

UC Davis

San Francisco Estuary and Watershed Science

Title

Delta Blue(green)s: The Effect of Drought and Drought-Management Actions on Microcystis in the Sacramento—San Joaquin Delta

Permalink

<https://escholarship.org/uc/item/1zq5s96r>

Journal

San Francisco Estuary and Watershed Science, 22(1)

Authors

Bouma—Gregson, Keith

Bosworth, David H.

Flynn, Theodore M.

et al.

Publication Date

2024

DOI

10.15447/sfews.2024v22iss1art2

Supplemental Material

<https://escholarship.org/uc/item/1zq5s96r#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

Delta Blue(green)s: The Effect of Drought and Drought-Management Actions on *Microcystis* in the Sacramento–San Joaquin Delta

Keith Bouma-Gregson¹, David Bosworth², Theodore M. Flynn², Amanda Maguire², Jenna Rinde³, Rosemary Hartman^{2*}

ABSTRACT

Cyanobacterial phytoplankton blooms are more prevalent in the freshwater Sacramento–San Joaquin Delta (Delta) since the late 1990s, including blooms driven by overgrowths of potentially toxigenic organisms of the genus *Microcystis*. Data from 2014 to 2021 were used to show how flow dynamics, water temperature, and water clarity drive occurrence of *Microcystis*. We used a *Microcystis* bloom in the central Delta from 2021 as a case study for how novel monitoring tools can track blooms in real-time and be used post hoc to evaluate the effects of management actions.

Microcystis was detected throughout the Delta in all but the highest-flow years, and bloom incidence and severity increased during drier years. In the South Delta, Franks Tract, lower

San Joaquin River, and Old River regions, where blooms are most prevalent, higher water temperatures and clarities, combined with lower exports from state and federal water projects, were the best explanatory factors for the occurrence of *Microcystis* blooms. Nutrient concentrations were lower in summer than in winter, but only became potentially limiting at high phytoplankton concentrations.

We used satellite data and *in situ* continuous monitoring of flow, phytoplankton communities, and water quality to track hydro-biogeochemical conditions during the 2021 case study *Microcystis* bloom in the Central Delta. We did not find evidence that changes to Delta outflow regulatory standards contributed to this bloom, but changes in flow caused by a salinity barrier placed in west False River may have exacerbated the bloom. The frequency and severity of droughts are expected to increase in the future as a result of climate change, and our study demonstrates how continued monitoring of cyanotoxins, water quality, and phytoplankton communities could help improve management of cyanobacterial blooms in the Delta and other estuaries.

SFEWS Volume 22 | Issue 1 | Article 2

<https://doi.org/10.15447/sfew.2024v22iss1art2>

* Corresponding author: Rosemary.Hartman@water.ca.gov

- 1 US Geological Survey
California Water Science Center
Sacramento, CA 95819 USA
- 2 California Department of Water Resources
West Sacramento, CA 95691 USA
- 3 California Department of Fish and Wildlife
West Sacramento, CA 95605 USA

KEY WORDS

Microcystis, harmful algal bloom, cyanobacteria, water quality, drought, estuary

INTRODUCTION

Communities of phytoplankton and cyanobacteria (blue-green algae) drive primary productivity in aquatic ecosystems worldwide, yet overgrowths of certain toxigenic species can form harmful algal blooms (HABs) that pose health risks to the humans and other organisms that inhabit these ecosystems (Banerjee et al. 2021; Chorus and Welker 2021). While saltwater HABs are generally caused by eukaryotic algae, predominantly freshwater regions typically experience HABs caused by cyanobacteria (cyanoHABs). Estuaries, a dynamic continuum of saline, brackish, and freshwater environments, can experience both types of HABs, and the increased frequency with which they occur is a growing concern for resource managers worldwide (Plaas and Paerl 2021; Zepernick et al. 2022).

CyanoHABs have occurred in the upper reaches of the San Francisco Estuary (the estuary) and the Sacramento–San Joaquin Delta (Delta) of California since the late 1990s (Hayes and Waller 1999), although *Microcystis* was reported in the San Joaquin River as early as 1913 and possibly earlier (Allen 1920). These blooms were described as having a green-flake appearance near the surface of the water, and later studies found them to comprise a mix of different taxa: *Aphanizomenon* spp., *Microcystis* spp., *Dolichospermum* (formerly *Anabaena*) spp., *Planktothrix* spp., and *Pseudanabaena* spp. (Lehman et al. 2010; Mioni et al. 2012). Most research in the Delta to date, however, has focused on *Microcystis* as the most visually apparent taxon and one that is most frequently tied to the production of toxins (Wilhelm et al. 2020). We will also focus on *Microcystis* in this paper, except when our monitoring tools do not allow us to distinguish between taxa.

The Delta is a hub for California water management (major rivers, landmarks, water-management facilities, and regional divisions used in this paper are shown in Figure 1). Water is regulated through many water rights, contracts, and environmental regulations (as discussed in Durand et al. 2020; Sommer 2020). However, California's Mediterranean climate, with cool, wet

winters and hot, dry summers, plus high inter-annual variation, complicates efforts of water managers to meet all water needs during Dry years. Consequences of extreme Dry years for the Delta include declines in many native fish species, increased temperatures, increased nutrients, decreased turbidity, decreased freshwater inflow, and salinity intrusion (Bosworth et al., this issue; Hartman, Stumpner et al., this issue). Preserving water quality in the Delta during these conditions often requires large-scale management actions, including changing operation of water-control structures, diversions, and export pumps; installing salinity barriers; facilitating water-market exchanges; increasing salmon-hatchery production and trucking juvenile hatchery salmon downstream; and mandating urban water conservation.

Resource managers in California are increasingly concerned over cyanoHABs in the Delta (Brown et al. 2016; Cloern et al. 2020; Kudela et al. 2023) because water diversions from this region provide nearly 27 million people in the state with drinking water, and irrigate 3 million acres of farmland (Durand et al. 2020). The flow of water in the Delta is heavily managed from upstream dam releases, within-Delta barriers, and strict controls on the timing and magnitude of water exports pumped from the Central Valley Project (CVP) and State Water Project (SWP) from the Delta (Moyle et al. 2018). The exported water is used for drinking and agricultural uses in the San Joaquin Valley and southern California. While research studies on the occurrence and drivers of cyanoHABs have increased since their discovery in the Delta, a landscape-scale understanding of what drives cyanoHAB formation has not been achieved.

Drivers of *Microcystis*

Research before 2023 has identified several drivers considered important in bloom formation (Figure 2). CyanoHABs are controlled primarily by light, temperature, and nutrients, which limit their growth rates, and by water-movement processes that transport them out of the Delta (Reynolds 1987; Paerl and Huisman 2008; Berg and Sutula 2015; Boesch 2019). Environmental conditions favoring the formation of cyanoHABs

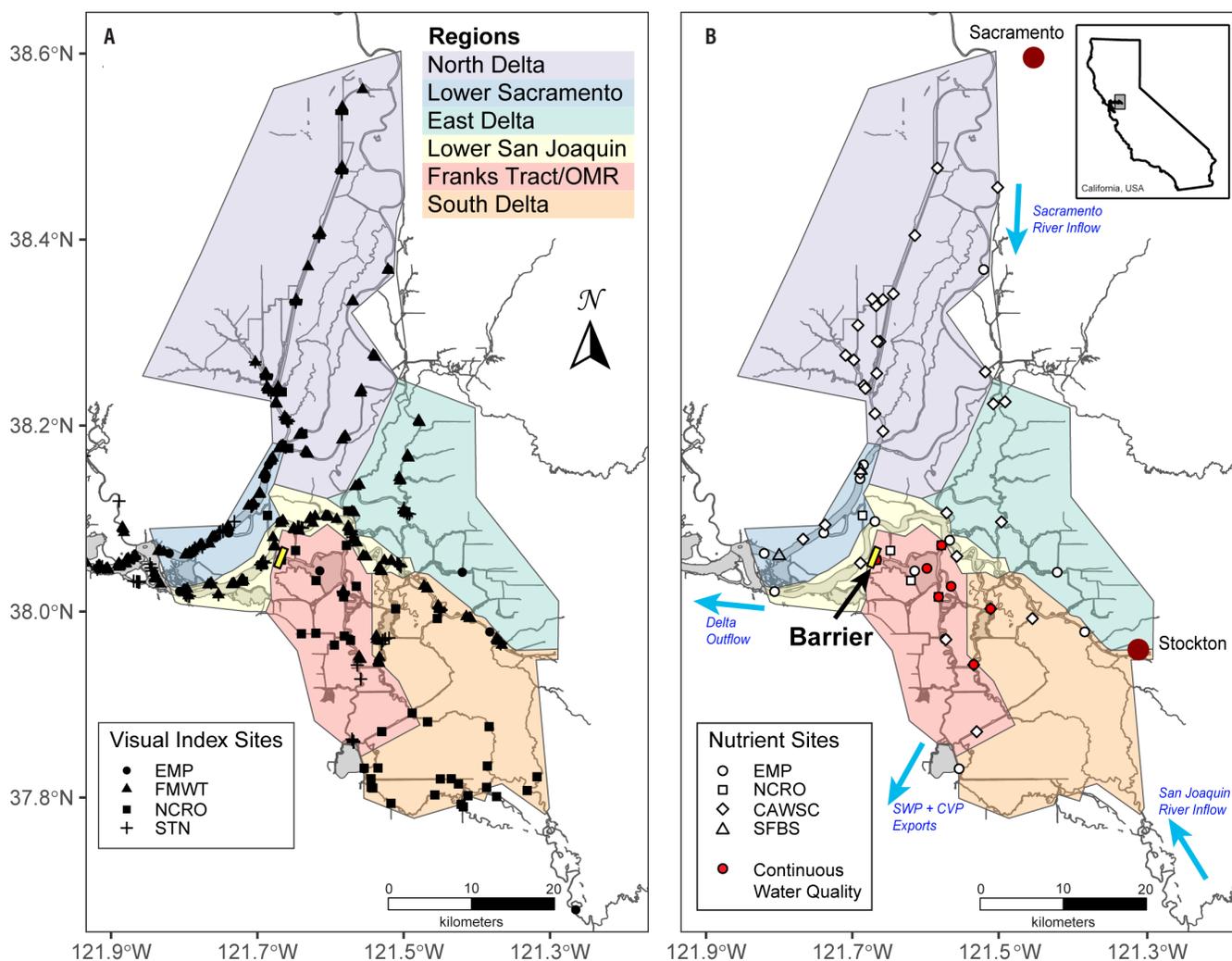


Figure 1 Maps showing the regions of the Delta used in this paper and monitoring stations used for (A) *Microcystis* visual index ratings and (B) nutrient and water-quality data along with major cities, the Emergency Drought Barrier (Barrier), and major flow parameters (Sacramento River inflow, San Joaquin River inflow, Delta outflow, and Central Valley Project (CVP) and State Water Project (SWP) exports).

in general, and *Microcystis* blooms in particular, include calm and stratified water, warm water temperatures, high availability of light, and an ample supply of nutrients (Paerl et al. 2011; Huber et al. 2012; Lehman et al. 2013; Lehman et al. 2018). Water temperature above 19 °C was considered a threshold for *Microcystis* detections in the Delta by Lehman et al. (2013). This temperature is often first exceeded in late spring, and water temperatures exceed 19 °C in the Delta throughout the summer months. Daytime water temperatures measured by long-term monitoring surveys have been increasing through time, though rates and amounts of increase vary

regionally and seasonally (Bashevkin et al. 2022a). Low light caused by high turbidity is thought to limit phytoplankton growth in the estuary in general (Jassby et al. 2002), with *Microcystis* being particularly reliant on high light conditions (Wu et al. 2009; Berg and Sutula 2015; Hellweger et al. 2022). However, turbidity in the Delta has been declining through time (Schoellhamer 2011), creating a more hospitable environment for *Microcystis*. Nutrients are seldom limiting in the Delta (Jassby et al. 2002; Kraus et al. 2017; Cloern 2019); however, nitrogen can be depleted during large blooms (Wilhelm et al. 2020), and the ratio of nitrogen to phosphorus and the form of

nitrogen present (ammonium vs. nitrate) are also believed to favor some phytoplankton taxa over others (Dahm et al. 2016; Glibert et al. 2016; Wan et al. 2019).

The more time available for cyanobacteria to grow and divide before being transported out of a system, the more likely they are to develop into a cyanoHAB. Changes in water residence time—the time a parcel of water remains in a given area (Monsen et al. 2002)—can therefore strongly influence bloom development (Bricker et al. 2008). Water residence time in the Delta is controlled by the combined interaction of tidal action, inflows, diversions, and physical characteristics of the Delta (Downing et al. 2016; Hammock et al. 2019). For simplicity, our conceptual model (Figure 2) represents all these hydrologic variables with the term “water movement.” On the larger scale, inflows dominate inter- and intra-annual differences in residence time, with major floods greatly reducing water residence time during the winter and spring months. Decreased flow typically occurs during July through September, which coincides with the occurrence of *Microcystis* blooms in the Delta (Lehman et al. 2013, 2018, 2022; Spier et al. 2013).

Here, we evaluate the effects of hydrologic variability (i.e., between dry and wet years) and water-management actions on the abundance of *Microcystis* in the Delta and apply our conceptual model (Figure 2) to a particular case study of drought management actions: the summer of 2021.

Case Study—Summer of 2021

While the conceptual model presented above provides some basis for predicting *when* *Microcystis* blooms will occur, predicting *how* these drivers will influence bloom development in the Delta during any particular year is still difficult. The problem becomes compounded when management actions occur only during Dry years when conditions are already highly favorable for bloom development. We present a case study of management actions and *Microcystis* blooms that occurred during the summer of 2021 to illustrate the difficulty in extracting the influence of management actions from other drivers.

Water year 2021 was the driest water year recorded in California since 1977, and 2021 followed the Dry year of 2020, meaning upstream reservoirs were already low. The unprecedented dry conditions required two major changes to water management that could have affected occurrence of cyanoHABs in the Delta. First, the State Water Resource Control Board granted a Temporary Urgency Change Order (TUCO) (SWRCB 2021) by allowing a relaxation of standards that the Water Rights Decision D-1641 (SWRCB 2021) required for the State Water Project (SWP) and Central Valley Project (CVP). TUCOs have been granted in the past in other Dry years, but each order has been unique and based on the unique hydrologic context. The 2021 TUCO had the following provisions:

- For June 1 through June 30, reduce the required minimum 14-day, running-average Delta outflow from 4,000 to 3,000 cubic feet per second ($\text{ft}^3 \text{s}^{-1}$) (from 113.3 to $85.0 \text{ m}^3 \text{ s}^{-1}$).
- For July 1 through July 31, reduce the required minimum monthly average Delta outflow from 4,000 to 3,000 $\text{ft}^3 \text{ s}^{-1}$ (from 113.3 to $85.0 \text{ m}^3 \text{ s}^{-1}$), with a 7-day running average of no less than 2,000 $\text{ft}^3 \text{ s}^{-1}$ ($56.6 \text{ m}^3 \text{ s}^{-1}$).
- For June 1 through July 31, limit the combined maximum export rate to no greater than 1,500 $\text{ft}^3 \text{ s}^{-1}$ ($42.5 \text{ m}^3 \text{ s}^{-1}$) when Delta outflow is below 4,000 $\text{ft}^3 \text{ s}^{-1}$ ($113.3 \text{ m}^3 \text{ s}^{-1}$).

Both decreased Delta outflow and decreased exports can increase water residence time in the South Delta and Franks Tract/Old-Middle River (OMR) regions (Figure 1), and increased water residence time is one of the major drivers hypothesized to increase *Microcystis* blooms (Lehman et al. 2022). Therefore, it was hypothesized that the TUCO might increase *Microcystis* blooms.

The second major action in response to the 2021 drought was the installation of an Emergency Drought Salinity Barrier in west False River (see Figure 1). The 2021 barrier was a temporary physical rock fill barrier that reduced the

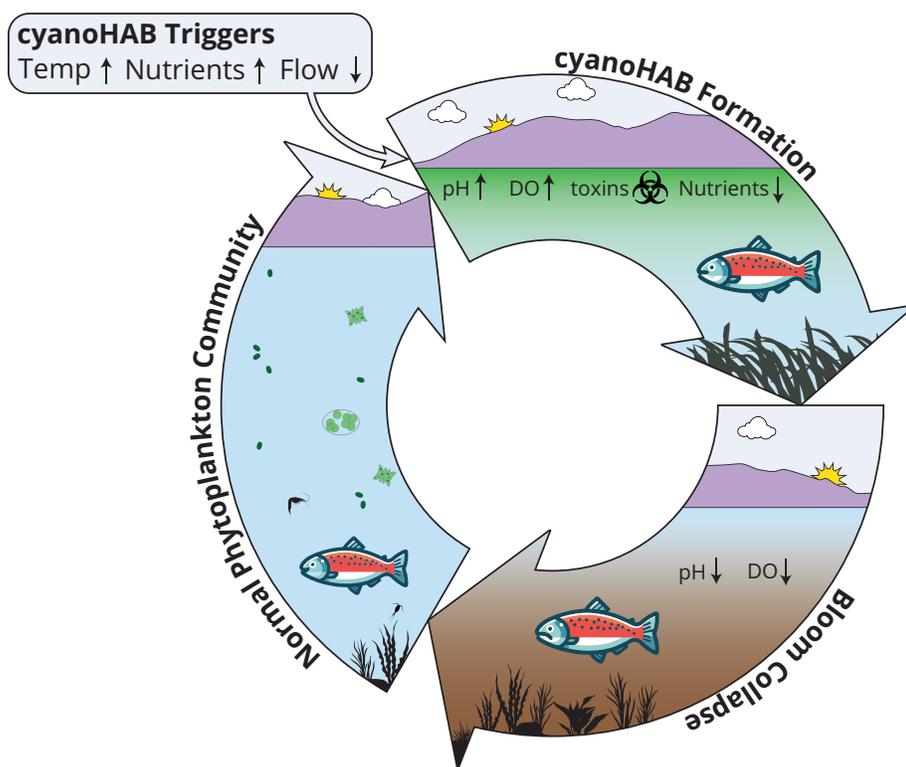


Figure 2 Conceptual model of factors hypothesized to trigger harmful algal blooms in the Delta and the effect of cyanoHABs on water quality in the Delta

intrusion of high-salinity water into the Franks Tract/OMR and South Delta regions. The barrier was installed in June of 2021 and was removed in October 2022. The barrier hydrologically closed west False River between Franks Tract and the San Joaquin River (Figure 1) and was structurally similar to the barrier installed in the same location in 2015.

Our research questions are as follows:

- How do *Microcystis* blooms vary across time and space in the Delta?
- What are the major drivers of *Microcystis* blooms in the Delta?
- Can we apply our knowledge of *Microcystis* drivers to assess how the water management actions that occurred in summer of 2021 affected *Microcystis*?

We use the example of HABs seen in the Franks Tract/OMR Region in the summer of 2021 to show

how different monitoring tools can be used to track the course of a cyanobacterial bloom and be used to assess the effects of these management actions.

METHODS

Drivers of *Microcystis* Analyzed from Visual Index Ratings

Most monitoring surveys that collect data on water quality and fisheries in the Delta also collect visual observations of *Microcystis* and other visually detectable algal blooms. Because *Microcystis* colonies are relatively easy to identify visually in the field, this visual ranking (*Microcystis* visual index rating) gives a general idea of when and where the most common harmful cyanobacteria in the Delta occur (Figure 3). While lacking quantitative rigor, these visual index ratings provide a spatially broad and temporally intense picture of patterns of *Microcystis* in the Delta that allow us to explore the relations between *Microcystis* blooms and environmental drivers.

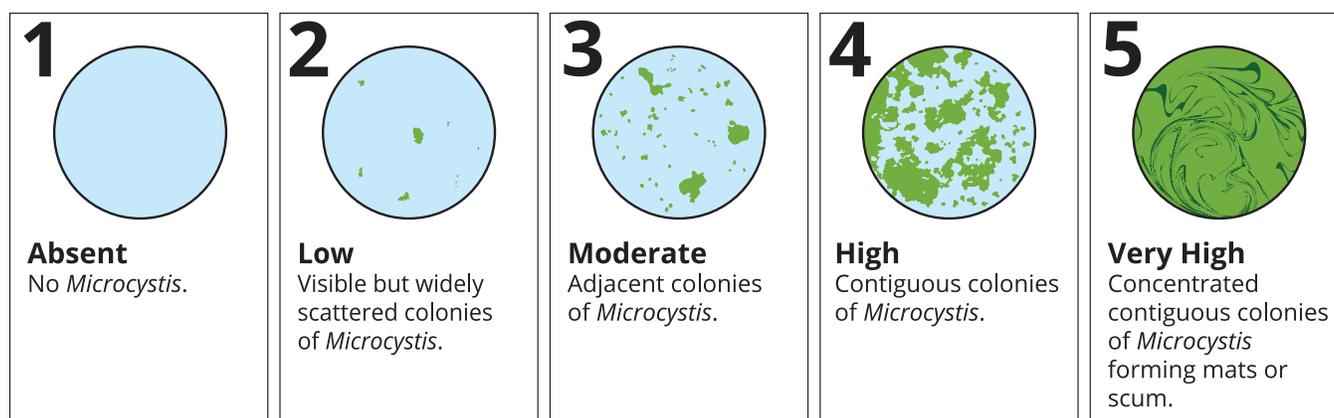


Figure 3 Scale for *Microcystis* visual index ratings used by monitoring programs in the Delta (Flynn et al. 2022)

Depending on the program that collects data, a visual index rating is taken either after a surface-water sample is brought on board a research vessel in a bucket, or when observers view surface water over the side of the boat. The *Microcystis* concentration is rated on a scale of 1 through 5, with 1 meaning “absent” and 5 meaning “very high” (Flynn et al. 2022). Visual index ratings were completed simultaneously with collections of data on water temperature, Secchi depth (as a measure of water clarity), and other water-quality parameters.

Visual assessment data came from four surveys: the Environmental Monitoring Program (EMP) conducted jointly by the California Department of Water Resources (CDWR), the California Department of Fish and Wildlife (CDFW), and the US Bureau of Reclamation (Reclamation); the Fall Midwater Trawl and Summer Towntnet surveys conducted by CDFW; and the South Delta monitoring program conducted by the North Central Region Office at CDWR. These data were subset to include only observations made during the summer and fall (June through October), because this is the time-frame during which cyanohABs usually occur. Datasets were also subset to include only observations in the regions outlined in Figure 1. Total observations varied by region of the Delta and years, but ranged from 360 to 1,372 data points per summer (Table 1). For more information about the surveys and their data collection methods, refer to the Supplemental Information and the integrated IEP Discrete Water Quality data

publication on the Environmental Data Initiative repository (<https://portal.edirepository.org/nis/mapbrowse?packageid=edi.731.5>; (Bashevkin et al. 2022b)).

Microcystis visual data were categorized for this analysis using a three-point scale to account for scale subjectivity. Values of 1 were re-coded as “absent,” values of 2 or 3 as “low,” and values of 4 or 5 as “high.” First, the annual pattern in the incidence of *Microcystis* among years across the entire Delta was assessed for 2014–2021. These years were chosen because they include the bulk of the available data, encompass the most recent two droughts, and include 2 years with emergency drought barriers. Then, the data were subset into regions (as defined in Figure 1) to determine whether any region had a disproportionately large change in *Microcystis* levels. Regions where frequency of *Microcystis* observations were particularly high received additional analysis.

The probability of having a high or low *Microcystis* visual index rating among water-year types were analyzed by fitting an ordinal model to the data using a Bayesian cumulative class ordinal model (Bürkner and Vuorre 2019) in the 'brms' R package (Bürkner 2017; Bürkner 2018). This model allowed us to assess the probability of three ranked ordinal classes (absent, low, and high *Microcystis* rating) against a variety of fixed and random predictor variables. Data were pre-processed to calculate the maximum *Microcystis* rating from each region and month from June through

Table 1 Number of *Microcystis* visual index ratings collected by all monitoring programs combined by season and year^a

Year	Water Year Type	East Delta	Lower Sac	Lower SJ	North Delta	Franks/OMR	South Delta
2007	Dry	22	45	63	40	18	25
2008	Critical	26	63	87	40	27	35
2009	Dry	30	62	90	67	29	38
2010	Below Normal	29	64	90	64	30	38
2011	Wet	30	64	90	112	30	38
2012	Below Normal	30	64	85	98	27	33
2013	Dry	30	64	90	111	30	38
2014	Critical	27	64	90	111	30	38
2015	Critical	35	84	113	117	40	43
2016	Below Normal	42	107	134	122	54	53
2017	Wet	44	109	133	135	95	125
2018	Below Normal	54	127	150	170	208	305
2019	Wet	51	242	144	384	177	231
2020	Dry	49	283	139	439	173	234
2021	Critical	42	221	110	345	126	190

a. Franks/OMR = Franks Tract and Old River, Middle River corridor; Lower Sac = Lower Sacramento River region; Lower SJ = Lower San Joaquin River region.

October for all years in the dataset. With these data, the probability of observing a *Microcystis* rating of absent, low, or high was modeled using water-year type and region as fixed effects, with a random intercept for station. Model code is provided in the Supplementary Information.

To assess the effect of change in Delta outflow, SWP and CVP exports, Secchi depth, and water temperature on the probability of detection of *Microcystis* in visual index rating surveys, the data were subset to the lower Sacramento River, lower San Joaquin River, Franks Tract/OMR, and South Delta regions. These regions have historically had higher cyanobacterial abundances than northern and western regions of the Delta (Lehman et al. 2005; Lehman et al. 2008; Mioni et al. 2012). Daily Delta outflow, San Joaquin River inflow, and SWP and CVP export data were compiled from CDWR's Dayflow model for the period 2014–2021 (CDWR 2002; CDWR 2022a). In the process of choosing predictor variables, we tested for high degrees of correlation between all variables, and found that San Joaquin River inflow and Delta outflow were too highly correlated (Pearson's correlation coefficient of 0.82) to include in the model, so we

used only Delta outflow, because changes to Delta outflow were included in the TUCO. Sacramento River inflow does not substantially influence water residence time in the South Delta and was not included as an explanatory variable in the final regression model (Hammock et al. 2019). Bayesian ordinal regressions were run on the probability of observing “absent,” “low,” or “high” *Microcystis* (response variables) as a function of Delta outflow, exports, Secchi depth, and water temperature at time of observation (predictor variables). Year (as a factor) and day of year were included as random-effect variables. Nutrient concentrations were not included in the model because nutrients are consumed during a bloom and thus are poorly correlated with *Microcystis* occurrence. All predictor variables were tested for collinearity before the model was run, and all predictor variables were normalized by subtracting the mean and dividing by the standard deviation. The regression was run using the *brm* function in the 'brms' R package, with 2,000 iterations per chain on two chains, and with the first 1,000 iterations discarded as warm-up (Bürkner 2018). All combinations of the four predictor variables (Delta outflow, exports, Secchi

depth, and water temperature) were run, and the best model was chosen as the model with the fewest predictors that had a Widely Applicable Information Criterion (WAIC) score within of 3 points of the lowest WAIC score. The best model was checked for model fit by using posterior predictive checks and examining diagnostic plots. This model was used to predict the difference in the probability of *Microcystis* observations at varying levels for each predictor in the top-ranked model. (Model code is provided in Appendix B.)

Nutrients

Discrete nutrient data (dissolved ammonium, dissolved nitrate + nitrite, and dissolved orthophosphate) were collected from three sources: the EMP conducted jointly by CDWR, CDFW, and Reclamation; the Central Delta monitoring program conducted by the CDWR's North Central Region office; and the San Francisco Bay Water Quality Survey (SFBS) conducted by the US Geological Survey (USGS) California Water Science Center (CAWSC). All nutrient grab samples collected by the EMP and the North Central Region Office were sampled at a depth of 1 m, while the samples collected by USGS were collected at various depths less than 5 m from the surface. For more information about the surveys, data collection methods, and quality assurance and quality control processing methods used for the nutrient data, refer to Appendix A and the integrated discrete data publication on the Environmental Data Initiative repository (Bashevkin et al. 2022b).

Data collected from 2014 through 2021 from the three surveys listed above were acquired through direct data requests or downloaded from either the 'discretewq' data package in R (Bashevkin et al. 2022b), CDWR's Water Data Library (CDWR 2022b), or the National Water Quality Monitoring Council's Water Quality Portal (NWQMC 2021). Data were integrated into one dataset, limiting the stations to only those where all three nutrient parameters (dissolved ammonium, dissolved nitrate+nitrite, and dissolved orthophosphate) were collected (Table A1). Average concentration across years by month and region were plotted to visually compare seasonal and regional variation

in nutrients and assess potential for nutrient limitation.

The potential for nitrogen or phosphorus limitation across the Delta in all reporting years was assessed with natural log-transformed dissolved nitrogen to dissolved phosphorus (N:P) ratios (Isles 2020). While nutrient limitation occurs only when ambient concentrations begin to limit cell divisions (Chorus and Spijkerman 2021), N:P ratio can be used to infer what nutrient may become limiting first. Only dissolved nutrient data were available for this analyses, so we could not calculate ratios of total nitrogen to total phosphorus. To calculate dissolved inorganic N:P ratio, we converted total dissolved inorganic nitrogen (nitrate and ammonium) to molar mass N, and total dissolved inorganic phosphorus to molar mass P. The molar mass N and molar mass P were then natural log-transformed ($\ln(N:P)$). We compared the calculated N:P ratio to the Redfield Ratio (16:1; Falkowski 2000) to characterize potential nutrient limitations. A ratio of $> 16:1$ indicates that phosphorus may become limiting before nitrogen, while a ratio $< 16:1$ indicates that nitrogen may become limiting before phosphorus (Reynolds 1999). However, this ratio is not fixed among algal cells, and limitation by only N or only P limitation can begin to occur within a range of ratios, depending on the physiological conditions of the cells N:P. At ratios near 16, N and P co-limitation is common, and potential limitation of a single element becomes stronger the further the measured ratios deviate from 16:1 (Guildford and Hecky 2000; Ptacnik et al. 2010). Differences in nutrient concentrations among years were tested with a mixed-effects model. Nutrient concentrations were \log_{10} -transformed and separated into spring (April, May, June) and summer (July, August, September) seasons. Differences in average concentrations were modeled with an interaction between region and year, and a random intercept for sampling site using the *lmer* function in the 'lme4' package in R (Bates et al. 2022). A post-hoc test was conducted to test for differences between years nested within each region using the 'emmeans' package in R (Lenth et al. 2022). Code for this analysis can be found in the Supplementary Information.

Monitoring Methods to Track the Bloom of 2021

Fluoroprobe

The EMP and USGS used vessels equipped with high-resolution sensors that collect data continuously on water quality and phytoplankton community composition while underway. During these surveys, the EMP monitors water quality using a YSI EXO2 water-quality sonde (Xylem, Inc.) to measure pH, turbidity, specific conductance, chlorophyll-*a* (with the Total Algae™ sensor), dissolved oxygen (DO), and water temperature. The EMP and USGS monitor phytoplankton community composition using a FluoroProbe instrument (bbe Moldaenke GmbH, Schwentinal, Germany) that differentiates among cyanobacteria, diatoms, green algae, and cryptophytes, based on the wavelength of the fluorescence given off by each taxonomic group's characteristic photo-pigments (Kring et al. 2014). USGS conducted spatially continuous mapping surveys in May, July, and October 2021; EMP discrete surveys are conducted monthly throughout the year. Each month, these agencies covered approximately 350 miles of channels in the Delta throughout 3 to 4 consecutive days.

FluoroProbe data collected by the EMP and USGS were spatially aligned to a common set of polygons to enable consistent comparisons across sampling areas and dates. Polygons were approximately 150 m in length, and the median value of all points within a polygon was calculated. Interpolated values were calculated in ArcGIS using the Spline with Barriers tool (Terzopoulos and Witkin 1988) and were used to create a continuous map of values (e.g., the concentration of pigments from cyanobacteria) across the mapped domain.

Satellite Remote Sensing

Satellite data, available from the San Francisco Estuary Institute's HAB Satellite Analysis Tool (<https://fhab.sfei.org/>, SFEI 2022), can provide estimates of cyanoHAB abundance with higher spatial and temporal coverage than grab samples and visual observations. Satellite imagery is collected by the Ocean Land Color Instrument on the Copernicus Sentinel-3 mission (pixel size

300 m by 300 m). The Cyanobacterial Index, CI_{cyano} , algorithm (Wynne et al. 2018) is applied to the Ocean Land Color Instrument data to estimate cyanoHAB abundance in the upper portion of the water column by analyzing wavelengths of light that interact strongly with chlorophyll-*a* and phycocyanin, an accessory pigment in photosynthesis specific to cyanobacteria. The CI_{cyano} algorithm returns estimates of cyanobacterial abundance in an exponential, satellite-specific, unitless scale.

Because of the limitations of the satellite-based sensor in distinguishing subtle differences in reflectance from cyanobacteria at levels that are very low (a CI_{cyano} of 6.310×10^{-05} is near natural background levels of cyanobacteria) or very high (CI_{cyano} of 6.327×10^{-02} in extremely dense scums), the minimum and maximum detectable levels have a smaller range than are possible using traditional water-grab samples. Because the smallest pixel size available is 22 acres, only larger areas of open water, such as Franks Tract, can be analyzed. Smaller sloughs are not large enough for accurate classification. Further information on these methods is detailed on the National Ocean Service website: <https://coastalscience.noaa.gov/research/stressor-impacts-mitigation/hab-monitoring-system/more-information/>.

Satellite mosaics of rasterized CI_{cyano} data across the Lower San Joaquin, Franks Tract/OMR, and South Delta (Clifton Court Forebay) regions for June through October in 2020 and 2021 were downloaded from the San Francisco Estuary Institute's HAB Satellite Analysis Tool (SFEI 2022). Raster pixels for two open-water regions in the Delta—Franks Tract and Mildred Island— were extracted from each file using the *exact_extract* function in the 'exactextractr' R package, version 0.7.1 (Baston 2021). These two regions were selected because the hydrology of Franks Tract is directly influenced by the barrier, while Mildred Island is not influenced by the barrier and is used to compare phytoplankton dynamics in Franks Tract with another flooded island. The two open-water regions were defined using polygons derived from CDFW's shapefile of Delta

waterways and expanded by 200 m around their perimeters to account for the large raster pixels.

Pixels were categorized into four CI_{cyano} categories (Low, Moderate, High, and Very High) based on the World Health Organization's (WHO's) recreational guidance level thresholds (WHO 2021). Additionally, pixels that were below the detection limit for the imagery-processing method ($CI_{\text{cyano}} \leq 6.310 \times 10^{-05}$) were categorized as "Non Detect." Including only pixels that were completely within one of the polygons of the two regions, the numbers of pixels within the "Non Detect," "Invalid," missing, and four CI_{cyano} categories were counted for each region and raster image. Using only days when there were greater than 25% valid pixels within a region, the time-series of pixel counts were visualized using area plots for each region and year.

Continuous Water-Quality Data

CDWR and USGS (US Geological Survey 2023) maintain a network of water-quality sondes and streamgages that collect data continuously (i.e., every 15 min) across the Delta. These stations measure water temperature, specific conductance, flow, DO, chlorophyll fluorescence (fCHL), turbidity, and pH using Yellow Springs Instruments (YSI) EXO2 sondes (Table 2). We requested quality-control data from CDWR personnel when available, and queried provisional data from the California Data Exchange Center (CDEC) if finalized data were not available. To assess how cyanoHABs affect water-quality parameters, we plotted the daily mean of data collected at stations in the South and Central Delta that experienced cyanobacteria blooms in 2021 versus day of the year for the past 7 years (2015 through 2021). We did not include 2014 in this analysis because the water quality station at Frank's Tract (FRK) was not installed until 2015.

Toxins

Regular monitoring for cyanotoxins has not been implemented in the Delta; however, two special studies of cyanotoxin dynamics and event-based monitoring provided coverage of the region that surrounds Franks Tract during the summer of 2021. The two sources of data are:

A special study conducted by Ellen Preece (Robertson-Bryan, Inc.), Tim Otten (Bend Genetics, LLC), and Janis Cooke (Central Valley Regional Water Quality Control Board; CVRWQCB) included collection of water samples for cyanotoxin analyses. This study was supported by the Delta Regional Monitoring Program and the State Water Resources Control Board Freshwater Harmful Algal Bloom Program. A single subsurface water-grab sample was collected from the eastern side of Franks Tract on July 2, 2021, and again on August 6, 2021. Bend Genetics, LLC (Sacramento, California) lysed and analyzed the samples for total microcystins/nodularins, using the enzyme-linked immunosorbent assay that targets the 3-amino-9-methoxy-2,6,8-trimethyl-10-phenyl-4,6-decadienoic acid region of microcystin (the ADDA ELISA method; USEPA 2016).

A special study of bioaccumulation of cyanotoxins in invertebrates in the Delta was conducted by David Senn (San Francisco Estuary Institute), Janis Cooke (CVRWQCB), Ellen Preece (Robertson-Bryan, Inc.), and Timothy Otten (Bend Genetics, LLC) (Senn et al. 2020). This study was funded by a State of California Proposition 1 grant administered by the Department of Fish and Wildlife Ecosystem Restoration Program (grant #Q2096021; Senn et al. 2020). Bend Genetics used ADDA ELISA (USEPA 2016) to collect and analyze whole-water samples for microcystins. Two stations—DHAB007 (in the western side of Franks Tract), and DHAB008 (in Old River)—provided data relevant to the Franks Tract bloom (Table 3).

Preliminary data from water-quality samples from both special studies were shared by the principal investigators and are presented here and in the accompanying data publication (Hartman et al. 2023).

RESULTS

Temporal and Spatial Trends

When visually assessing the relative frequency of *Microcystis* visual index ratings (absent, low, and high) (see Figure 4), the 3 water years classified as Wet during the time-series (2011, 2017, and 2019) have much lower frequency of

Table 2 Stations used for continuous water-quality analysis^a

CDWR Station Code	Operator	USGS Station ID	Station Name	Latitude	Longitude	Sensors
FAL	USGS/CDWR ¹	11313440	False River near Oakley	38.05547	-121.667	fCHL, DO, SC, Turbidity, Water Temp
HLT	USGS/CDWR ¹	11312685	Middle River near Holt	38.00310	-121.5108	fCHL, DO, Turbidity, Water Temp
HOL	USGS/CDWR ¹	11313431	Holland Cut Near Bethel Island	38.01582	-121.582	DO, SC, Turbidity, Water Temp
OSJ	USGS/CDWR ¹	11313452	Old River at Franks Tract near Terminous	38.07125	-121.578	fCHL, DO, SC, Turbidity, Water Temp
FRK	CDWR	NA	Franks Tract Mid Tract	38.04642	-121.598	fCHL, DO, pH, SC, Turbidity, Water Temp

a. fCHL = Chlorophyll fluorescence; DO = dissolved oxygen; SC = specific conductance; Temp = temperature. Data from USGS National Water Information System (USGS 2023).

Table 3 Locations of Cyanotoxin monitoring data

Station	Latitude	Longitude	Region
DHAB007	38.0486	-121.6234	Franks Tract, western side
DHAB008	37.9641	-121.5737	Old River near Holland Tract
Franks Tract	38.0379	-121.586	Franks Tract, eastern side

Microcystis observations; years classified as Below Normal, Dry, or Critical have higher *Microcystis* observations. The model that predicts incidence of *Microcystis* by region indicated a significantly higher probability of absence and lower probability of low *Microcystis* in wet years in all regions (Figure 5; Table 4). Of the remaining water year types, Critical years tended to have higher probabilities of observing *Microcystis* than Dry years, which tended toward higher incidence of *Microcystis* than Below-Normal years, but these differences were not significant at the 95% credible interval.

Microcystis Visual Index Rating Data

After running Bayesian mixed models for all possible combinations of Delta outflow, SWP and CVP exports, water temperature, and Secchi depth against the probability of *Microcystis* observation in the South Delta, San Joaquin River, lower Sacramento River, and Franks Tract/OMR regions (Figure 1) during the summer and fall (Hartman et al. 2023), code for all tested models provided in Appendix B), two models had equal support when ranked with WAIC (Table 5).

The two models were Exports + Temperature + Secchi + Outflow, and Exports + Temperature + Secchi. Because the addition of Outflow did not significantly improve the model, we chose the model without outflow for further analysis.

The best model (Figure 6; Table 6) showed that as water temperature increases, the probability of “0 *Microcystis* absent observations” declines, and the probability of “high *Microcystis* observations” increases. Low levels of *Microcystis* increase between 15 and 25 °C, then decrease above 25 °C as high *Microcystis* increases steeply. A similar pattern occurs with Secchi depth. As Secchi depth increases, the probability of no *Microcystis* observations declines, and the probability of high *Microcystis* observations increases. Low levels of *Microcystis* increase between 0 and 225 cm, then decrease above 225 cm as high *Microcystis* increases. As project exports increase, probability of no *Microcystis* increases, while probability of low and high *Microcystis* decrease. This is a relatively flat relation, with an increase in probability of absence of only 4% to 8% (depending on day of the year), with a change in

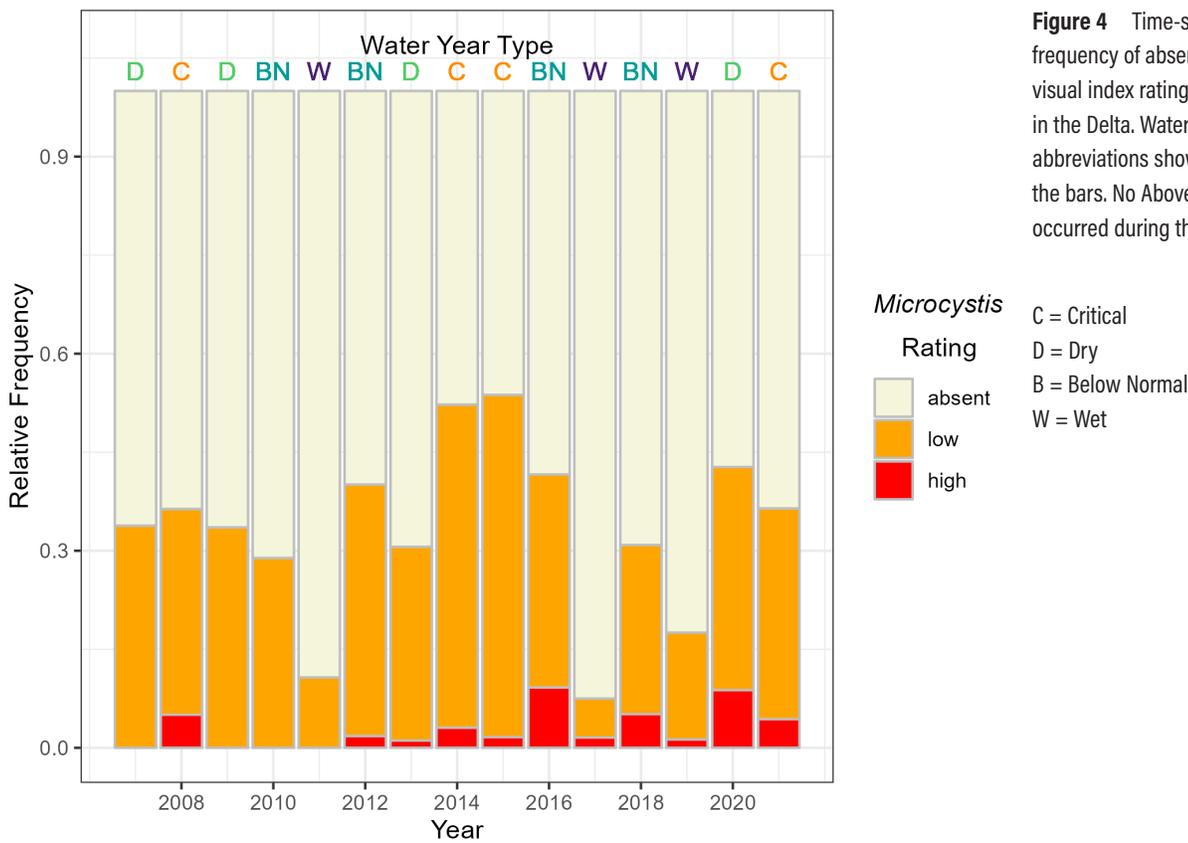


Figure 4 Time-series of relative frequency of absent, low, and high visual index ratings of *Microcystis* in the Delta. Water Year Type abbreviations shown at the top of the bars. No Above-Normal years occurred during this period.

Table 4 Bayesian ordinal regression parameters estimating *Microcystis* visual index rating from region and water year type. Model parameter estimates, estimate standard error, lower and upper 95% credible interval (CI) and Rhat. Rhat indicates whether chains have converged, with Rhat >1.1 indicating chains have not converged and model fit may be poor. Code for analysis available in Appendix B.

Parameter	Estimate	Estimate error	Lower 95% CI	Upper 95% CI	Rhat
Intercept[Absent:Low]	0.95	0.23	0.51	1.40	1.0005
Intercept[Low:High]	2.85	0.23	2.40	3.32	1.0002
RegionFranksDOMR	1.80	0.26	1.29	2.31	1.0001
RegionLowerSac	0.70	0.27	0.18	1.23	1.0012
RegionLowerSJ	1.70	0.26	1.19	2.21	1.0003
RegionNorthDelta	-0.32	0.26	-0.84	0.20	1.0001
RegionSouthDelta	1.55	0.25	1.05	2.04	1.0001
Yr_typeCritical[Absent:Low]	0.57	0.07	0.43	0.72	1.0003
Yr_typeCritical[Low:High]	-0.11	0.10	-0.30	0.09	1.0004
Yr_typeDry[Absent:Low]	0.14	0.07	0.01	0.28	1.0000
Yr_typeDry[Low:High]	-0.04	0.09	-0.22	0.14	1.0001
Yr_typeWet[Absent:Low]	-1.07	0.07	-1.21	-0.93	1.0000
Yr_typeWet[Low:High]	-0.71	0.12	-0.95	-0.49	1.0005
sd(Intercept)	0.54	0.05	0.45	0.65	1.0008

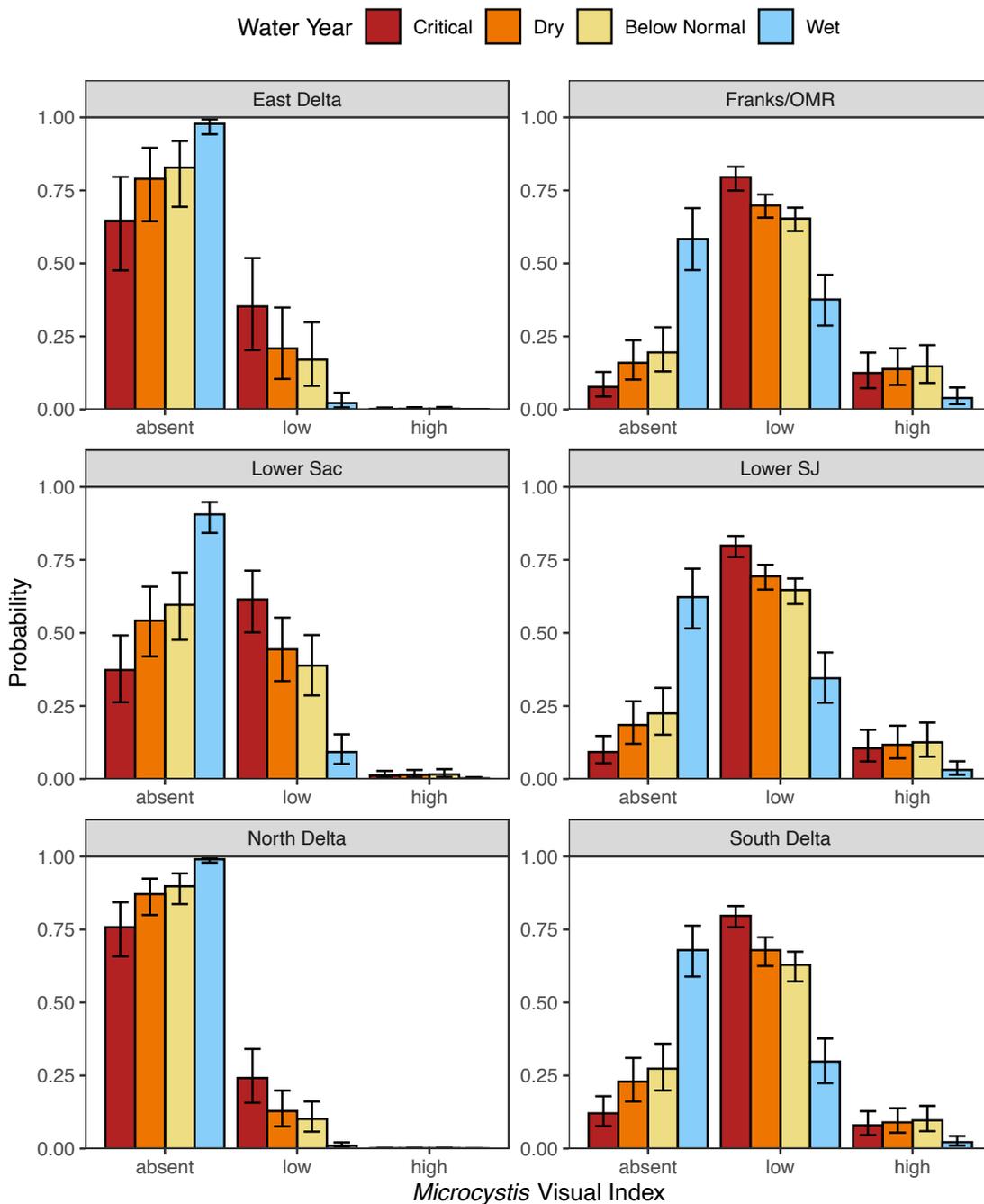


Figure 5 Model results predicting the probability of a given *Microcystis* visual index rating (absent, low, high) occurring during each Sacramento Valley Water Year Hydrological Classification Index in each region from 2007 to 2021 during the months of June through October. Error bars show the 95% credible interval.

Table 5 Model comparison of all Bayesian mixed models predicting presence of *Microcystis* (Absent, Low, or High) in the integrated dataset of visual assessment data (Hartman et al. 2023). Code for model available in Appendix A.^a

Model Terms	WAIC	SE WAIC	Delta WAIC
Temperature + Secchi + Exports	2023.30	55.74	
Temperature + Outflow + Secchi + Exports	2024.64	55.87	1.33
Temperature + Outflow + Secchi	2053.51	56.12	30.20
Temperature + Secchi	2054.05	56.03	30.75
Temperature + Outflow + Exports	2082.09	55.16	58.78
Temperature	2114.48	55.58	91.18
Temperature + Outflow	2115.93	55.66	92.63
Secchi + Exports	2139.95	55.33	116.65
Outflow + Secchi + Exports	2142.99	55.45	119.69
Secchi	2159.43	55.76	136.12
Outflow + Secchi	2162.42	55.63	139.12
Exports	2268.79	53.88	245.49
Exports + Outflow	2270.83	53.95	247.53
Outflow	2288.82	54.36	265.52

a. WAIC = Widely Acceptable Information Criterion. SE WAIC = Standard error in WAIC. Delta WAIC = Difference in WAIC between model and best model. The model with the lowest WAIC is considered the best fit.

Table 6 Top ranked model of frequency of *Microcystis* visual index rating in the South Delta from 2014–2021 with model parameter estimates, estimate standard error, lower and upper 95% credible interval (CI) and Rhat. Rhat indicates whether chains have converged, with Rhat >1.1 indicating chains have not converged and model fit may be poor. Code for analysis available in Appendix B.

Parameter	Estimate	Estimate error	Lower 95% CI	Upper 95% CI	Rhat
Intercept[Absent:Low]	-0.991	0.564	-2.114	0.123	1.001
Intercept[Low:High]	3.482	0.580	2.365	4.628	1.001
Water Temperature	1.232	0.113	1.016	1.458	1.000
Project Exports	-0.837	0.172	-1.168	-0.508	1.001
Secchi Depth	0.573	0.069	0.442	0.705	1.000
Year	1.538	0.472	0.899	2.700	1.001
Day of Year	1.822	0.171	1.504	2.171	1.005

exports from 42.5 to 85 m³ s⁻¹, and an additional increase of 10% to 16% with a change in exports from 85 to 170 m³ s⁻¹. The wide credible intervals on Figure 6 indicate that very large changes in outflow are necessary for a meaningful change in probability of *Microcystis*.

Nutrients

Nitrogen and phosphorus concentrations varied by region and season, with the highest concentrations of ammonium in the North Delta and confluence (Figure 7, note varying y-axes), and the highest concentrations of nitrate and

orthophosphate in the South Delta (Figures 8 and 9, note varying y-axes). There was no consistent pattern between water year type and ammonium concentration among seasons or regions. Sometimes wet years had higher ammonium (Franks/OMR, summer 2019 vs. summer 2014, $p < 0.05$, Table A5), and sometimes Critical years had higher ammonium (North Delta, spring 2019 vs. spring 2014, $p < 0.05$, Table A6). For nitrate, the pattern was more consistent with the Critical years of 2014 and 2015 having higher ($p < 0.05$) nitrate concentrations than many Wet and Below Normal water years in

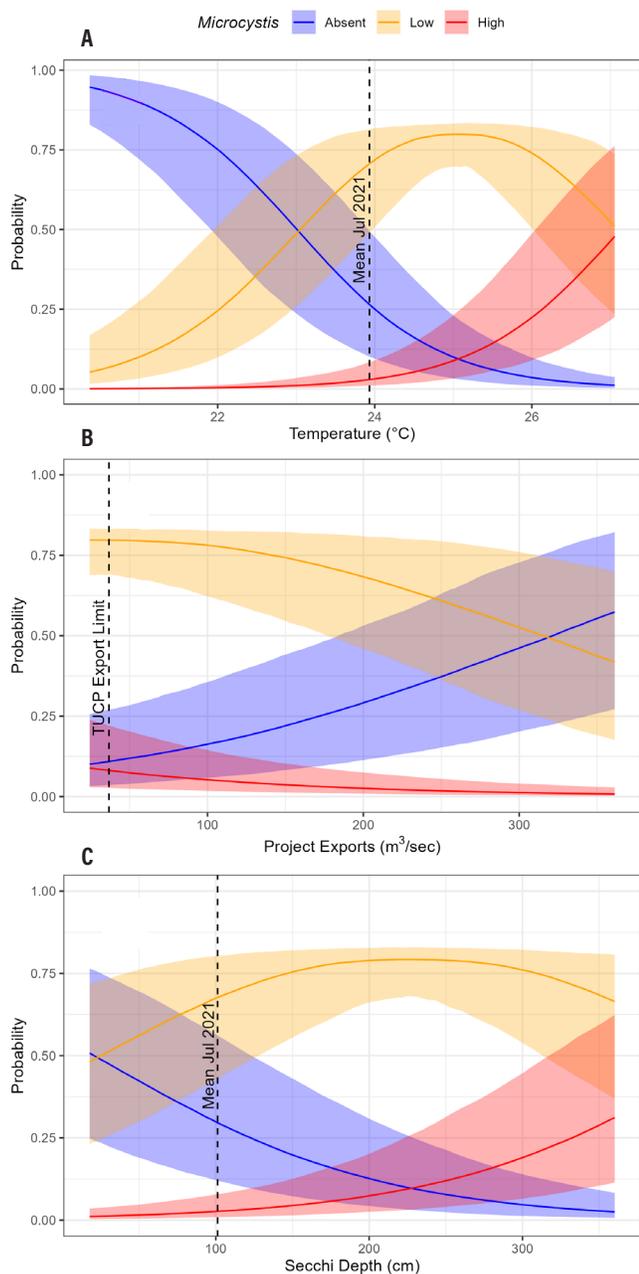


Figure 6 Conditional plots showing the predicted value (+/- 95% credible interval) of *Microcystis* with varying rates of (A) water temperature, (B) combined State Water Project and Central Valley Project water exports and (C) Secchi depth, as derived from Bayesian mixed model of environmental drivers (Table 5).

both spring and summer (Table A7 and Table A8). Nitrate concentrations in summer 2021 are lower than the summer concentrations in 2014 and 2015, the other Critical water years, likely as a result of the Regional San WWTP upgrade, which came online in 2021 and reduced inorganic nitrogen loads into the Sacramento River. However, orthophosphate was never significantly higher in a Wet year than a Critical year (Table A9 and Table A10). Average dissolved inorganic nitrogen to phosphorus (N:P) ratios were mostly below the Redfield ratio (16:1) (Figure 10). In all water year types the low N:P ratio suggests that nitrogen would become limiting before phosphorus, if limiting concentrations were reached.

2021 Case Study

Toxin Analysis

Microcystin concentrations in the Franks Tract/OMR region in the vicinity of the bloom were relatively low, mostly below $0.8 \mu\text{g L}^{-1}$, which is the threshold concentration used by the California Cyanobacterial Harmful Algal Bloom (CCHAB) network for recommending that a “Caution” advisory be issued (CCHAB Network 2022). The highest concentration of microcystins ($2.99 \mu\text{g L}^{-1}$) measured during the bloom occurred on August 11 at station HAB008 on the Old River (Table 3), south of the main bloom in Franks Tract (Figure 11).

Fluoroprobe Data

The temporal progression of the Franks Tract bloom and cyanobacteria in the surrounding waterways was captured with boat-based mapping surveys that measured cyanobacterial fCHL with a Fluoroprobe. In early June, Fluoroprobe cyanobacterial fCHL was $\leq 10 \mu\text{g L}^{-1}$ across the Franks Tract/OMR Region (Figure 11). During July 15–19, 2021, cyanobacterial fCHL in Franks Tract increased above $10 \mu\text{g L}^{-1}$, but surrounding rivers and channels remained below $10 \mu\text{g L}^{-1}$. Cyanobacterial fCHL eventually exceeded $50 \mu\text{g L}^{-1}$ in Franks Tract during July 26–27, 2021, and remained above $40 \mu\text{g L}^{-1}$ during the August 2021 surveys. Cyanobacterial fCHL also exceeded $20 \mu\text{g L}^{-1}$ in the San Joaquin River and Old River during the August 2021 surveys. By the time of

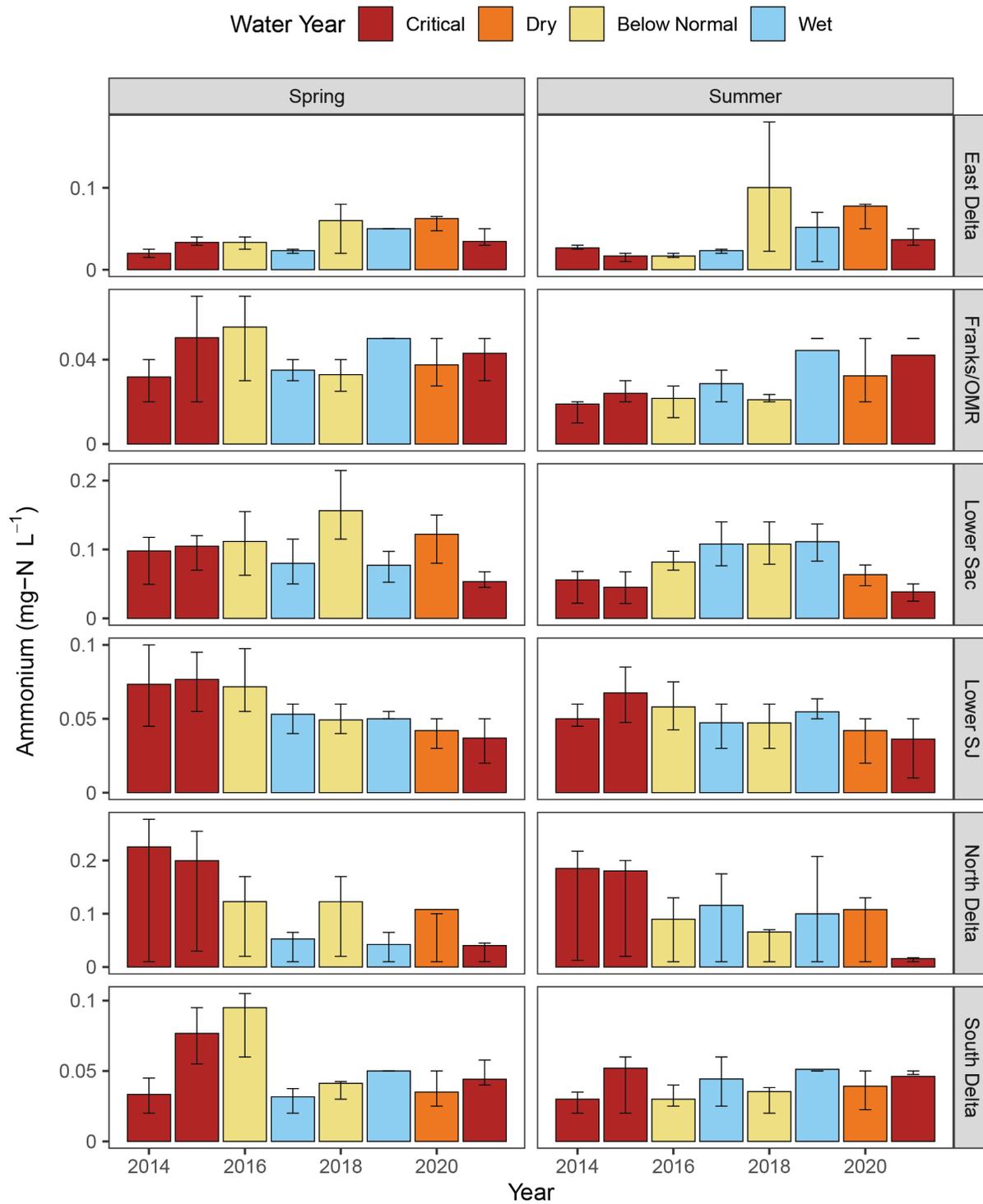


Figure 7 Average concentration (mg-N L⁻¹) of dissolved ammonium, by season, region, and year for calendar years 2014–2021. Error bars represent 25% and 75% quartiles. Note the different y-axes between panels.

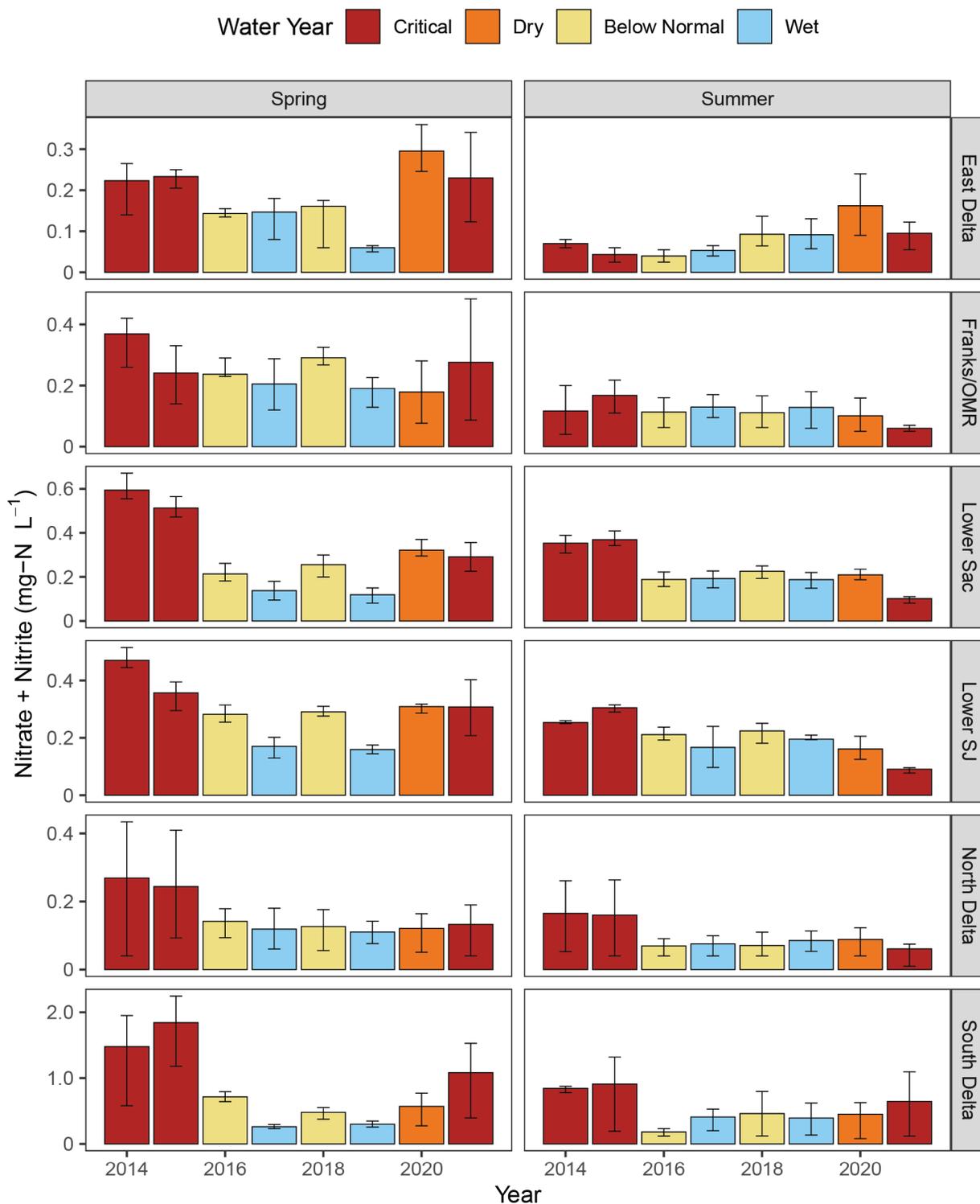


Figure 8 Average concentration (mg-N L^{-1}) of dissolved nitrate + nitrite, by season, region, and year for calendar years 2014–2021. Error bars represent 25% and 75% quartiles. Note the different y-axes between panels.

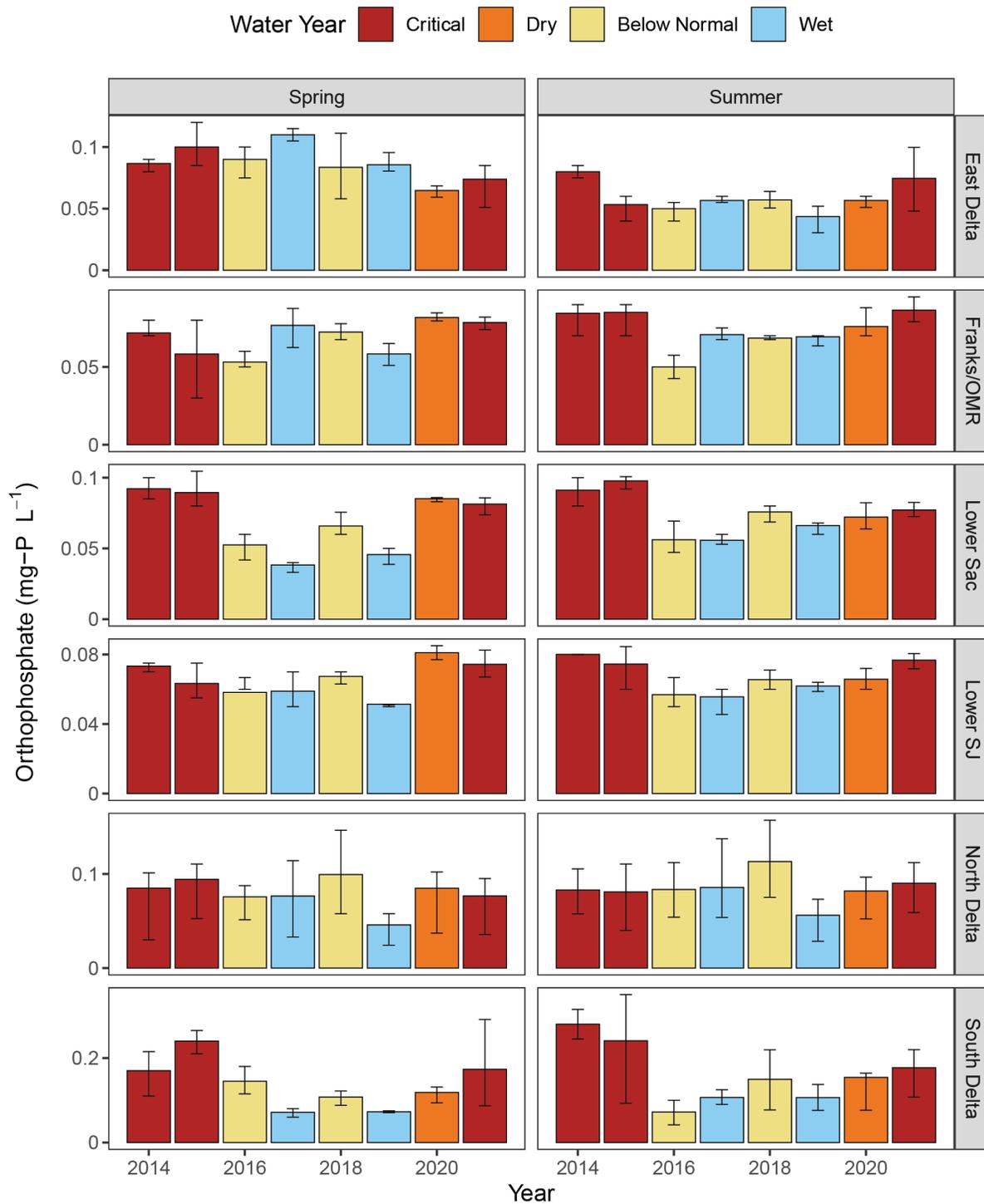


Figure 9 Average concentration (mg-P L⁻¹) of dissolved orthophosphate, by season, region, and year for calendar years 2014-2021. Error bars represent 25% and 75% quartiles. Note the different y-axes between panels.

the September 10–14, 2021, surveys, the bloom had ended, and cyanobacterial fCHL was below $5 \mu\text{g L}^{-1}$.

Satellite Data

The July–August 2021 cyanobacteria bloom in Franks Tract documented by the boat-based mapping surveys was also observed in the satellite data (Figure 12). The bloom of 2020 was more severe than in 2021. During the peak of this bloom from mid-July through mid-August 2021, at least one-third of the valid pixels were in the High or Very High categories, with a maximum of 90% in late July 2021. Spatially, the pixels with the highest CI_{cyano} categories were concentrated in the southeast corner of Franks Tract throughout the bloom in 2021 (Figure 13). In contrast, almost all pixels were in the Non-Detect category within Franks Tract in 2020, without a cyanobacteria bloom (Figure 12).

Satellite data indicated that the nearby comparison site at Mildred Island had cyanobacteria blooms in 2020 and 2021 (Figure 12). The bloom in 2020 was more severe than in 2021. Mildred Island had some instances in 2020 when at least half of the valid pixels were in the High CI_{cyano} category, with a maximum of 80% at the beginning of September. In 2021, the percentage of pixels categorized as High remained below 20%. There were a few gaps in the satellite dataset at the end of August and beginning of September 2020 that may have obscured the extent of the cyanobacteria blooms in Mildred Island. These gaps extended for longer than a week and may have occurred during times when there was dense smoke in the area from regional wildfires.

Water Quality

A focused assessment of continuous water-quality data collected at Franks Tract and adjacent sites (Figure 1) over the summer of 2021 indicated substantial differences in parameters linked to increased photosynthesis, i.e., DO and pH, compared to previous years. The DO (Figure 14) and pH concentrations (Figure 15) in Franks Tract began increasing in July 2021, and by August 2021, pH levels and DO concentrations were the highest

recorded since 2015. DO concentrations were also substantially higher during July and August ($>12 \text{ mg L}^{-1}$) at the Franks Tract station (FRK) than at several adjoining monitoring stations (Figure 14). The maximum daily pH peaked in early September 2021 before declining rapidly (Table A2), while the DO maxima was reached later in September 2021 before also declining (Table A3).

During the bloom, daily DO maxima peaked at more than 200% saturation with atmospheric O_2 and averaged more than 170% saturation for the months of July and August 2021, the highest on record for this station (Table A3). Values of DO saturation greater than 100% indicate high rates of photosynthesis in Franks Tract, from production of phytoplankton and aquatic vegetation. Daily chlorophyll fluorescence concentrations measured using sondes were higher in 2021 than in 2020 (Table A4) but were lower than the highest concentrations measured using the FluoroProbe (Figure 11, Figure A1). Small spikes of chlorophyll-*a* ($<10 \mu\text{g L}^{-1}$) detected at nearby stations (Figure A1) were much less than concentrations observed by the FluoroProbe (present a range of observed concentration $>10 \mu\text{g L}^{-1}$). Nitrogen concentrations declined sharply during the summer across the Delta, falling below the reporting limit in Franks Tract (Figure 16), while orthophosphate concentrations remained relatively stable (Figure 17).

DISCUSSION

We found that *Microcystis* was more common in the Delta when low flows, high water clarity, and high water temperature predominated. This finding aligns with both our conceptual model (Figure 2) and previous research (Lehman et al. 2013, 2018, 2022). By analyzing records of *Microcystis* visual index ratings (Flynn et al. 2022), we achieved a higher spatial resolution, higher temporal resolution, and a longer dataset (15+ years) than previous studies of cyanoHABs in the Delta (e.g., Lehman et al. 2022). This work demonstrates how modern *in situ* monitoring data (such as the FluoroProbe data) and remote sensing tools (such as the Ocean Land Color Instrument

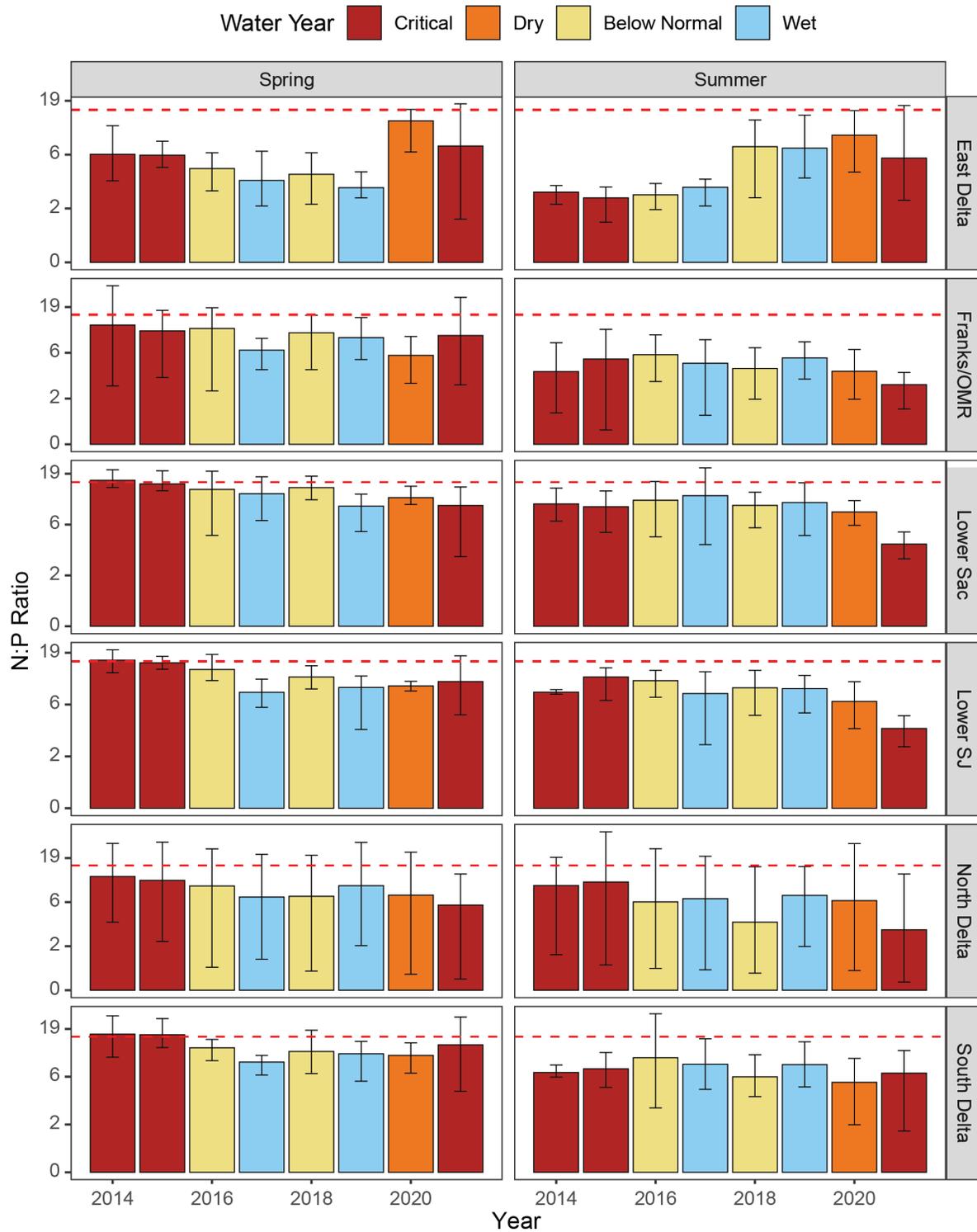
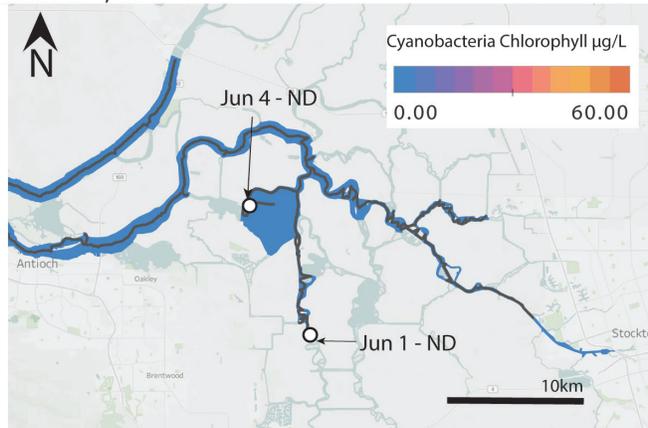
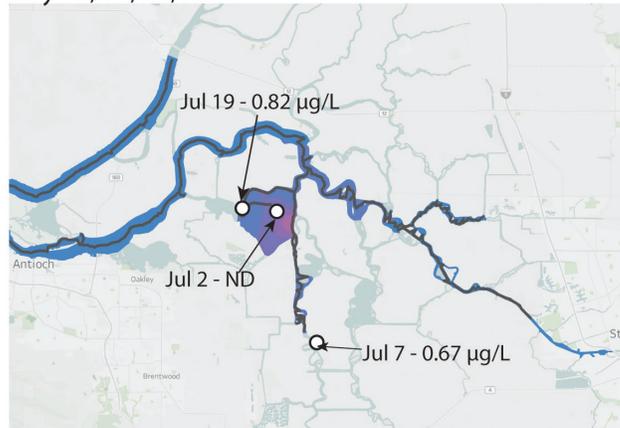


Figure 10 Mean N:P ratios by season, region, and year for all surveyed years in the Delta (calendar years 2014-2021). Note that the y-axis is spaced on the log scale. The error bars represent the maximum and minimum values. The red-dashed horizontal line is the Redfield ratio (16:1).

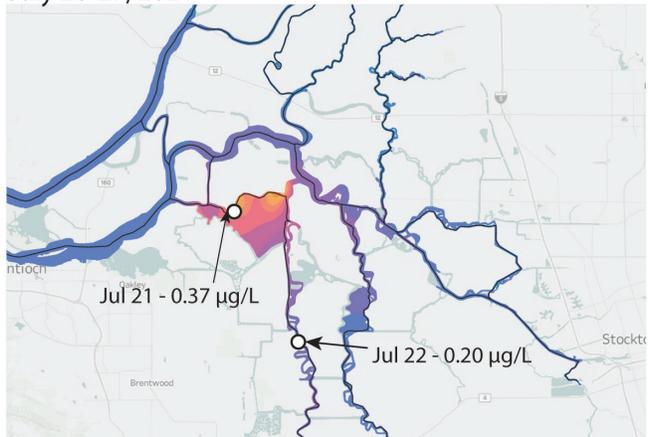
June 2-4, 2021



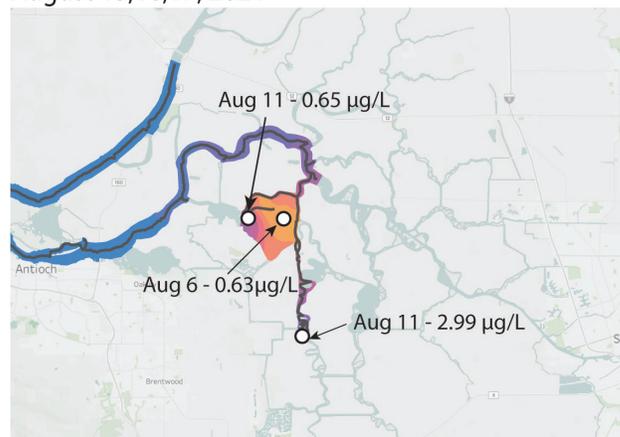
July 15, 16, 19, 2021



July 26-27, 2021



August 13, 16, 17, 2021



September 10, 13, 14, 2021

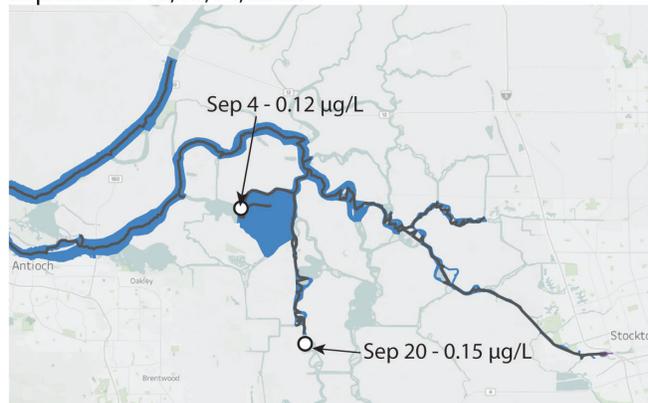


Figure 11 Cyanotoxin concentrations (in $\mu\text{g L}^{-1}$, with ND meaning 'non-detect' for values below the detection limit of the analysis method) from discrete samples (*white points*) collected for cyanotoxin special studies displayed with maps of cyanobacterial chlorophyll fluorescence as measured by a boat-based FluoroProbe during sampling surveys. Each *panel* is labelled with the date of the FluoroProbe surveys. The July 26-27, 2021, cyanobacterial chlorophyll data were collected by the USGS. All other cyanobacterial chlorophyll data were collected by the EMP. Cyanobacterial chlorophyll is interpolated across the channel width and the actual boat tracks are shown as *black lines*.

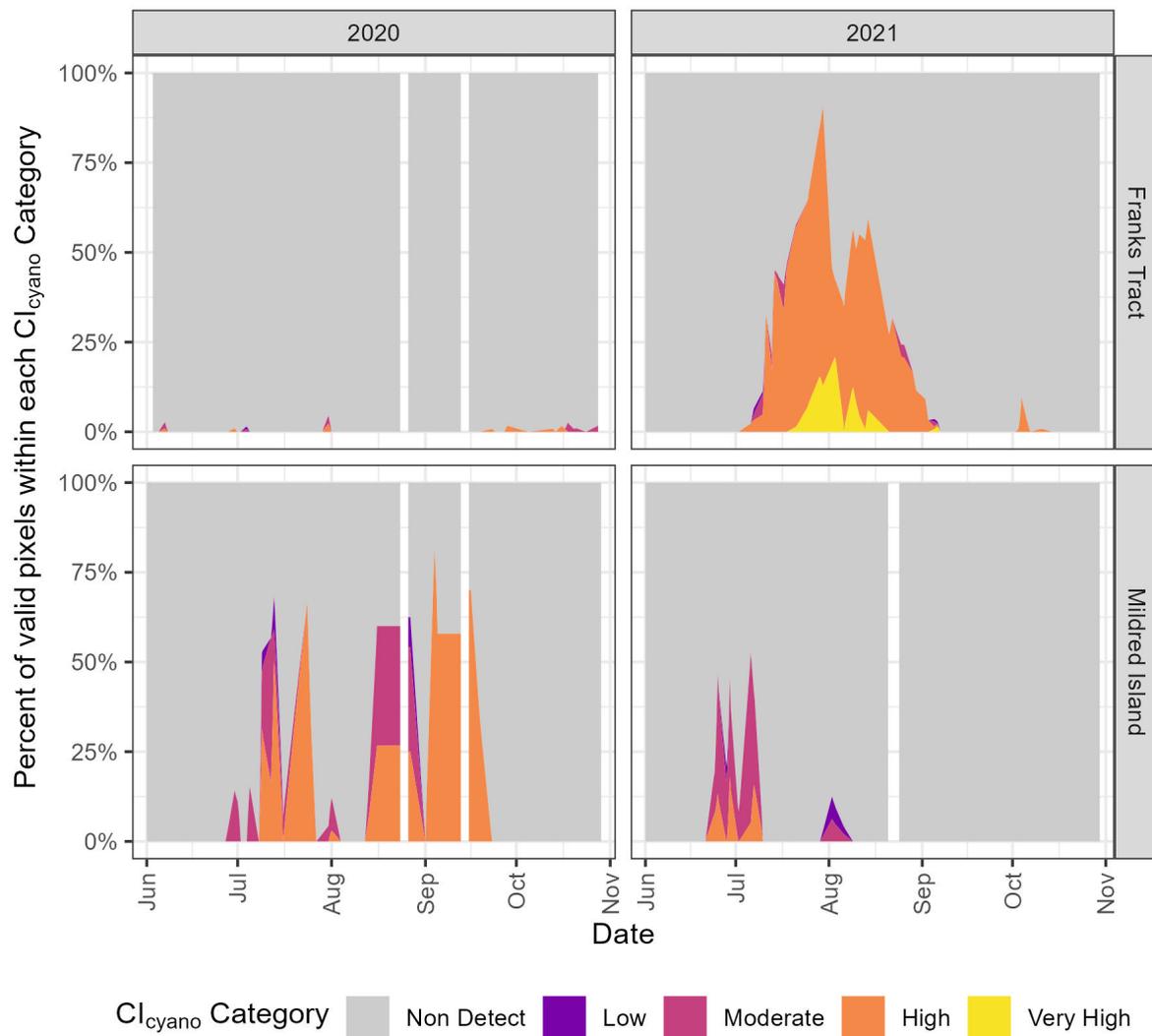


Figure 12 Time-series of the percent of valid pixels within each Cyanobacteria Index (CI_{cyano}) category for Summer-Fall in calendar years 2020 and 2021 within Franks Tract and Mildred Island.

onboard the Sentinel-3 satellite) can be combined with visual indices to more completely assess how water management actions may affect cyanoHABs in the Delta. Our results demonstrate clear relations among environmental conditions that affect cyanoHAB formation, but distinguishing the effects of management actions from the effects of drought remains challenging.

Regional and Temporal Trends

Figure 4 shows that throughout our period of study, *Microcystis* was frequently observed in the Delta. This aligns with previous studies in the system (Lehman et al. 2017, 2022) and larger

global trends (Huisman et al. 2018 and references therein). *Microcystis* was more likely to be observed during drier years when flows, water clarity, and summer water temperatures were more conducive to bloom formation (Figures 4 and 5). Previous work also found that *Microcystis* abundance was greater in drier years throughout the estuary (Lehman et al. 2017; Lehman et al. 2022), though within-year spatial and temporal variation could result in different intensities of blooms during successive Dry years (Lehman et al. 2018).

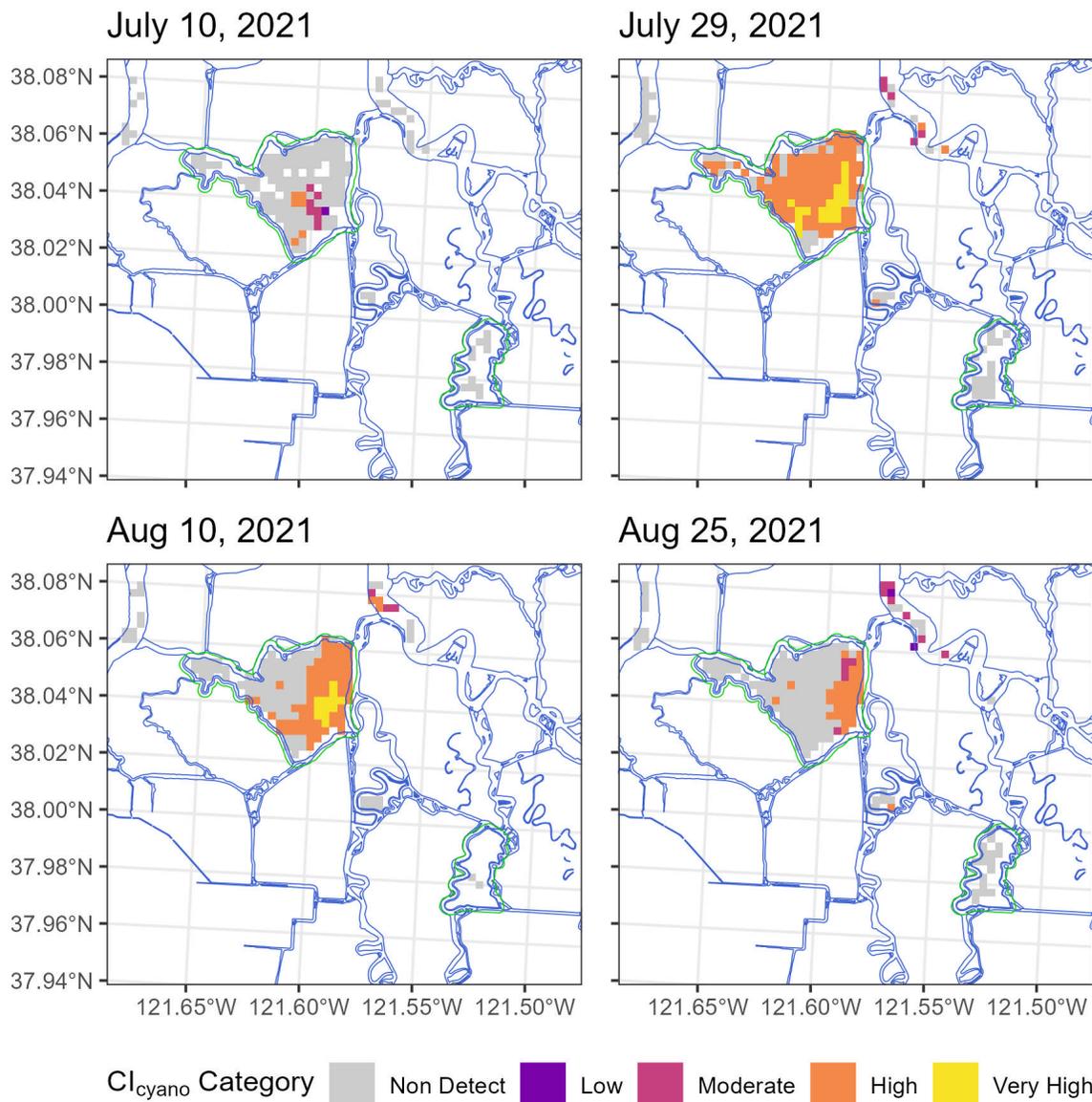


Figure 13 Maps of Cyanobacteria Index (CI_{cyano}) categories at the beginning (July 10), peak (July 29 and August 10), and end (August 25) of the cyanobacterial bloom in Franks Tract during Summer 2021. Area visualized by the satellite is highlighted in green.

The higher incidences of *Microcystis* blooms observed in the South Delta, lower San Joaquin River, and Franks Tract/OMR regions compared to other regions in the Delta (Figure 5) had also been documented previously (Lehman et al. 2005, 2013); these regions typically display higher water temperatures, lower salinity, and higher water clarity than the rest of the Delta (Lehman et al. 2005, 2013). During Wet years, incidences of *Microcystis* blooms decreased substantially in the North and East Delta, but incidences of *Microcystis*

blooms did not decrease in the South Delta and Franks Tract/OMR regions despite increased flows (Figure 5). Similarly, Lehman et al. (2022) found that lower outflows in 2014 contributed to high abundance and toxicity of *Microcystis* in the Central Delta, but even the extreme wet year of 2017 did not eliminate *Microcystis* from the area. Our analysis shows that these patterns are consistent throughout a longer time-frame than previously studied, and highlights the persistence of *Microcystis* in a system, once established.

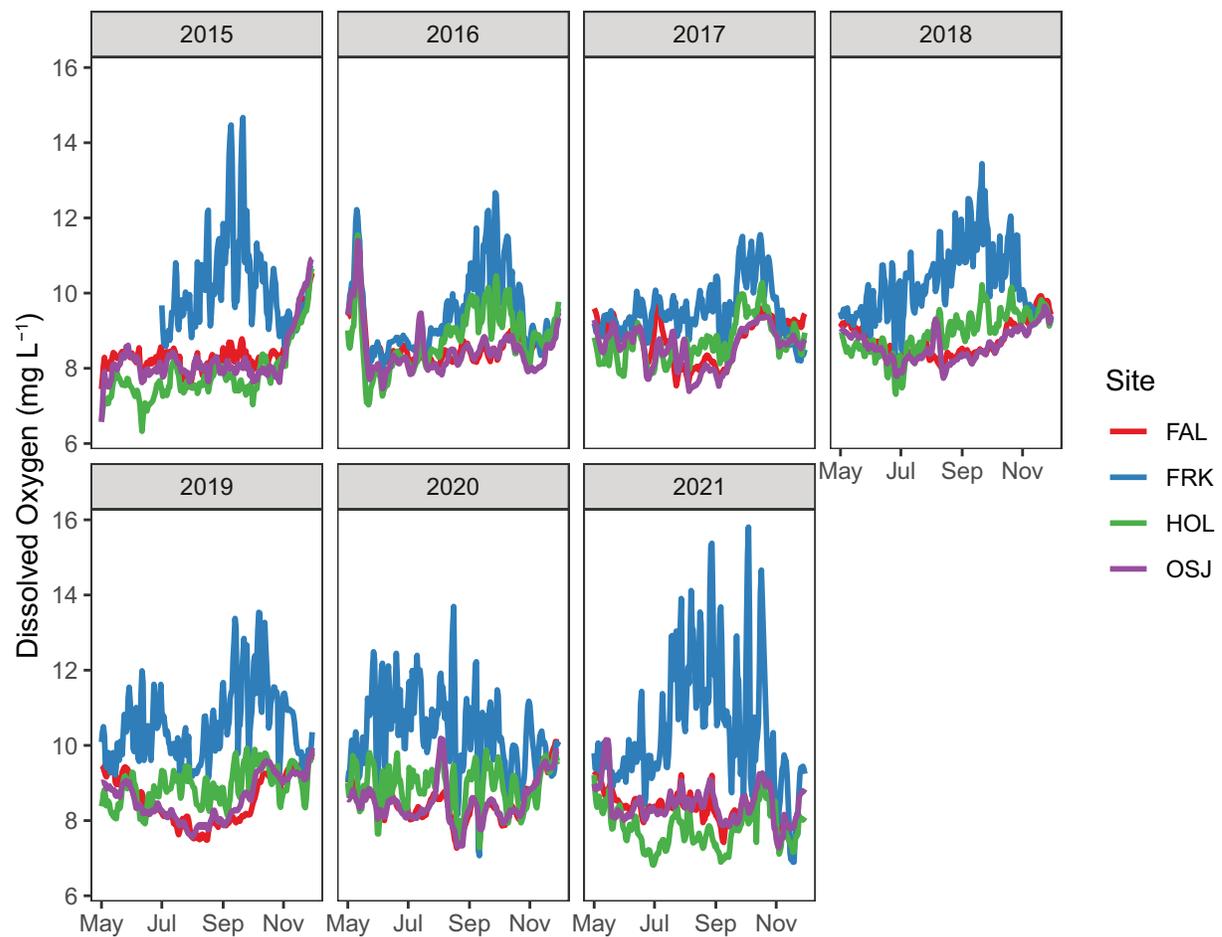


Figure 14 Daily mean concentration of dissolved oxygen (mg L^{-1}) in and around Franks Tract from May through November of calendar years 2015–2021. Data collected using a YSI EX02 water-quality sonde equipped with an optical dissolved-oxygen sensor.

Nutrients

Because of their high concentrations in the Delta, nutrients are seldom considered limiting to the growth of cyanobacteria and other types of phytoplankton (Jassby et al. 2002; Berg and Sutula 2015; Kudela et al. 2023). However, this abundance is still likely a contributing factor to the increased frequency and severity of cyanobacteria blooms seen during the past 20 years. Three factors regulate how nutrient conditions control the growth and biomass accumulation of phytoplankton, including cyanobacteria (Reynolds 1992; Chorus and Spijkerman 2021). First, the concentration of dissolved inorganic nutrients affects the rate of cellular nutrient uptake. Second, once nutrients enter the cell, their intracellular concentrations must remain

sufficient to support cell metabolism and growth. Lastly, the total amount of nutrients within a system like the Delta will partially control total phytoplankton biomass and constrain the extent to which a bloom can occur. For example, in the Franks Tract/OMR Region, the concentration of nitrate + nitrite was $0.5\text{--}1.0 \text{ mg L}^{-1}$ during March and April of 2021, but decreased to $<0.125 \text{ mg L}^{-1}$ by July 2021 when a *Microcystis* bloom developed (Figures 16 and 8). If the initial pool of available nutrients were lower, less total biomass might have accumulated during the bloom. In our 2021 case study, nutrient concentrations were highly variable in the North Delta, East Delta, and South Delta regions but did not decline during the summer season when the potential for *Microcystis* bloom formation was greatest. Despite the ample

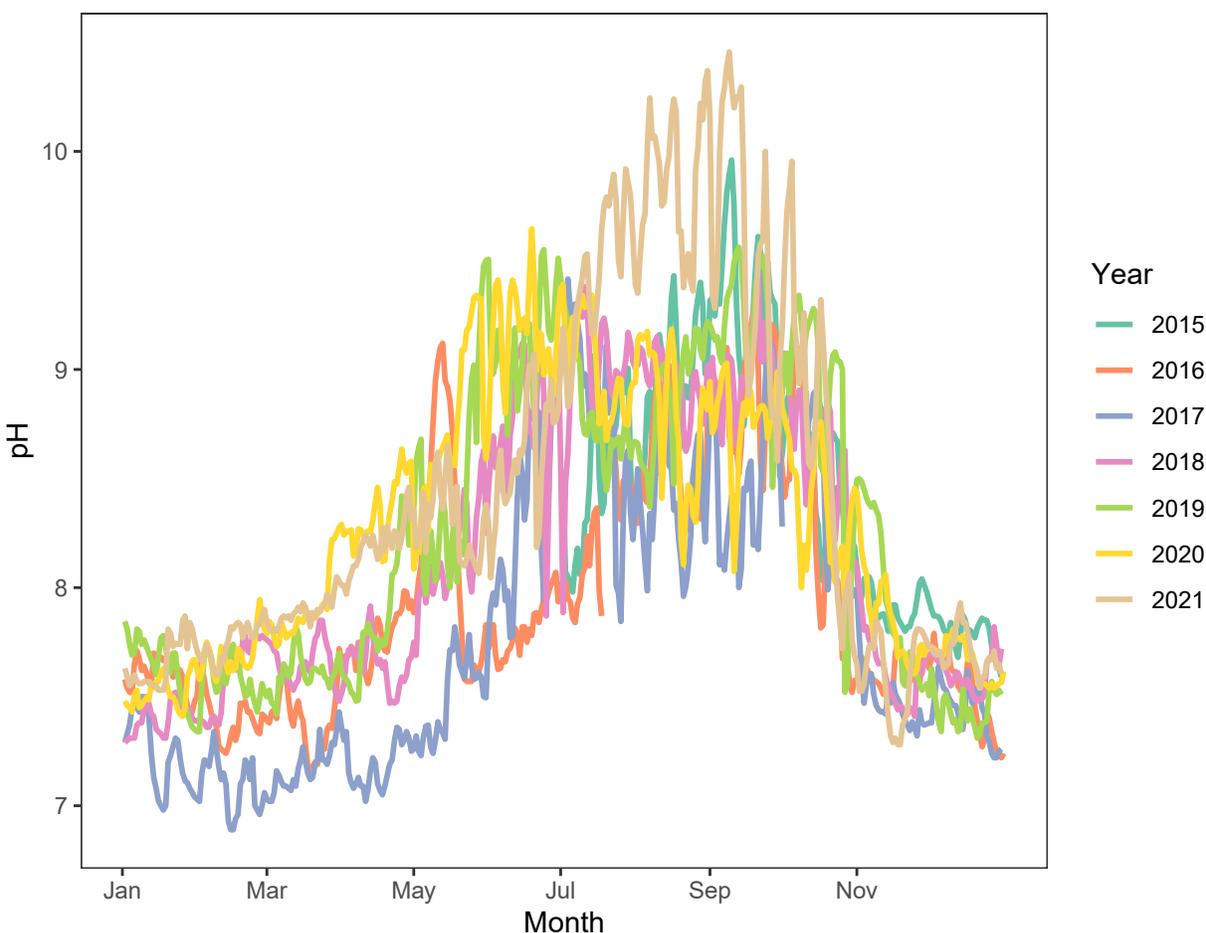


Figure 15 Daily median pH at FRK during calendar years 2015–2021. Data collected using a YSI EX02 water-quality sonde equipped with a pH Smart Sensor.

availability of nutrients in these regions, large cyanobacterial blooms in the open waterways sampled by IEP’s monitoring programs failed to materialize in these regions. Nutrients were actually higher in these regions than in the Franks Tract/OMR Region where a cyanoHAB did form (Figures 16 and 17), indicating that nutrients are necessary for bloom formations but are not solely responsible for bloom formations in the Delta. *Microcystis* biomass was greatest during July and August 2021 in the Franks Tract/OMR Region, where nitrogen depletion began in the spring and continued through June (Figure 16). Unlike nitrogen, orthophosphate concentrations throughout the Delta were stable throughout 2021, without any noticeable declines (Figure 17).

In the South Delta region, nutrient concentrations were highest at station P8 near the Stockton Wastewater Treatment Plant (WWTP) (Figures 1, 16 and 17). Previous isotopic studies have shown that nitrate from the San Joaquin River mixes with nitrate from the Sacramento River between Medford Island and Windmill Cove (river miles 26–34), far enough downstream to enter Columbia and Turner cuts (Kendall et al. 2015; Novick et al. 2015). Tidally influenced flows or high volumes of export pumping could therefore disperse the abundant nutrients near the Stockton WWTP into the South Delta and OMR regions, through Turner Cut into the channels of Middle and Old rivers, and downstream to the Sacramento River, which is the dominant source of water to the Delta (Jabusch et al. 2018). This dilution and dispersion, along with uptake of nutrients by phytoplankton

and other autotrophic organisms, explain why the high concentrations of nitrate found near Stockton are not present downstream along the San Joaquin River or in Franks Tract. However, comprehensive tracking of nutrient flux through the Franks Tract/OMR and South Delta regions remains challenging because of the complexity of flows in the area. As a result, the process of using nutrient modeling to predict where *Microcystis* blooms will form is not well established. Even so, collecting additional data on nutrients in the South Delta and East Delta using real-time instruments such as the submersible ultraviolet nitrate analyzer (SUNA) probe (Sea-Bird Scientific) may benefit regional models and provide resource managers with a better understanding of the fate and transport of nutrients from the Stockton WWTP.

The influence of different chemical forms of nitrogen (i.e., nitrate or ammonium) on phytoplankton growth and community composition has been studied extensively in the San Francisco Bay and the Delta (Dugdale et al. 2007; Parker et al. 2012; Lee et al. 2015; Lehman et al. 2015; Berg et al. 2017; Strong et al. 2021). In our study, nitrate was highest in the South Delta, and ammonium was highest in the North Delta and lower Sacramento River (Figures 7 and 8). However, concentrations of nitrate in the South Delta ($\sim 2 \text{ mg L}^{-1}$) were almost an order of magnitude higher than the highest ammonium concentrations (0.25 mg L^{-1}) detected in the North Delta (Figure 7). While the abundance of *Microcystis* is positively correlated to regions with higher nitrate concentrations (Franks Tract/OMR and the South Delta), Lee et al. (2015) showed that *Microcystis* in the Delta uptake ammonium faster than nitrate. Additionally, stable isotope experiments by Lehman et al. (2015) reported that *Microcystis* grow primarily using ammonium as a source of nitrogen. However, other *in vitro* or field experiments elsewhere have shown *Microcystis* can grow well using nitrate, or has no preference for the form of inorganic nitrogen it uses (Berg and Sutula 2015; Gobler et al. 2016; Chaffin et al. 2018; Erratt et al. 2018). Metabolic flexibility allows *Microcystis* to flourish in a variety of inorganic nutrient contexts, which may partially

explain the success of *Microcystis* in forming large blooms worldwide in a variety of environmental contexts (Dick et al. 2021). More research could help determine if and how nitrogen form controls the formation and magnitude of cyanobacterial blooms in the Delta.

When nutrient concentrations are considered saturating, the N:P ratio has less influence in controlling the phytoplankton community (Reynolds 1999; Chorus and Spijkerman 2021). Phosphorus limitation in the Delta is likely infrequent because concentrations are always well above concentrations of $\sim 0.003 \text{ mg P L}^{-1}$, the concentration at which phosphorus limitation could be considered to potentially be occurring (Reynolds 2006; Chorus and Spijkerman 2021). The absence of a summer decline in phosphate concentrations (Figures 9 and 17) is also a consistently observed pattern for a phosphorus-replete system. For nitrogen, phytoplankton can usually satisfy their immediate nitrogen demand when dissolved inorganic nitrogen concentrations are above 0.1 mg L^{-1} , below which nitrogen might begin to be considered as a factor that may limit cell division rates and population growth (Reynolds 2006; Chorus and Spijkerman 2021). During summer 2021, dissolved inorganic N concentrations approached 0.1 mg L^{-1} in the Franks Tract/OMR region (Figure 16). During this time the N:P ratio drops below 6, which, combined with the low inorganic nitrogen concentration, indicates that cells may have become limited by nitrogen during the height of the bloom, even though nitrogen was well in excess before the bloom. These results support recent findings that controlling N input into systems prone to cyanoHAB formation may be as important as controlling P (Paerl et al. 2011; Hellweger et al. 2022).

Drivers

Results of our analyses supported our conceptual model that the major drivers behind *Microcystis* occurrence and severity in the Delta are water temperature, light availability, and flow, and these drivers help explain the increased frequency of blooms observed during the past 20 years. Nutrients may have also been an important

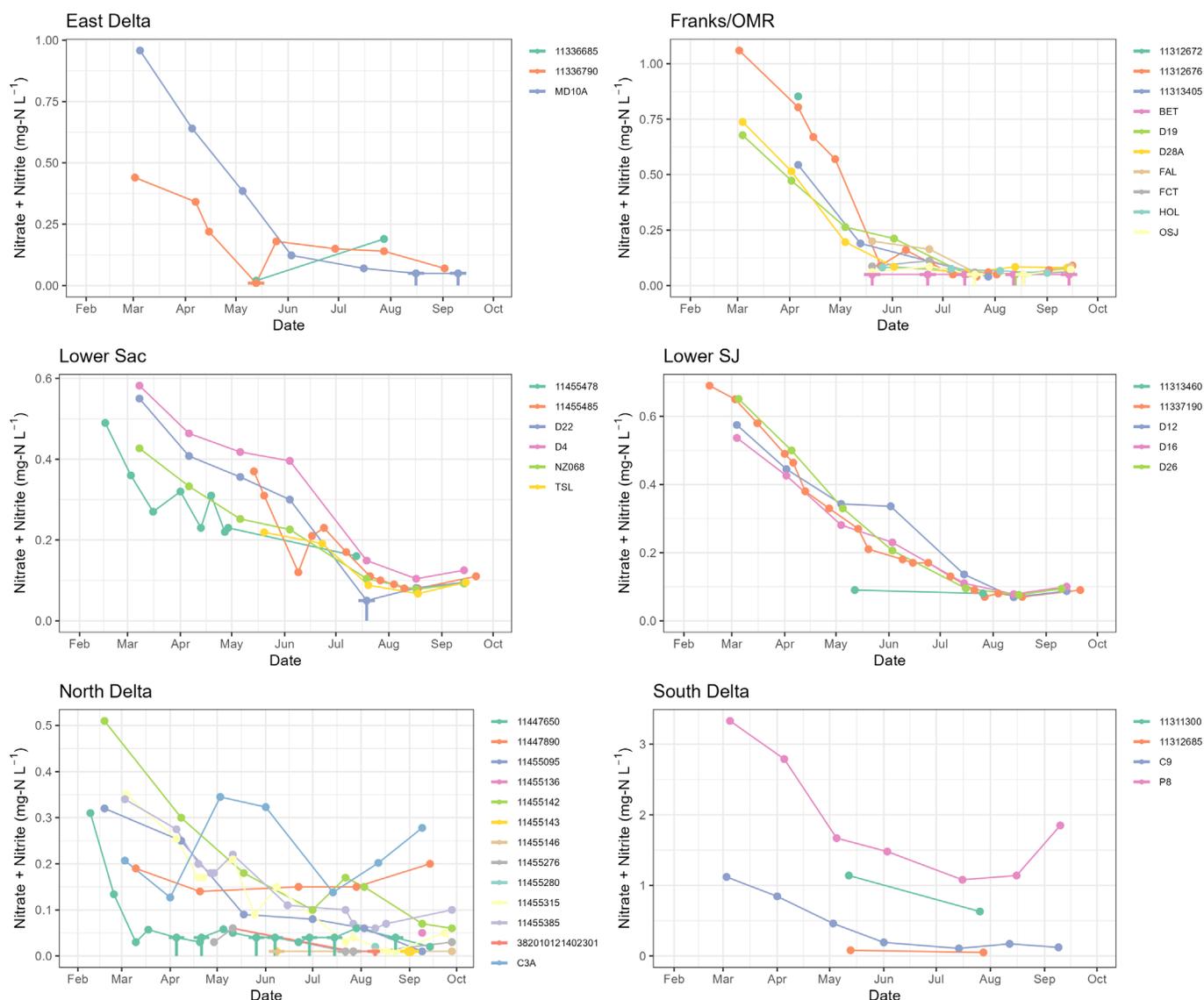


Figure 16 Time-series of dissolved nitrate + nitrite during spring and summer 2021. Note the different y-axis scales across regions. Samples measuring below the reporting limits are notated with *vertical lines* that are capped at the reporting limit. USGS data from National Water Information System (US Geological Survey 2023)

driver, but nutrient concentrations were not used in models to directly predict *Microcystis* occurrence because of the complexities with seasonal nutrient concentration trends and negative correlations between bloom biomass and dissolved nutrient concentrations.

Nutrients may not be the primary factor that drives a phytoplankton bloom, but they can control how much phytoplankton biomass can accrue. Higher springtime nitrate concentrations

in the Delta could result in more cyanobacterial biomass in the summer. In the South Delta, where cyanobacterial blooms are more common, the Critical years of 2015 and 2021 had higher spring nitrate concentrations than Wet years 2017 and 2019 (Figure 8). The higher temperatures, lower flow, and lower turbidity conditions during drier years (Bosworth et al., this issue), are the direct factors that drive phytoplankton to more fully utilize the higher springtime nutrient supply that can accrue during droughts.

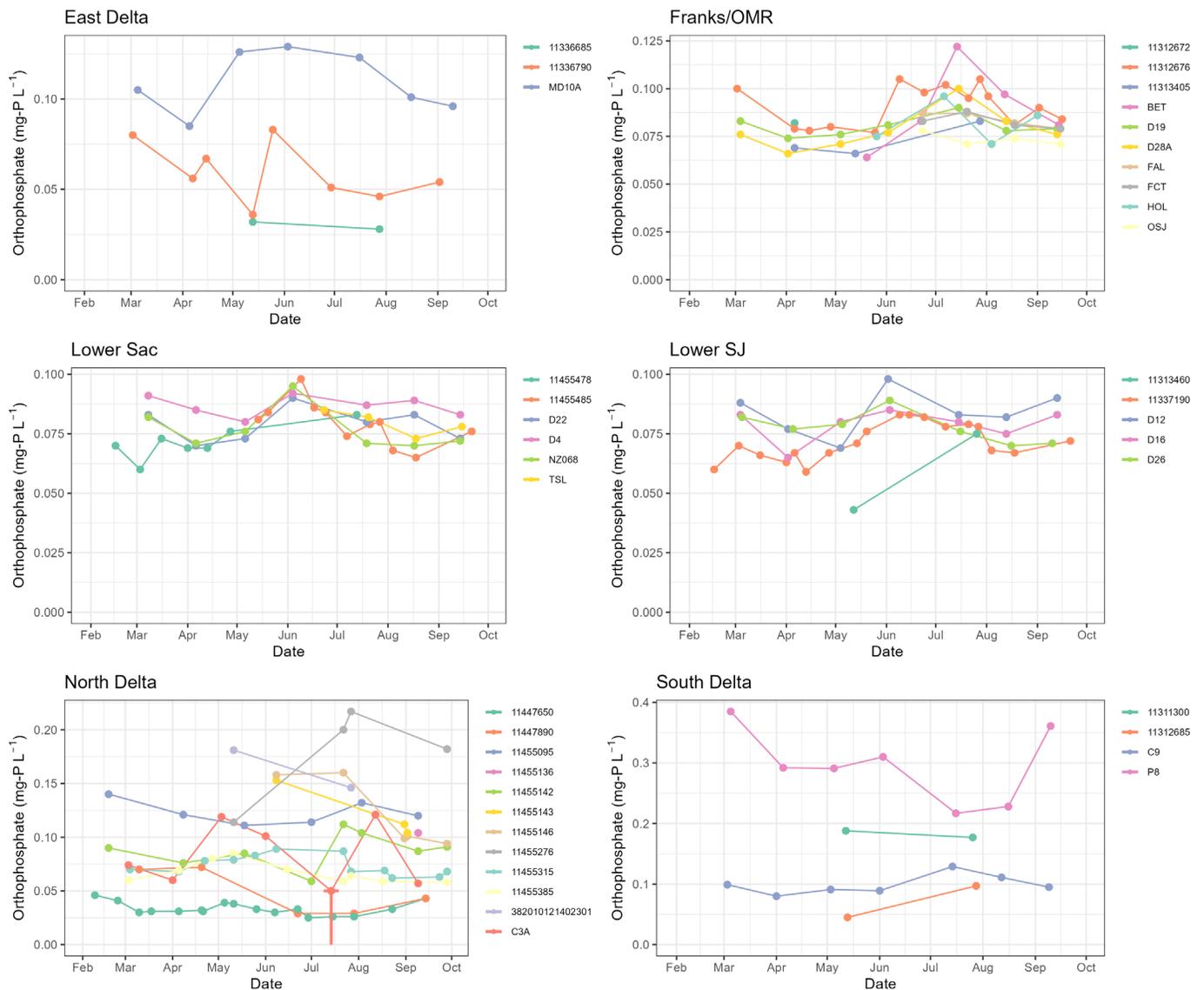


Figure 17 Time-series of discrete orthophosphate during spring and summer 2021. Note the different y-axis scales across regions. Sample measuring below the reporting limit is notated with a vertical line that is capped at the reporting limit. USGS data from National Water Information System (US Geological Survey 2023).

Water temperature is a well-established predictor of cyanobacteria in the Delta as well as other systems (Lehman et al. 2013; Pick 2016; de Souza et al. 2018; Lehman et al. 2022), with water temperature above 19 °C being a particularly important threshold above which *Microcystis* blooms occur (Lehman et al. 2013). Our top-ranked model included water temperature as a predictor, which supported previous research. Correlations between increased severity of *Microcystis* and observed changes to the climate

are supported by the past 5 years being some of the hottest years in recorded history, with the US experiencing the hottest air temperatures in June and July on record in 2021 (NOAA National Centers for Environmental Information 2022). Water temperatures in the Delta are frequently hotter during low outflow years and droughts (Bashevkin and Mahardja 2022; Bosworth et al., this issue), and 15 of the past 20 years have been classified as Below Normal, Dry, or Critical. Therefore, the recent increased frequency of

Microcystis observations would be predicted based on increases to temperature alone.

The association of warmer years with drier years likely makes *Microcystis* blooms more common during droughts. Overall, drier water years had higher incidence of *Microcystis* observations (Figures 4 and 5), likely because water residence time is an important factor in predicting *Microcystis*, and water residence time is longer in drier years (Hartman, Stumpner et al., this issue). More detailed studies that directly model water residence time could help confirm this hypothesis. The similar frequency of high *Microcystis* in Critical, Dry, and Below Normal years suggests that very large changes in flow are needed to cause an appreciable change to *Microcystis* abundance.

We found SWP and CVP water exports to be the best flow predictor of *Microcystis* in the Delta that we tested in this analysis, and previous research has shown that SWP and CVP water exports significantly decrease water residence time, especially along the San Joaquin River (Hammock et al. 2019). Multiple factors contribute to the realized water residence time in the South Delta region, but SWP and CVP water exports can frequently be higher than Delta outflow during the summer when inflow is low, which can cause large negative flows in the South Delta (SWRCB 2018; Cloern 2019). Therefore, SWP and CVP water exports have a larger controlling influence on water residence time than outflow during these periods. Changes to San Joaquin River flow may have a similarly large influence on South Delta water residence time; however, regulatory mandates control the ratio of San Joaquin River inflow and SWP and CVP water exports, complicating efforts to separate these two drivers.

Light availability (as indexed by Secchi depth) was the other major predictor of *Microcystis* in the South Delta region. The San Francisco Estuary as a whole has lower productivity than other estuaries with similar nutrient inputs (Cloern 2001), but low light availability is believed to limit overall pelagic production in the San Francisco Estuary (Jassby et al. 2002; Dahm et al. 2016).

Water clarity is highest during the summers, when *Microcystis* is most common, and water clarity tends to be higher in drought years (Bosworth et al., this issue). Furthermore, water clarity has increased significantly during the past 30 years because upstream dams block sediment transport and the proliferation of submerged aquatic vegetation (SAV) (Schoellhamer 2011; Hestir et al. 2016). Increases in frequency of severe droughts, water temperatures, and water clarity provide more suitable conditions for *Microcystis* blooms.

2021 Case Study

A large cyanobacterial bloom that occurred in Franks Tract during July and August 2021 was apparent in datasets with high spatial resolution (FluoroProbe and satellite data) and high temporal resolution (continuous pH and DO data). The FluoroProbe and satellite datasets had elevated cyanobacterial fCHL, and CI_{cyano} values were observed in Franks Tract in FluoroProbe and satellite datasets, respectively, during this period (Figures 11, 12, and 13). In addition, continuous DO and pH values were higher at FRK during the summer of 2021 than at other nearby stations and other years (Figures 14 and 15). Higher than average DO and pH values indicate increased rates of photosynthesis (Raven et al. 2020). However, in Franks Tract, SAV altered its distribution when drought barriers have been installed (Kimmerer et al. 2019; Hartman et al. 2022), and photosynthesis by SAV would also increase DO concentrations. In 2015, a year when the barrier was installed but there was no cyanobacterial bloom, DO concentrations did not exceed 12 mg L^{-1} until after September 1. However, in July and August 2021, a cyanobacterial bloom occurred and DO concentrations exceeded 12 mg L^{-1} . While we cannot disentangle the contributions of cyanobacteria and SAV to DO concentrations, the high DO values ($>12 \text{ mg L}^{-1}$) in July and August 2021 do not occur in any other year, and 2021 was the only year in the study period with a documented cyanobacterial bloom, leading us to conclude that a large proportion of DO in Franks Tract was produced by cyanobacteria.

Despite the observed cyanoHAB bloom, microcystin concentrations mostly remained below the “Caution” advisory level of $0.8 \mu\text{g L}^{-1}$ (CCHAB Network 2022) in and near Franks Tract in 2021. Similar average microcystin concentrations were observed previously during extremely dry summers, such as in 2014, when toxin concentrations in the open waters of the Central Delta ranged from ~ 0.4 to $\sim 1.3 \mu\text{g L}^{-1}$ (Lehman et al. 2018); however, enclosed marinas and dead-end sloughs consistently experience much higher microcystin concentrations ($> 50 \mu\text{g L}^{-1}$) (Hartman et al. 2022; Kudela et al. 2023). The lack of consistent microcystin monitoring in the Central Delta limits our ability to put the Franks Tract bloom into context. Furthermore, the small number of samples collected in 2021 limits our ability to describe the full extent of toxicity during the bloom.

The barrier in west False River may have contributed to the formation of cyanoHABs in Franks Tract. Satellite data (Figure 12), and continuous DO and pH data (Figures 14 and 15) indicated cyanoHABs were not observed in 2020, which was a Dry year during which a barrier was not in place. However, 2015 was another Dry year with a barrier in west False River, and evidence for cyanoHABs was not observed in 2015. Kimmerer et al. (2019) looked at potential effects of the barrier installed in 2015 and found no evidence that the barrier affected the *Microcystis* visual index ratings observed at Franks Tract in 2015. However, the high DO concentrations and pH values measured in September 2015 were only exceeded by DO concentrations and pH values measured in 2021 (Figures 14 and 15), indicating high rates of photosynthesis (Raven et al. 2020). These high rates of photosynthesis in September were likely caused by elevated biomass of submersed vegetation rather than cyanobacteria. FluoroProbe or cyanoHAB satellite data were not available for 2015. In the future, FluoroProbe or cyanoHAB satellite data may provide more insights into the conditions in and near Franks Tract during another Dry year with a barrier in place.

Comparing the occurrence of a cyanoHAB bloom in Franks Tract near the barrier in 2021 to a lack of a cyanoHAB bloom in 2020 when the barrier was not in place indicates the barrier may have played some role in the formation of the bloom; however, available data cannot be used to confirm a cause-and-effect relation. Satellite data show the bloom initiating in the southeast side of Franks Tract, in the region farthest from the barrier (Figure 13). Modeling and monitoring completed during the 2015 and 2021 barrier installations indicated that current speeds and flow increased on the eastern side and decreased on the western side of the tract. Modeling of water age as a proxy for water residence time (Monsen et al. 2002) indicated water age decreased in the east and increased in the west (Hartman et al. 2022). We predicted that blooms would form in the western side of the tract, closest to the barrier, which would have the lowest current speeds and flows and highest water ages associated with barrier installation. However, satellite data showed cyanobacteria density was lowest in the area closest to the barrier (Figure 13). This counter-intuitive situation may have been caused by the dense submerged vegetation that dominated the western side of the tract (Hartman et al. 2022) because submerged vegetation can reduce cyanobacteria blooms (Nezbrytska et al. 2022). Prevailing winds in the region are typically from the west (Bever et al. 2018), so a bloom in the eastern side of the tract may have been caused by surface scum being pushed by the wind. Wind-induced turbulence can also cause *Microcystis* to disaggregate (O'Brien et al. 2004), potentially making them more visible to the satellites. Additional research could help further distinguish drivers of episodic cyanoHABs.

Outside of Franks Tract, similar *Microcystis* concentrations were observed in other areas of the Delta in 2021 as in previous Dry years (Figure 4), providing little evidence for an effect of the TUCO on frequency or intensity of *Microcystis* across the Delta. The predictive model of *Microcystis* occurrence in the South Delta indicated that reduced SWP and CVP water exports increase the probability of *Microcystis* occurrence, and the TUCO restricted SWP and

CVP water exports to below $42.5 \text{ m}^3 \text{ s}^{-1}$ (SWRCB 2022). However, the relation between exports and *Microcystis* is relatively flat at low export rates and has wide credible intervals (Figure 6). A large increase in exports (over $56 \text{ m}^3 \text{ s}^{-1}$) would have been required for the model to predict a meaningful reduction in *Microcystis* occurrence. Given the extremely dry conditions and reduced water storage in 2021, increasing SWP and CVP water exports enough to reduce *Microcystis* in the South Delta would not have been feasible because dry conditions with low reservoir storage historically corresponds greatly reduced SWP and CVP allocations (CDWR 2020). Also, while SWP and CVP water exports were the best predictive flow variable identified in this analysis, exports are only one of many hydrodynamic factors that contribute to water movement in the Franks Tract/OMR and South Delta regions. Inflow, tidal dynamics, wind–wave mixing, outflow, aquatic vegetation, channel morphology, and within-Delta diversions also contribute to water residence time and formation of blooms in the Delta (Lehman et al. 2017; Hammock et al. 2019).

Finally, the 2021 case study demonstrates the importance of incorporating multiple sources of monitoring data and embracing new monitoring tools in assessing cyanoHABs in the Delta. The Delta does not have a monitoring program currently dedicated to assessing cyanoHABs. However, by leveraging data collected for existing fish and water-quality surveys, using remote sensing data, and integrating data collected by special studies, we created a picture of the distribution of cyanoHABs in the Delta. Investing in new tools in the future could help increase our ability to monitor, predict, and mitigate cyanoHABs.

RECOMMENDATIONS

Droughts are expected to increase in frequency and severity in the future, and the scientific community could benefit from more routine cyanotoxin monitoring and the development of additional tools. Routine cyanotoxin data would improve understanding of baseline conditions and provide opportunities to compare drought

and non-drought years. The benefits that would be provided by funded HAB monitoring was a recurring theme from the recent Harmful Algal Bloom workshop held by the Delta Stewardship Council (Birdwell and Lee 2022).

Additional tools can also be developed to better understand, predict, and mitigate cyanoHABs. Examining advanced data-modeling techniques may help optimize the integration of various datasets to predict or better understand drivers of blooms. A spatio-temporal model developed using satellite-derived data and local environmental conditions might be feasible and could be used for short-term forecasting of cyanoHABs (such as explored by Myer et al. 2020). An improved understanding about the feasibility of large-scale implementation of different mitigation approaches and technologies would inform decisions made by Delta resource managers. Mitigation efforts have three general categories of approaches: (1) physical (e.g. screens, surface mixers, aeration), (2) chemical (e.g., hydrogen peroxide, binding agents for phosphorous), or (3) biological (e.g., bio-manipulation) (Paerl et al. 2018; Burford et al. 2019; Kibuye et al. 2021). Aeration, surface-water mixers, and hydrogen peroxide could be used in the Bay–Delta in small hotspot regions (marinas) but would require permitting to ensure no non-target effects on sensitive aquatic life. Local-scale mitigation, or control technologies or treatments might effectively counteract any increases in bloom intensity at known hotspots that could result from Delta-wide flow management alterations, which often occur during droughts. Overall, the large scale of the Delta makes a single solution impossible, so a variety of management tools will be needed.

Lastly, routine monitoring and advanced tools would help optimize water management in a way that does not contribute to cyanoHAB formation. Many drivers of cyanoHABs (i.e., water movement, nutrients, and light) may be altered by management actions (e.g., barriers, TUCOs, and wastewater treatment plant upgrades). As management actions are implemented, additional HABs-related monitoring—including toxin,

community composition, and water quality analyses—would help understand how the actions affected phytoplankton and HABs before, during, and after the action. Event-based monitoring, where data are collected when a bloom is detected, can also help fill gaps in system-wide monitoring networks. With careful planning and additional tools available, resource managers could better assess how drought and drought-management actions affect cyanoHABs.

ACKNOWLEDGMENTS

We would like to thank Sarah Perry (CDWR), Tyler Salman (CDWR), Karen Odkins (CDFW), Ellen Preece (CDWR) and Timothy Otten (Bend Genetics, LLC) for their assistance with data contributions and formatting. We would also like to thank all the field staff of the Interagency Ecological Program long-term monitoring surveys, the California Department of Water Resources' North Central Region Office, and USGS CA Water Science Center Biogeochemistry Group for their tireless work collecting the field data that contributed to this publication. This study was conducted under the auspices of the Interagency Ecological Program. The views presented here are those of the authors and do not necessarily represent the views of the Interagency Ecological Program. This journal article has been peer reviewed and approved for publication consistent with USGS Fundamental Science Practices (<https://pubs.usgs.gov/circ/1367/>). Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US Government.

REFERENCES

- Allen WE. 1920. A quantitative and statistical study of the plankton of the San Joaquin River and its tributaries in and near Stockton, California, in 1913. Berkeley (CA): University of California Press. 292 p.
- Banerjee S, Maity S, Guchhait R, Chatterjee A, Biswas C, Adhikari M, Pramanick K. 2021. Toxic effects of cyanotoxins in teleost fish: a comprehensive review. *Aquat Toxicol*. [accessed 2023 Feb 23]; 240:105971. <https://doi.org/10.1016/j.aquatox.2021.105971>
- Bashevkin SM, Mahardja B. 2022. Seasonally variable relationships between surface water temperature and inflow in the upper San Francisco Estuary. *Limnol Oceanogr*. [accessed 2023 Jan 4];67:684–702. <https://doi.org/10.1002/lno.12027>
- Bashevkin SM, Mahardja B, Brown LR. 2022a. Warming in the upper San Francisco Estuary: patterns of water temperature change from 5 decades of data. *Limnol Oceanogr*. [accessed 2023 Jan 3] 67(5):1065–1080. <https://doi.org/10.1002/lno.12057>
- Bashevkin SM, Perry SE, Stumpner EB. 2022b. Six decades (1959–2021) of water quality in the upper San Francisco Estuary: an integrated database of 15 discrete monitoring surveys in the Sacramento San Joaquin Delta, Suisun Bay, Suisun Marsh, and San Francisco Bay. Version 5. Environmental Data Initiative. [accessed 2022 Nov 30]. <https://doi.org/10.6073/pasta/c9b3da65a8c89cbfa6fc28d26f938c22>
- Baston D. 2021. exactextractr: fast extraction from raster datasets using polygons. *Comprehensive R Archive Network (CRAN)*. [accessed 2023 Feb 23]. Available from: <https://cran.r-project.org/web/packages/exactextractr/index.html>
- Bates D, Maechler M, Bolker B, Walker S. 2022. lme4: linear mixed-effects models using 'Eigen' and S4. 1.1–30 edition: The Comprehensive R Archive Network (CRAN). [accessed 2022 Jul 8]. Available from: <https://cran.r-project.org/web/packages/lme4/index.html>
- Berg GM, Driscoll S, Hayashi K, Ross M, Kudela R. 2017. Variation in growth rate, carbon assimilation, and photosynthetic efficiency in response to nitrogen source and concentration in phytoplankton isolated from upper San Francisco Bay. *J Phycol*. [accessed 2023 Feb 23]; 53(3):664–679. <https://doi.org/10.1111/jpy.12535>

- 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 number 12-135-250). [accessed 2023 Feb 23]. Available from: https://amarine.com/wp-content/uploads/2018/01/Cyano_Review_Final.pdf
- Bever AJ, MacWilliams ML, Fullerton DK. 2018. Influence of an observed decadal decline in wind speed on turbidity in the San Francisco Estuary. *Estuaries Coasts*. [accessed 2023 Feb 23];41(7):1943–1967. <https://doi.org/10.1007/s12237-018-0403-x>
- Birdwell T, Lee T. 2022. Delta Harmful Algal Blooms Workshop Information Sheet. Sacramento (CA): Delta Science Program. [accessed 2023 Feb 23]. Available from: https://www.researchgate.net/publication/365964769_Delta_Harmful_Algal_Blooms_Workshop_Information_Sheet
- Boesch DF. 2019. Barriers and bridges in abating coastal eutrophication. *Frontiers in marine science*. 6. [accessed 2023 Feb 23] <https://doi.org/10.3389/fmars.2019.00123>
- Bosworth DH, Bashevkin SM, Bouma–Gregson K, Hartman R, Stumpner EB. 2024. The anatomy of a drought in the upper San Francisco estuary: water quality and lower-trophic responses to multi-year droughts over a long-term record (1975–2021). *San Franc Estuary Watershed Sci*. <https://doi.org/10.15447/sfews.2024v22iss1art1>
- Bricker SB, Longstaff B, Dennison W, Jones A, Boicourt K, Wicks C, Woerner J. 2008. Effects of nutrient enrichment in the nation's estuaries: a decade of change. *Harmful Algae*. [accessed 2023 Feb 23];8(1):21–32. <https://doi.org/10.1016/j.hal.2008.08.028>
- Brown LR, Kimmerer W, Conrad JL, Lesmeister S, Mueller–Solger A. 2016. Food webs of the Delta, Suisun Bay, and Suisun Marsh: an update on current understanding and possibilities for management. *San Franc Estuary Watershed Sci*. [accessed 2023 Feb 13];14(3). <https://doi.org/10.15447/sfews.2016v14iss3art4>
- Burford MA, Gobler CJ, Hamilton DP, Visser PM, Lurling M, Codd GA. 2019. Solutions for managing cyanobacterial blooms. Scientific Committee on Oceanic Research. [accessed December 13 2022]. Available from: http://www.globalhab.info/files/Cyano_mitigation_GlobalHAB2019.pdf
- Bürkner P–C. 2017. 'brms': an R package for Bayesian multilevel models using *Stan*. *J Stat Softw*. [accessed 2021 Nov 2];80(1). <https://doi.org/10.18637/jss.v080.i01>
- Bürkner P–C. 2018. Advanced Bayesian multilevel modeling with the R package 'brms'. *R J*. [accessed 2023 Feb 23];10:395–411. Available from: <https://journal.r-project.org/archive/2018/RJ-2018-017/RJ-2018-017.pdf>
- Bürkner P–C, Vuorre M. 2019. Ordinal regression models in psychology: a tutorial. *Adv Methods Practices Psychological Sci*. [accessed 2023 Feb 23];2(1):77–101. <https://doi.org/10.1177/2515245918823199>
- [CDWR] California Department of Water Resources. 2002. Dayflow: and estimate of daily average Delta outflow. Dayflow documentation 1997 through present. [accessed 2023 Jan 4]. Sacramento (CA): California Natural Resources Agency Open Data. Available from: <https://data.cnra.ca.gov/dataset/dayflow/resource/776b90ca-673e-4b56-8cf3-ec26792708c3>
- [CDWR] California Department of Water Resources. 2020. California's most significant droughts: comparing historical and recent conditions. Sacramento (CA): CDWR. [accessed 2023 Feb 6]. Available from: https://cawaterlibrary.net/wp-content/uploads/2017/05/CalSignificantDroughts_v10_int.pdf
- [CDWR] California Department of Water Resources. 2022a. Dayflow: and estimate of daily average Delta Outflow. [accessed 2023 Feb 6]. Sacramento (CA): California Natural Resources Agency Open Data. Available from: <https://data.cnra.ca.gov/dataset/dayflow/resource/776b90ca-673e-4b56-8cf3-ec26792708c3>
- [CDWR] California Department of Water Resources 2022b. Water data library. [accessed 2022 Dec 10]. Available from: <https://wdl.water.ca.gov/waterdatalibrary/WaterQualityDataLib.aspx>
- [CCHAB Network] California Cyanobacteria and Harmful Algal Blooms Network. 2022. California voluntary guidance for response to HABs in recreational inland waters. [Sacramento (CA)]: CCHAB Network. [accessed 2023 Apr 13]. Available from: https://mywaterquality.ca.gov/habs/resources/habs_response.html#general_public_res

- Chaffin JD, Davis TW, Smith DJ, Baer MM, Dick GJ. 2018. Interactions between nitrogen form, loading rate, and light intensity on *Microcystis* and *Planktothrix* growth and microcystin production. *Harmful Algae*. [accessed 2023 Feb 23];73:84–97. <https://doi.org/10.1016/j.hal.2018.02.001>
- Chorus I, Spijkerman E. 2021. What Colin Reynolds could tell us about nutrient limitation, N:P ratios and eutrophication control. *Hydrobiologia*. [accessed 2023 Feb 23]; 848(1):95–111. <https://doi.org/10.1007/s10750-020-04377-w>
- Chorus I, Welker M, editors. 2021. Toxic cyanobacteria in water: a guide to their public health consequences, monitoring and management. Boca Raton (FL): CRC Press. 859 p.
- Cloern JE. 2001. Our evolving conceptual model of the coastal eutrophication problem. *Mar Ecol Prog Ser*. [accessed 2023 Feb 23];210:223–253. <https://doi.org/10.3354/meps210223>
- Cloern JE. 2019. Patterns, pace, and processes of water-quality variability in a long-studied estuary. *Limnol Oceanogr*. [accessed 2023 Feb 23];64(S1):S192–S208. <https://doi.org/10.1002/lno.10958>
- Cloern JE, Schraga TS, Nejad E, Martin C. 2020. Nutrient status of San Francisco Bay and its management implications. *Estuaries Coasts*. [accessed 2023 Feb 23];43:1299–1317. <https://doi.org/10.1007/s12237-020-00737-w>
- 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>
- de Souza MS, Muelbert JH, Costa LDF, Klering EV, Yunes JS. 2018. Environmental variability and cyanobacterial booms in a subtropical coastal lagoon: searching for a sign of climate change effects. *Frontiers Microbiol*. [accessed 2023 Feb 23];9(1727). <https://doi.org/10.3389/fmicb.2018.01727>
- Dick GJ, Duhaime MB, Evans JT, Errera RM, Godwin CM, Kharbush JJ, Nitschky HS, Powers MA, Vanderploeg HA, Schmidt KC, et al. 2021. The genetic and ecophysiological diversity of *Microcystis*. *Environ Microbiol*. [accessed 2023 Feb 23];23(12):7278–7313. <https://doi.org/10.1111/1462-2920.15615>
- Downing BD, Bergamaschi BA, Kendall C, Kraus TEC, Dennis KJ, Carter JA, Von Dessenneck TS. 2016. Using continuous underway isotope measurements to map water residence time in hydrodynamically complex tidal environments. *Environ Sci Tech*. 50(24):13387–13396. [accessed 2023 Feb 23] <http://doi.org/10.1021/acs.est.6b05745>
- Dugdale RC, Wilkerson FP, Hogue VE, Marchi A. 2007. The role of ammonium and nitrate in spring bloom development in San Francisco Bay. *Estuar Coast Shelf Sci*. [accessed 2023 Feb 23];73:17–29. <https://doi.org/10.1016/j.ecss.2006.12.008>
- Durand JR, Bombardelli F, Fleenor WE, Henneberry Y, Herman J, Jeffres C, Leinfelder-Miles M, Lund JR, Lusardi R, Manfree AD, et al. 2020. Drought and the Sacramento-San Joaquin Delta, 2012–2016: environmental review and lessons. *San Franc Estuary Watershed Sci*. [accessed 2023 Jan 4]; 18(2). <https://doi.org/10.15447/sfews.2020v18iss2art2>
- Erratt KJ, Creed IF, Trick CG. 2018. Comparative effects of ammonium, nitrate and urea on growth and photosynthetic efficiency of three bloom-forming cyanobacteria. *Freshw Biol*. [accessed 2023 Feb 23];63(7):626–638. <https://doi.org/10.1111/fwb.13099>
- Falkowski PG. 2000. Rationalizing elemental ratios in unicellular algae. *J Phycol*. [accessed 2023 Feb 23];36(1):3–6. <https://doi.org/10.1046/j.1529-8817.2000.99161.x>
- Flynn T, Lehman P, Lesmeister S, Waller S. 2022. A visual scale for *Microcystis* bloom severity. figshare. Figure. [accessed 2023 Feb 23] <https://doi.org/10.6084/m9.figshare.19239882.v1>
- Glibert PM, Wilkerson FP, Dugdale RC, Raven JA, Dupont CL, Leavitt PR, Parker AE, Burkholder JM, Kana TM. 2016. Pluses and minuses of ammonium and nitrate uptake and assimilation by phytoplankton and implications for productivity and community composition, with emphasis on nitrogen-enriched conditions. *Limnol Oceanogr*. [accessed 2023 Feb 23];61(1):165–197 <https://doi.org/10.1002/lno.10203>

- Gobler CJ, Burkholder JM, Davis TW, Harke MJ, Johengen T, Stow CA, Van de Waal DB. 2016. The dual role of nitrogen supply in controlling the growth and toxicity of cyanobacterial blooms. *Harmful Algae*. 54:87-97. [accessed 2023 Feb 23] doi: <https://doi.org/10.1016/j.hal.2016.01.010>
- Guildford SJ, Hecky RE. 2000. Total nitrogen, total phosphorus, and nutrient limitation in lakes and oceans: Is there a common relationship? *Limnol Oceanogr*. [accessed 2023 Jan 6];45(6):1213-1223. <https://doi.org/10.4319/lo.2000.45.6.1213>
- Hammock BG, Moose SP, Solis SS, Goharian E, Teh SJ. 2019. Hydrodynamic modeling coupled with long-term field data provide evidence for suppression of phytoplankton by invasive clams and freshwater exports in the San Francisco Estuary. *Environ Manag*. [accessed 2023 Jan 4];63:703-717. <https://doi.org/10.1007/s00267-019-01159-6>
- Hartman R, Bosworth D, Rasmussen N, Flynn T, Bouma-Gregson K, Khanna S, Frantzich J. 2023. Harmful algal bloom and aquatic weeds data from the Sacramento-San Joaquin Delta, collected to evaluate the impact of the 2021 Temporary Urgency Change Order and Emergency Drought Barrier. Version 1. Environmental Data Initiative. Environmental Data Initiative. [accessed 2023 Apr 13]. <https://doi.org/10.6073/pasta/9e53e6f97568cacbf5f307a5645efc3>
- 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. Sacramento (CA): Report to the State Water Resources Control Board. [accessed 2023 Jan 6]. 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, Interagency Ecological Program 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/sfew.2024v22iss1art5>
- Hayes SP, Waller S. 1999. An extensive, patchy *Microcystis aeruginosa* bloom detected in the Delta. IEP Newsletter. [accessed 2023 Feb 23];12:11-12. <https://iep.ca.gov/Publications/Library>
- Hellweger FL, Martin RM, Eigemann F, Smith DJ, Dick GJ, Wilhelm SW. 2022. Models predict planned phosphorus load reduction will make Lake Erie more toxic. *Science*. [accessed 2023 Feb 23];376(6596):1001-1005. <https://doi.org/10.1126/science.abm6791>
- 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>
- Huber V, Wagner C, Gerten D, Adrian R. 2012. To bloom or not to bloom: contrasting responses of cyanobacteria to recent heat waves explained by critical thresholds of abiotic drivers. *Oecologia*. [accessed 2023 Jan 6];169(1):245-256. <https://doi.org/10.1007/s00442-011-2186-7>
- Huisman J, Codd GA, Paerl HW, Ibelings BW, Verspagen JMH, Visser PM. 2018. Cyanobacterial blooms. *Nat Rev Microbiol*. [accessed 2023 Jan 4];16(8):471-483. <https://doi.org/10.1038/s41579-018-0040-1>
- Isles PDF. 2020. The misuse of ratios in ecological stoichiometry. *Ecology*. [accessed 2023 Jan 6];101(11):e03153. <https://doi.org/10.1002/ecy.3153>
- Jabusch T, Trowbridge P, Heberger M, Guerin M. 2018. Modeling to assist identification of temporal and spatial data gaps for nutrient monitoring. Delta Regional Monitoring Program nutrients synthesis. [accessed 2023 Feb 23]. Available from: <https://www.sfei.org/documents/delta-nutrients-modeling>
- 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>
- Kendall C, Young MB, Silva SR, Kraus TEC, Peek S, Guerin M. 2015. Tracing nutrient and organic matter sources and biogeochemical processes in the Sacramento River and Northern Delta: proof of concept using stable isotope data. Menlo Park (CA): US Geological Survey.

- Kibuye FA, Zamyadi A, Wert EC. 2021. A critical review on operation and performance of source water control strategies for cyanobacterial blooms: Part II—mechanical and biological control methods. *Harmful Algae*. [accessed 2023 Jan 6];109:102119.
<https://doi.org/10.1016/j.hal.2021.102119>
- 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/sfew.2019v17iss3art2>
- Kring SA, Figary SE, Boyer GL, Watson SB, Twiss MR. 2014. Rapid in situ measures of phytoplankton communities using the bbe FluoroProbe: evaluation of spectral calibration, instrument intercompatibility, and performance range. *Can J Fish Aquatic Sci*. [accessed 2023 Feb 23];71(7):1087–1095.
<https://doi.org/10.1139/cjfas-2013-0599>
- Kudela RM, Howard MD, Monismith S, Paerl HW. 2023. Status, trends, and drivers of harmful algal blooms along the freshwater-to-marine gradient in the San Francisco Bay–Delta system. *San Franc Estuary Watershed Sci*. [accessed 2023 Jan 6];20(4).
<http://doi.org/10.15447/sfew.2023v20iss4art6>
- Lee J, Parker AE, Wilkerson FP, Dugdale RC. 2015. Uptake and inhibition kinetics of nitrogen in *Microcystis aeruginosa*: results from cultures and field assemblages collected in the San Francisco Bay Delta, CA. *Harmful Algae*. [accessed 2023 Jan 6];47:126–140.
<https://doi.org/10.1016/j.hal.2015.06.002>
- Lehman P, Marr K, Boyer G, Acuna S, Teh S. 2013. Long-term trends and causal factors associated with *Microcystis* abundance and toxicity in San Francisco Estuary and implications for climate change impacts. *Hydrobiologia*. [accessed 2023 Jan 4];718:141–158.
<https://doi.org/10.1007/s10750-013-1612-8>
- Lehman P, Teh S, Boyer G, Nobriga M, Bass E, Hogle C. 2010. Initial impacts of *Microcystis aeruginosa* blooms on the aquatic food web in the San Francisco Estuary. *Hydrobiologia*. [accessed 2023 Feb 23];637(1):229–248.
<https://doi.org/10.1007/s10750-009-9999-y>
- 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, Boyer G, Satchwell M, Waller S. 2008. The influence of environmental conditions on the seasonal variation of *Microcystis* cell density and microcystins concentration in San Francisco Estuary. *Hydrobiologia*. [accessed 2023 Feb 23];600(1):187–204.
<https://doi.org/10.1007/s10750-007-9231-x>
- Lehman PW, Kendall C, Guerin MA, Young MB, Silva SR, Boyer GL, Teh SJ. 2015. Characterization of the *Microcystis* bloom and its nitrogen supply in San Francisco Estuary using stable isotopes. *Estuaries Coasts*. [accessed 2023 Feb 6];38(1):165–178. <https://doi.org/10.1007/s12237-014-9811-8>
- 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(Supplement C):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. *Aquatic Microbial Ecology*. [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. *Quatern Intl*. [accessed 2023 Jan 4];621:16–25. <https://doi.org/10.1016/j.quaint.2019.12.003>
- Lenth RV, Buerkner P, Herve M, Love J, Riebl H, Singmann H. 2022. emmeans: estimated marginal means, aka least-squares means. Version 1.8.1. CRAN: Comprehensive R Archive Network. [accessed 2021 Aug 16]. Available from: <https://cran.r-project.org/web/packages/emmeans/index.html>

- Mioni C, Kudela R, Baxa D. 2012. Harmful cyanobacteria blooms and their toxins in Clear Lake and the Sacramento–San Joaquin Delta (California). Surface Water Ambient Monitoring Program report 10-058-150. [accessed 2023 Feb 22]. Available from: https://www.waterboards.ca.gov/waterrights/water_issues/programs/bay_delta/california_waterfix/exhibits/docs/petitioners_exhibit/dwr/DWR-728.pdf
- Monsen NE, Cloern JE, Lucas LV, Monismith SG. 2002. A comment on the use of flushing time, residence time, and age as transport time scales. *Limnol Oceanogr.* [accessed 2023 Feb 23];47(5):1545–1553. <http://doi.org/10.4319/lo.2002.47.5.1545>
- Moyle PB, Hobbs JA, Durand JR. 2018. Delta Smelt and water politics in California. *Fisheries.* [accessed 2023 Feb 23];43(1):42–50. <https://doi.org/10.1002/fsh.10014>
- Myer MH, Urquhart E, Schaeffer BA, Johnston JM. 2020. Spatio-temporal modeling for forecasting high-risk freshwater cyanobacterial harmful algal blooms in Florida. *Frontiers Environ Sci.* [accessed 2023 Jan 6];8:1–13. <https://doi.org/10.3389/fenvs.2020.581091>
- Nezbrytska I, Usenko O, Konovets I, Leontieva T, Abramiuk I, Goncharova M, Bilous O. 2022. Potential use of aquatic vascular plants to control cyanobacterial blooms: a review. *Water.* [accessed 2023 Jan 6];14(11):1727. <https://www.mdpi.com/2073-4441/14/11/1727>
- [NOAA NCEI] National Oceanic and Atmospheric Administration, National Centers for Environmental Information. 2022. Climate at a Glance: National Rankings, published November 2022. [accessed 2022 Nov 22]. Available from: <https://www.ncei.noaa.gov/access/monitoring/climate-at-a-glance/national/rankings>
- 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. Richmond (CA): San Francisco Estuary Institute. [accessed 2023 Feb 6]. Available from: http://www.sfei.org/sites/default/files/biblio_files/785%20Delta%20synthesis%20modeling.pdf
- NWQMC. 2021. Water Quality Portal. Washington (DC): National Water Quality Monitoring Council, United States Geological Survey (USGS), Environmental Protection Agency (EPA).
- O'Brien K, Meyer D, Waite A, Ivey G, Hamilton D. 2004. Disaggregation of *Microcystis aeruginosa* colonies under turbulent mixing: Laboratory experiments in a grid-stirred tank. *Hydrobiologia.* [accessed 2023 Feb 23];519:143–152. <https://doi.org/10.1023/B:HYDR.0000026501.02125.cf>
- Paerl HW, Hall NS, Calandrino ES. 2011. Controlling harmful cyanobacterial blooms in a world experiencing anthropogenic and climatic-induced change. *Sci Total Environ.* [accessed 2023 Feb 23];409(10):1739–1745. <https://doi.org/10.1016/j.scitotenv.2011.02.001>
- Paerl HW, Huisman J. 2008. Blooms like it hot. *Science.* [accessed 2023 Feb 23];320(5872):57–58. <https://doi.org/10.1126/science.1155398>
- Paerl HW, Otten TG, Kudela R. 2018. Mitigating the expansion of harmful algal blooms across the freshwater-to-marine continuum. *Environ Sci Tech.* [accessed 2023 Feb 23];52(10):5519–5529. <https://doi.org/10.1021/acs.est.7b05950>
- Parker AE, Dugdale RC, Wilkerson FP. 2012. Elevated ammonium concentrations from wastewater discharge depress primary productivity in the Sacramento River and the northern San Francisco Estuary. *Mar Poll Bull.* [accessed 2023 Feb 23];64(3):574–586. <http://dx.doi.org/10.1016/j.marpolbul.2011.12.016>
- Pick FR. 2016. Blooming algae: a Canadian perspective on the rise of toxic cyanobacteria. *Can J Fish Aquat Sci.* [accessed 2023 Feb 23];73(7):1149–1158. <https://doi.org/10.1139/cjfas-2015-0470>
- Plaas HE, Paerl HW. 2021. Toxic cyanobacteria: a growing threat to water and air quality. *Environ Sci Tech.* 55(1):44–64. [accessed 2023 Jan 4] <https://doi.org/10.1021/acs.est.0c06653>
- Ptacinik R, Andersen T, Tamminen T. 2010. Performance of the Redfield Ratio and a family of nutrient limitation indicators as thresholds for phytoplankton N vs. P limitation. *Ecosystems.* [accessed 2023 Feb 23];13(8):1201–1214. <https://doi.org/10.1007/s10021-010-9380-z>

- Raven JA, Gobler CJ, Hansen PJ. 2020. Dynamic CO₂ and pH levels in coastal, estuarine, and inland waters: Theoretical and observed effects on harmful algal blooms. *Harmful Algae*. [accessed 2023 Feb 23];91:101594.
<https://doi.org/10.1016/j.hal.2019.03.012>
- Reynolds C. 1992. Eutrophication and the management of planktonic algae: what Vollenweider couldn't tell us. In: Sutcliffe DW, Jones JG, editors. *Eutrophication : research and application to water supply*. London (UK): Freshwater Biological Association. p. 4–29. Available from: <http://hdl.handle.net/1834/22792>
- Reynolds CS. 1987. Cyanobacterial water-blooms. In: Callow JA, editor. *Advances in botanical research*. [Cambridge (MA)]: Academic Press. p. 67–143.
- Reynolds CS. 1999. Non-determinism to probability, or N : P in the community ecology of phytoplankton:nutrient ratios. *Archiv Fur Hydrobiol*. [accessed 2023 Feb 23];146:23–35.
<https://doi.org/10.1127/archiv-hydrobiol/146/1999/23>
- Reynolds CS. 2006. Nutrient uptake and assimilation in phytoplankton. *The ecology of phytoplankton*. Cambridge (UK): Cambridge University Press. p. 145–177.
- 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>
- Senn D, Preece E, Cooke J, Otten T. 2020. Identifying cyanobacterial harmful algal bloom toxins in Delta invertebrates: implications for native species and human health. *Delta Water Quality and Ecosystem Restoration Grant Program*. Grant Number Q2096021. Sacramento (CA): California Department of Fish and Wildlife.
- SFEI. 2022. HAB Satellite Analysis Tool. Richmond (CA): San Francisco Estuary Institute. Available from: <https://fhab.sfei.org/>
- Sommer T. 2020. How to respond? An introduction to current Bay–Delta natural resources management options. *San Franc Estuary Watershed Sci*. [accessed 2023 Feb 28];18(3).
<https://doi.org/10.15447/sfew.2020v18iss3art1>
- Spier C, Stringfellow W, Hanlon J, Estiandan M, Koski T, Kaaria J. 2013. Unprecedented bloom of toxin-producing cyanobacteria in the southern Bay–Delta Estuary and its potential negative impact on the aquatic food web. University of the Pacific Ecological Engineering Research Program Report 4.5.1. [accessed 2023 Feb 23]. Available from: https://www.waterboards.ca.gov/waterrights/water_issues/programs/bay_delta/california_waterfix/exhibits/docs/petitioners_exhibit/dwr/DWR-745.pdf
- Strong AL, Mills MM, Huang IB, van Dijken GL, Driscoll SE, Berg GM, Kudela RM, Monismith SG, Francis CA, Arrigo KR. 2021. Response of lower Sacramento River phytoplankton to high-ammonium wastewater effluent. *Elementa: Sci Anthro*. [accessed 2021 May 20];9(1).
<https://doi.org/10.1525/elementa.2021.040>
- [SWRCB] State Water Resources Control Board. 2018. Water Quality Control Plan for the San Francisco Bay/Sacramento–San Joaquin Delta Estuary. Resolution no. 2018-0059. Sacramento (CA): SWRCB. [accessed 2023 Feb 23]. Available from: https://www.waterboards.ca.gov/plans_policies/docs/2018wqcp.pdf
- [SWRCB] State Water Resources Control Board. 2021. Order conditionally approving a petition for temporary urgency changes to license and permit terms and conditions requiring compliance with Delta water quality objectives in response to drought conditions. Sacramento (CA): California Environmental Protection Agency, and SWRCB. [accessed 2023 Feb 23]. Available fom: https://www.waterboards.ca.gov/waterrights/water_issues/programs/drought/docs/tucp/2015/tucp_order070315.pdf
- [SWRCB] State Water Resources Control Board. 2022. Order WR 2022-0095. Sacramento (CA): California Environmental Protection Agency, SWRCB. [accessed 2023 Feb 23]. Available from: https://www.waterboards.ca.gov/waterrights/board_decisions/adopted_orders/orders/2022/wro2022_0095.pdf
- Terzopoulos D, Witkin A. 1988. Physically based models with rigid and deformable components. *IEEE Comput Graph Appl*. [accessed 2023 Feb 23];8(6):41–51. <https://doi.org/10.1109/38.20317>

- [USEPA] US Environmental Protection Agency. 2016. Method 546: determination of total microcystins and nodularins in drinking water and ambient water by Adda enzyme-linked immunosorbent assay. USEPA. [accessed 2023 Apr 13]. Available from: <https://www.epa.gov/sites/default/files/2016-09/documents/method-546-determination-total-microcystins-nodularins-drinking-water-ambient-water-adda-enzyme-linked-immunosorbent-assay.pdf>
- Wan L, Chen X, Deng Q, Yang L, Li X, Zhang J, Song C, Zhou Y, Cao X. 2019. Phosphorus strategy in bloom-forming cyanobacteria (*Dolichospermum* and *Microcystis*) and its role in their succession. *Harmful Algae*. [accessed 2023 Feb 23];84:46–55. <https://doi.org/10.1016/j.hal.2019.02.007>
- Wilhelm SW, Bullerjahn GS, McKay RML, Moran MA. 2020. The complicated and confusing ecology of *Microcystis* blooms. *mBio*. 11(3):e00529–00520. [accessed 2023 Jan 4]. <https://doi.org/10.1128/mBio.00529-20>
- World Health Organization (WHO). 2021. WHO guidelines on recreational water quality: volume 1: coastal and fresh waters. Geneva (CH): World Health Organization.
- Wu Z, Shi J, Li R. 2009. Comparative studies on photosynthesis and phosphate metabolism of *Cylindrospermopsis raciborskii* with *Microcystis aeruginosa* and *Aphanizomenon flos-aquae*. *Harmful Algae*. [accessed 2023 Feb 23];8(6):910–915. <https://doi.org/10.1016/j.hal.2009.05.002>
- Wynne T, Meredith A, Briggs T, Litaker W, R. Stumpf. 2018. Harmful algal bloom forecasting branch ocean color satellite imagery processing guidelines. NOAA Technical Memorandum NOS NCCOS 252. Silver Spring (MD): National Oceanic and Atmospheric Administration. [accessed 2023 Feb 23].
- Zepernick BN, Wilhelm SW, Bullerjahn GS, Paerl HW. 2022. Climate change and the aquatic continuum: a cyanobacterial comeback story. *Environ Microbiol Rep*. [accessed 2023 Feb 23];15(1):3–12. <https://doi.org/10.1111/1758-2229.13122>