for their assistance with data contributions, data analysis, and formatting. We would also like to thank all the field and laboratory staff of the Interagency Ecological Program (IEP) long-term monitoring surveys, US Geological Survey (USGS), CDWR's North Central Region Office, and CDWR's Bryte Laboratory for their tireless work collecting and analyzing the data that contributed to this study. We would like to thank Ted Flynn (CDWR), Jared Frantzich (CDWR), and other reviewers for helpful comments that improved the manuscript. This study was conducted under the auspices of the IEP. The views and conclusions in this article represent the views of the authors from the California Department of Water Resources, the Delta Stewardship Council, and the California State Water Resources Control Board. The views and conclusions of this article do not necessarily represent the views of the IEP. This article has been peer reviewed and approved for publication consistent with USGS Fundamental Science Practices (https://pubs.usgs.gov/circ/1367/). Funding for Keith Bouma-Gregson was provided by CDWR. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US Government.

REFERENCES

Acuna S, Deng DF, Lehman P, Teh S. 2012. Sublethal dietary effects of *Microcystis* on Sacramento splittail, *Pogonichthys macrolepidotus*. Aquat Toxicol. [accessed 2023 Feb 6];110-111:1-8. https://doi.org/10.1016/j.aquatox.2011.12.004

Arthur JF, Ball MD. 1979. Factors influencing the low phytoplankton standing crop in Suisun Bay during the 1976–1977 drought. Sacramento (CA): US Bureau of Reclamation. 100 p.

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

Bashevkin SM, Barros A, Hartman R. 2021. 'deltamapr': spatial data for the Bay–Delta, v. 1.0.0. GitHub. [accessed 2023 Feb 6]. https://github.com/InteragencyEcologicalProgram/deltamapr/tree/d0a6f9c22aa074f906176e99a0ed70f97f26fffd

Bashevkin SM, Bosworth D, 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 Jun 19]. https://doi.org/10.6073/pasta/8dbd29c8c 22f3295bbc5d3819fb51d00

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(3):684-702.

https://doi.org/10.1002/lno.12027

Beck MW, Jabusch TW, Trowbridge PR, Senn DB. 2018. Four decades of water quality change in the upper San Francisco Estuary. Estuarine Coastal Shelf Sci. [accessed 2023 Feb 6];212:11-22. https://doi.org/10.1016/j.ecss.2018.06.021

Bennett WA, Burau JR. 2015. Riders on the storm: selective tidal movements facilitate the spawning migration of threatened Delta Smelt in the San Francisco Estuary. Estuaries and Coasts. [accessed 2023 Jan 6];38(3):826-835.

https://doi.org/10.1007/s12237-014-9877-3

- Berg M, Sutula M. 2015. Factors affecting the growth of cyanobacteria with special emphasis on the Sacramento–San Joaquin Delta. Prepared for the Central Valley Regional Water Quality Control Board (Agreement No. 12-135-250). Southern California Coastal Water Research Project Technical Report 869. [accessed 2023 Feb 23]. Available from: https://amarine.com/wp-content/uploads/2018/01/Cyano_Review_Final.pdf
- 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 Dec 21];14(1). https://doi.org/10.15447/sfews.2016v14iss1art3
- Bosworth DH, Hartman R, Bashevkin SM, Stumpner EB, Bouma-Gregson K. 2024. InteragencyEcologicalProgram/WQ-LT-Publication: Manuscript-Resubmittal 1, v2.0.0. Zenodo. [accessed 2024 Jan 11]. https://doi.org/10.5281/zenodo.10493268
- Bouma-Gregson K, Bosworth D, Flynn TM, Maguire A, Rinde J, Hartman R. 2024. Delta Blue(green)s: the impact 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, Bauer ML. 2010. Effects of hydrologic infrastructure on flow regimes of California's Central Valley rivers: implications for fish populations. River Res Appl. [accessed 2023 Jan 3];26(6):751-765. https://doi.org/10.1002/rra.1293
- Bruesewitz DA, Hoellein TJ, Mooney RF, Gardner WS, Buskey EJ. 2017. Wastewater influences nitrogen dynamics in a coastal catchment during a prolonged drought. Limnol Oceanogr. [accessed 2023 Jun 30];62(S1):S239-S257. https://doi.org/10.1002/lno.10576
- [CDFW] California Department of Fish and Wildlife. 2020. Incidental take permit for long-term operation of the State Water Project in the Sacramento–San Joaquin Delta. Sacramento (CA): California Department of Fish and Wildlife. Incidental Take Permit No. 2081-2019-066-00. [accessed 2023 Feb 6]. Available from: https://water.ca.gov/-/media/DWR-Website/Web-Pages/Programs/State-Water-Project/Files/ITP-for-Long-Term-SWP-Operations.pdf

- [CDWR] California Department of Water Resources. 2020. California's most significant droughts: comparing historical and recent conditions. Sacramento (CA): California Department of Water Resources. [accessed 2023 Feb 6]. 202 p. Available from: https://cawaterlibrary.net/wp-content/uploads/2017/05/CalSignficantDroughts_v10_int.pdf
- [CDWR] California Department of Water Resources. 2022a. Chronological reconstructed Sacramento and San Joaquin Valley Water Year Hydrologic Classification indices. California Data Exchange Center. [accessed 2023 Feb 6]. https://cdec.water.ca.gov/reportapp/javareports?name=WSIHIST
- [CDWR] California Department of Water Resources. 2022b. Dayflow: and estimate of daily average Delta Outflow. California Natural Resources Agency Open Data. [accessed 2023 Feb 6]. https://data.cnra.ca.gov/dataset/dayflow
- [CDWR] California Department of Water Resources. 2022c. New water year begins amid preparations for continued drought [blog post]. CDWR News Releases. [accessed 2022 Dec 19]. October 3, 2022. Available from: https://water.ca.gov/News/News-Releases/2022/Oct-22/New-Water-Year-Begins-Amid-Preparations-for-Continued-Drought
- Cira EK, Palmer TA, Wetz MS. 2021. Phytoplankton dynamics in a low-inflow estuary (Baffin Bay, TX) during drought and high-rainfall conditions associated with an El Niño event. Estuaries Coasts. [accessed 2023 Jun 30];44(7):1752-1764. https://doi.org/10.1007/s12237-021-00904-7
- Cloern JE, Alpine AE, Cole BE, Wong RLJ, Arthur JF, Ball MD. 1983. River discharge controls phytoplankton dynamics in the northern San Francisco Bay estuary. Estuarine Coastal Shelf Sci. [accessed 2023 Feb 28];16(4):415-429. https://doi.org/10.1016/0272-7714(83)90103-8
- Cloern JE, Jassby AD. 2012. Drivers of change in estuarine-coastal ecosystems: Discoveries from four decades of study in San Francisco Bay. Rev Geophys. [accessed 2023 Dec 22];50(4):RG4001. http://doi.org/10.1029/2012RG000397
- Dahm CN, Parker AE, Adelson AE, Christman MA, Bergamaschi BA. 2016. Nutrient dynamics of the Delta: effects on primary producers. San Franc Estuary Watershed Sci. [accessed 2023 Jan 6];14(4). https://doi.org/10.15447/sfews.2016v14iss4art4

- Davis B, Bush E, Lehman P, Pien C. 2022.

 Temperature thresholds for aquatic species in the Sacramento–San Joaquin Delta ver 2.

 Environmental Data Initiative. [accessed 2023 Feb 13]. https://doi.org/10.6073/pasta/0ffa27c1302fd8f6197ea5ffd9feff9e
- Davis BE, Hansen MJ, Cocherell DE, Nguyen TX, Sommer T, Baxter RD, Fangue NA, Todgham AE. 2019. Consequences of temperature and temperature variability on swimming activity, group structure, and predation of endangered delta smelt. Freshw Biol. [accessed 2023 Feb 6];64(12):2156-2175.

https://doi.org/10.1111/fwb.13403

DeCicco LA, Hirsch RM, Lorenz D, Watkins WD, Johnson M. 2022. 'dataRetrieval': R packages for discovering and retrieving water data available from federal hydrologic web services. v. 2.7.12. Comprehensive R Archive Network (CRAN). [accessed 2023 Jun 29].

https://doi.org/10.5066/P9X4L3GE

Dettinger M. 2011. Climate change, atmospheric rivers, and floods in California–a multimodel analysis of storm frequency and magnitude changes. J Am Water Res Assoc. [accessed 2022 Jan 09];47(3):514-523.

https://doi.org/10.1111/j.1752-1688.2011.00546.x

Dettinger M, Anderson J, Anderson M, Brown L, Cayan D, Maurer E. 2016. Climate change and the Delta. San Franc Estuary Watershed Sci. [accessed 2023 Jan 12];14(3).

http://doi.org/10.15447/sfews.2016v14iss3art5

Domagalski J, Saleh D. 2015. Sources and transport of phosphorus to rivers in California and adjacent states, US, as determined by SPARROW modeling. J Am Water Res 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, LeinfelderMiles M, Lund JR, Lusardi R, Manfree AD,
Medellín-Azuara J, Milligan B, Moyle PB. 2020.
Drought and the Sacramento-San Joaquin Delta,
2012–2016: ssons. San Franc Estuary Watershed
Sci. [accessed 2023 Jan 4];18(2).

https://doi.org/10.15447/sfews.2020v18iss2art2

Enright C, Culberson SD. 2009. Salinity trends, variability and control in the northern reach of the San Francisco Estuary. San Franc Estuary Watershed Sci. [accessed 2023 Feb 6];7(2). https://doi.org/10.15447/sfews.2009v7iss2art3

Ferrari MCO, Ranaker 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 Fishes. [accessed 2023 Jan 12];97:79-90. https://doi.org/10.1007/s10641-013-0125-7

[FLOAT-MAST] Flow Alteration-Management Analysis and Synthesis Team. 2021. Synthesis of data and studies relating to Delta Smelt biology in the San Francisco Estuary, emphasizing water year 2017. Sacramento (CA): Interagency Ecological Program. IEP Technical Report 95. [accessed 2022 Feb 23]. Available from: https://cadwr.app.box.com/v/InteragencyEcologicalProgram/file/838721643382

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).

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

Glibert PM. 2010. Long-term changes in nutrient loading and stoichiometry and their relationships with changes in the food web and dominant pelagic fish species in the San Francisco Estuary, California. Rev Fisheries Sci. [accessed 2023 Feb 6];18(2):211-232.

https://doi.org/10.1080/10641262.2010.492059

Glibert PM, Dugdale R, Wilkerson FP, Parker AE, Alexander J, Antell E, Blaser S, Johnson A, Lee J, Lee T, Murasko S, Strong S. 2014. Major–but rarespring 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

Godin G. 1972. The analysis of tides. Toronto (Canada): Univ. of Toronto Press. 264 p.

Goertler P, Mahardja B, Sommer T. 2021. Striped bass (*Morone saxatilis*) migration timing driven by estuary outflow and sea surface temperature in the San Francisco Bay–Delta, California. Sci Rep. [accessed 2023 Jan 3];11.

https://doi.org/10.1038/s41598-020-80517-5

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 Manage. [accessed 2023 Jan 4];63:703-717.

https://doi.org/10.1007/s00267-019-01159-6

- Hartman R, Rasmussen N, Bosworth D, Berg M, Ateljevich E, Flynn T, Wolf B, Pennington T, Khanna S. 2022. Temporary urgency change petition of 2021 and emergency drought salinity barrier; impact on harmful algal blooms and aquatic weeds in the Delta. Report to the State Water Resources Control Board. Sacramento (CA): California Department of Water Resources. [accessed 2023 Jan 6]. 239 p. Available from: https://www.waterboards.ca.gov/drought/tucp/docs/2022/2022-10-14-habs-weeds-report.pdf
- Hartman R, Stumpner E, Burdi C, Bosworth D, Maguire A, IEP Drought Synthesis Team. 2024. Dry me a river: ecological effects of drought in the upper San Francisco Estuary. San Franc Estuary Watershed Sci.

https://doi.org/10.15447/sfews.2024v22iss1art5

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, Fangue NA, Geist J, Komoroske LM, Truong J, McPherson R, Connon RE. 2016. Assessments at multiple levels of biological organization allow for an integrative determination of physiological tolerances to turbidity in an endangered fish species. Conserv Phys. [accessed 2017 Oct 2];4(1):cow004. https://doi.org/10.1093/conphys/cow004

- 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. Integrative Comparative Biol. [accessed 2023 Jan 12];53(4):620-634. https://doi.org/10.1093/icb/ict082
- Hayes SP, Waller S. 1999. An extensive, patchy *Microcystis aeruginosa* bloom detected in the Delta. Sacramento (CA): Interagency Ecological Program. IEP Newsletter. [accessed 2023 Feb 23]; vol 12.
- 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 Coasts. [accessed 2023 Jan 4];39(4):1100-1112.

https://doi.org/10.1007/s12237-015-0055-z

Hoitink AJF, Jay DA. 2016. Tidal river dynamics: implications for deltas. Rev Geophys. [accessed 2023 Dec 28];54(1):240-272.

https://doi.org/10.1002/2015RG000507

- Hutton PH, Rath JS, Roy SB. 2017a. Freshwater flow to the San Francisco Bay–Delta estuary over nine decades. Part 1: trend evaluation. Hydrol Processes. [accessed 2023 Jan 6];31(14):2500-2515. https://doi.org/10.1002/hyp.11201
- Hutton PH, Rath JS, Roy SB. 2017b. Freshwater flow to the San Francisco Bay–Delta estuary over nine decades. Part 2: change attribution. Hydrol Processes. [accessed 2023 Jan 4];31(14):2516-2529. https://doi.org/10.1002/hyp.11195
- Jabusch T, Trowbridge P, 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. SFEI Contribution #865. Richmond (CA): Aquatic Science Center. [accessed 2023 Jan 4]. 119 p. Available from: https://www.sfei.org/documents/delta-nutrient-status-2018
- Jassby A. 2008. Phytoplankton in the upper San Francisco Estuary: recent biomass trends, their causes and their trophic significance. San Franc Estuary Watershed Sci. [accessed 2012 Jan 5];6(1). https://doi.org/10.15447/sfews.2008v6iss1art2
- Jassby AD, Cloern JE, Cole BE. 2002. Annual primary production: Patterns and mechanisms of change in a nutrient-rich tidal ecosystem. Limnol Oceanogr. [accessed 2023 Feb 6];47(3):698-712. https://doi.org/10.4319/lo.2002.47.3.0698

Jungbluth M, Lee C, Patel C, Ignoffo T, Bergamaschi B, Kimmerer W. 2021. Production of the copepod *Pseudodiaptomus forbesi* is not enhanced by ingestion of the diatom *Aulacoseira* granulata during a bloom. Estuaries Coasts. [accessed 2023 Jan 6];44:1083-1099.

https://doi.org/10.1007/s12237-020-00843-9

Kimmerer WJ. 2002a. Physical, biological, and management responses to variable freshwater flow into the San Francisco Estuary. Estuaries. [accessed 2023 Jan 6];25:1275-1290. https://doi.org/10.1007/BF02692224

Kimmerer WJ. 2002b. Effects of freshwater flow on abundance of estuarine organisms: physical effects or trophic linkages? Mar Ecol Prog Ser. [accessed 2021 Sep 27];243:39-55.

https://doi.org/10.3354/meps243039

Kimmerer WJ. 2004. Open water processes of the San Francisco Bay Estuary: from physical forcing to biological responses. San Franc Estuary Watershed Sci. [accessed 2023 Jan 6];2(1). https://doi.org/10.15447/sfews.2004v2iss1art1

Kimmerer WJ, Burau JR, Bennett WA. 2002. Persistence of tidally-oriented vertical migration by zooplankton in a temperate estuary. Estuaries. [accessed 2021 Sep 27];25(3):359-371. https://doi.org/10.1007/BF02695979

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 Coasts. [accessed 2023 Jan 4];37:1202-1218.

https://doi.org/10.1007/s12237-013-9753-6

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

Kraus TEC, Carpenter KD, Bergamaschi BA, Parker AE, Stumpner EB, Downing BD, Travis NM, Wilkerson FP, Kendall C, Mussen TD. 2017. A riverscale Lagrangian experiment examining controls on phytoplankton dynamics in the presence and absence of treated wastewater effluent high in ammonium. Limnol Oceanogr. [accessed 2023 Jan 6];62(3):1234-1253.

https://doi.org/10.1002/lno.10497

Kudela R, Howard M, Monismith S, Paerl H. 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 2023 Dec 27];20(4).

https://doi.org/10.15447/sfews.2023v20iss4art6

Kurobe T, Lehman PW, Haque ME, Sedda T, Lesmeister S, Teh S. 2018. Evaluation of water quality during successive severe drought years within *Microcystis* blooms using fish embryo toxicity tests for the San Francisco Estuary, California. Sci Total Environ. [accessed 2023 Jan 6];610-611:1029-1037.

https://doi.org/10.1016/j.scitotenv.2017.07.267

Lehman PW. 1992. Environmental factors associated with long-term changes in chlorophyll concentration in the Sacramento-San Joaquin delta and Suisun Bay, California. Estuaries. [accessed 2024 Mar 13];15(3):335-348. https://doi.org/10.2307/1352781

Lehman PW. 1996. Changes in chlorophyll *a* concentration and phytoplankton community composition with water-year type in the upper San Francisco Estuary. In: Hollibaugh JT, editor. 1996. San Francisco Bay: the ecosystem. San Francisco (CA): American Association for the Advancement of Science, Pacific Division. p. 351-374.

Lehman PW, Boyer G, Hall C, Waller S, Gehrts K. 2005. Distribution and toxicity of a new colonial *Microcystis aeruginosa* bloom in the San Francisco Estuary, California. Hydrobiologia. [accessed 2023 Jan 6];541:87-99.

https://doi.org/10.1007/s10750-004-4670-0

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, Lesmeister S, Lam C, Tung A, Xiong M, Teh SJ. 2018. Strong differences characterize *Microcystis* blooms between successive severe drought years in the San Francisco Estuary, California, USA. Aquat Microbial Ecol. [accessed 2023 Jun 20];81(3):293-299. https://doi.org/10.3354/ame01876 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 International. [accessed 2023 Jan 4];621:16-25.

https://doi.org/10.1016/j.quaint.2019.12.003

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

- Lenth RV, Buerkner P, Herve M, Love J, Riebl H, Singmann H. 2022. Package 'emmeans': estimated marginal means, aka least-squares means, v. 1.8.1. Comprehensive R Archive Network. [accessed 2021 Aug 16]. https://cran.r-project.org/web/packages/emmeans/index.html
- 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 Coasts. [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
- Lucas LV, Thompson JK, Brown LR. 2009. Why are diverse relationships observed between phytoplankton biomass and transport time? Limnol Oceanogr. [accessed 2023 Dec 28];54(1):381-390. https://doi.org/10.4319/lo.2009.54.1.0381
- Lund J, Medellin-Azuara J, Durand J, Stone K. 2018. Lessons from California's 2012–2016 drought. J Water Resour Planning Manage. [accessed 2023 Feb 6]:144(10).

https://doi.org/10.1061/(ASCE)WR.1943-5452.0000984

Lürling M. 2021. Grazing resistance in phytoplankton. Hydrobiologia. [accessed 2023 Jun 20];848(1):237-249.

https://doi.org/10.1007/s10750-020-04370-3

- Mahardja B, Conrad JL, Lusher L, Schreier BM. 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 Dec 22];14(1). https://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). https://doi.org/10.1002/eap.2243
- Moftakhari H, Jay DA, Talke SA, Kukulka T, Bromirski PD. 2013. A novel approach to flow estimation in tidal rivers. Water Resourc Res. [accessed 2023 Jul 5];49(8):4817-4832. https://doi.org/10.1002/wrcr.20363
- Monismith SG. 2016. A note on Delta outflow. San Franc Estuary Watershed Sci. [accessed 2023 Jan 12];14(3).

https://doi.org/10.15447/sfews.2016v14iss3art3

- Moritz S, Bartz-Beielstein T. 2017. 'imputeTS': time series missing value imputation in R. R Journal. [accessed 2023 Jan 6];9(1):207-218. https://doi.org/10.32614/RJ-2017-009
- Mount J, Gray B, Chappelle C, Gartrell G, Grantham T, Moyle P, Seavy N, Szeptycki L, Thompson BB. 2017. Managing California's freshwater ecosystems, lessons from the 2012–16 drought. San Francisco (CA): Public Policy Institute of California. [accessed 2023 Jan 10]. 54 p. Available from: https://www.ppic.org/wp-content/uploads/r_1117jmr.pdf
- Müller-Navarra DC, Brett MT, Liston AM, Goldman CR. 2000. A highly unsaturated fatty acid predicts carbon transfer between primary producers and consumers. Nature. [accessed 2023 Jun 20];403(6765):74-77. https://doi.org/10.1038/47469
- Nichols FH. 1985. Increased benthic grazing: An alternative explanation for low phytoplankton biomass in northern San Francisco Bay during the 1976–1977 drought. Estuarine Coastal Shelf Sci. [accessed 2023 Jul 5];21(3):379-388.

https://doi.org/10.1016/0272-7714(85)90018-6

Nichols FH, Thompson JK, Schemel LE. 1990. Remarkable invasion of San Francisco Bay (California USA) by the Asian clam *Potamocorbula amurensis*. II. Displacement of a former community. Mar Ecol Prog Ser. [accessed 2023 Feb 13];66(1/2):95-102.

https://www.jstor.org/stable/24844649

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

- Novick E, Holleman R, Jabusch T, Sun J,
 Trowbridge P, Senn D, Guerin M, Kendall C,
 Young M, Peek S. 2015. Characterizing and
 quantifying nutrient sources, sinks and
 transformations in the Delta: synthesis, modeling,
 and recommendations for monitoring. San
 Francisco (CA): San Francisco Estuary Institute.
 [accessed 2023 Feb 6]. 28 p. Available from: http://
 www.sfei.org/sites/default/files/biblio_files/785%20
 Delta%20synthesis%20modeling.pdf
- Orsi JJ, Mecum WL. 1986. Zooplankton distribution and abundance in the Sacramento–San Joaquin Delta in relation to certain environmental factors. Estuaries. [accessed 2023 Feb 28];9(4B):326-339. https://doi.org/10.2307/1351412
- Owens S, Ignoffo TR, Frantzich J, Slaughter A, Kimmerer W. 2019. High growth rates of a dominant calanoid copepod in the northern San Francisco Estuary. J Plankt Res. [accessed 2020 Jun 14];41(6):939-954.

https://doi.org/10.1093/plankt/fbz064

Peltomaa ET, Aalto SL, Vuorio KM, Taipale SJ. 2017. The importance of phytoplankton biomolecule availability for secondary production. Front Ecol Evol. [accessed 2023 Jun 20];5(2017). https://doi.org/10.3389/fevo.2017.00128

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

- Pierce DW, Kalansky JF, Cayan DR. 2018. Climate, drought, and sea level rise scenarios for California's fourth climate change assessment. California Energy Commission and California Natural Resources Agency. [accessed 2023 Jun 22]. Available from: https://www.energy.ca.gov/sites/default/files/2019-11/Projections_CCCA4-CEC-2018-006_ADA.pdf
- 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 Inc., Ascent Environmental Inc. 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. 230 p.
- Romine JG, Perry RW, Stumpner PR, Blake AR, Burau JR. 2021. Effects of tidally varying river flow on entrainment of juvenile salmon into Sutter and Steamboat sloughs. San Franc Estuary Watershed Sci. [accessed 2023 Jan 12];19(2). https://doi.org/10.15447/sfews.2021v19iss2art4
- Ruess L, Müller-Navarra DC. 2019. Essential biomolecules in food webs. Front Ecol Evol. [accessed 2023 Jun 20];7(2019). https://doi.org/10.3389/fevo.2019.00269
- Ryderheim F, Grønning J, Kiørboe T. 2022. Thicker shells reduce copepod grazing on diatoms. Limnol Oceanogr Lett. [accessed 2023 Jun 20];7(5):435-442. https://doi.org/10.1002/lol2.10243
- Saleh D, Domagalski J. 2015. SPARROW modeling of nitrogen sources and transport in rivers and streams of California and adjacent states, US. J Am Water Res 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

Schacter CR, Peterson SH, Herzog MP, Hartman CA, Casazza ML, Ackerman JT. 2021. Wetland availability and salinity concentrations for breeding waterfowl in Suisun Marsh, California. San Franc Estuary Watershed Sci. [accessed 2023 Dec 22];19(3).

https://doi.org/10.15447/sfews.2021v19iss3art5

Schoellhamer DH. 2002. Comparison of the basinscale effect of dredging operations and natural estuarine processes on suspended sediment concentration. Estuaries. [accessed 2023 Feb 6];25(3):488-495.

https://doi.org/10.1007/BF02695990

Schoellhamer DH. 2011. Sudden clearing of estuarine waters upon crossing the threshold from transport to supply regulation of sediment transport as an erodible sediment pool is depleted: San Francisco Bay, 1999. Estuaries Coasts. [accessed 2023 Feb 6];34(5):885-899. https://doi.org/10.1007/s12237-011-9382-x

Schoellhamer DH, Wright SA, Drexler J. 2012.
A conceptual model of sedimentation in the Sacramento–San Joaquin Delta. San Franc Estuary Watershed Sci. [accessed 2023 Jun 20];10(3). https://doi.org/10.15447/sfews.2012v10iss3art3

Senn D, Kraus T, Richey A, Bergamaschi B, Brown L, Conrad L, Francis C, Kimmerer W, Kudela R, Otten T, Parker A, Robinson A, Mueller-Solger A, Stern D, Thompson J. 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]. 44 p. Available from: https://sfbaynutrients.sfei.org/sites/default/files/delta_nutrient_upgrade_draft_may302019.pdf

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).

https://doi.org/10.15447/sfews.2013v11iss2art4

Sommer TR, Harrell WC, Solger AM, Tom B, Kimmerer W. 2004. Effects of flow variation on channel and floodplain biota and habitats of the Sacramento River, California, USA. Aquat Conserv. [accessed 2023 Feb 6];14(3):247-261. https://doi.org/10.1002/aqc.620 [SWRCB] State Water Resources Control Board. 2000. Revised Water Right Decision 1641. In the matter of implementation of water quality objectives for the San Francisco Bay/Sacramento-San Joaquin Delta Estuary. A petition to change points of diversion of the Central Valley Project and the State Water Project in the southern Delta, and a petition to change places of use and purposes of use of the Central Valley Project. Sacramento (CA): State Water Resources Control Board, California Environmental Protection Agency. Available from: https://www.waterboards.ca.gov/waterrights/board_decisions/adopted_orders/decisions/d1600_d1649/wrd1641_1999dec29.pdf

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).

https://doi.org/10.1029/2019wr026245

Swain DL, Langenbrunner B, Neelin JD, Hall A. 2018. Increasing precipitation volatility in twenty-first-century California. Nature Climate Change. [accessed 2023 Jan 4];8(5):427-433.

https://doi.org/10.1038/s41558-018-0140-y

Thomas PK, Kunze C, Van de Waal DB, Hillebrand H, Striebel M. 2022. Elemental and biochemical nutrient limitation of zooplankton: a meta-analysis. Ecol Lett. [accessed 2023 Jun 20];25(12):2776-2792.

https://doi.org/10.1111/ele.14125

[USWS] US Fish and Wildlife Service. 2019. Biological opinion for the reinitiation of consultation of the coordinated operations of the Central Valley Project and State Water Project. Sacramento (CA): US Fish and Wildlife Service. Service File No. 08FBTD00-2019-F-0164. [accessed 2023 Feb 6]. Available from: https://www.usbr.gov/mp/bdo/docs/ba-final-biological-assessment.pdf

[USGS] US Geological Survey. 2023. USGS water data for the nation. US Geological Survey National Water Information System database. [accessed 2023 Jun 29]. https://doi.org/10.5066/F7P55KJN

van Vliet MTH, Ludwig F, Zwolsman JJG, Weedon GP, Kabat P. 2011. Global river temperatures and sensitivity to atmospheric warming and changes in river flow. Water Resour Res. [accessed 2023 Jan 6];47(2).

https://doi.org/10.1029/2010WR009198

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

Wagner RW, Stacey M, Brown LR, Dettinger M. 2011. Statistical models of temperature in the Sacramento–San Joaquin Delta under climate-change scenarios and ecological implications. Estuaries Coasts. [accessed 2023 Feb 6];34(3):544-556. https://doi.org/10.1007/s12237-010-9369-z

Walker K, Rudis B. 2023. 'tigris': Load Census TIGER/ Line Shapefiles, v. 2.0.3. Comprehensive R Archive Network (CRAN). [accessed 2023 Jul 27].

https://cran.r-project.org/package=tigris

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

NOTES

Nelson PA, Hartman R, Keller E, Sawyer EB.
Historical fluctuations in fish populations during droughts in the San Francisco Estuary. Draft manuscript submitted to San Francisco Estuary and Watershed Science. Available from:

Peter.Nelson@water.ca.gov

https://doi.org/10.15447/sfews.2024v22iss1art1