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RESEARCH

Regional Variability in Conditions Favoring Cyanobacterial Harmful Algal Blooms in the Sacramento–San Joaquin Delta

Ellen P. Preece^{*1}, Gry Mine Berg², Karen Odkins³, Tricia Lee⁴, Jenna Rinde³

ABSTRACT

Cyanobacterial harmful algal blooms (CHABs), often comprising the cyanobacteria genus *Microcystis*, are an increasing water-quality concern in the large, hydrologically complex, Sacramento–San Joaquin Delta (Delta). Monitoring CHABs in estuarine environments is challenging because of the dynamic physical, chemical, and biological gradients across the freshwater–saltwater continuum. Here we provide an overview and synthesis of environmental drivers known to influence CHAB formation. We analyzed long-term environmental data—including flow, turbidity, temperature, salinity, and nutrients compiled from routine monitoring stations—to assess variability across seven defined regions of the Delta. Our results highlight significant differences in environmental

conditions among regions. The upper San Joaquin River (USJR) region has previously been recognized as one of the areas in the Delta most prone to CHAB events, and in our analyses exhibited the highest summer water temperatures, elevated nutrient concentrations, and low turbidity all conditions that favor CHAB development. In contrast, the lower San Joaquin River (LSJR) and lower Sacramento River (LSR) regions had cooler temperatures and higher turbidity, which are generally less favorable for bloom formation. While water temperatures in the East Delta (ED) were relatively cool, they increased more rapidly than in other regions, with an observed warming trend in June of approximately 0.2 °C per year. The ED was also the region that had the least amount of environmental monitoring relative to the other study regions and had no consistent nutrient data. Enhanced monitoring in the ED and continued monitoring in the other regions will be critical for tracking climate-driven changes in environmental conditions that support CHAB proliferation.

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INTRODUCTION

Situated between the Sacramento and San Joaquin rivers at the head of San Francisco Bay, the Sacramento–San Joaquin Delta (Delta) comprises approximately 700 miles of sloughs, river channels, creeks, flooded islands, and marinas,

across an area approximately 900 square miles (2,300 km²) in size (Whipple et al. 2012; Cloern et al. 2021). This large network of sloughs and river channels—connected to San Francisco Bay at the confluence of the two rivers—is hydraulically forced by riverine inflows, diversion of water to southern California via two aqueduct systems, agricultural intakes and water drainages within the Delta, and propagation of water with semi-diurnal tide. On average, the Sacramento River comprises ~85% of the total freshwater inflow to the Delta, with the San Joaquin River comprising close to ~11% and the remainder made up by smaller rivers (Kimmerer 2002). The Delta has a typical Mediterranean climate, with precipitation generally falling only between October through March. Delta inflows are sensitive to cycles of drought and precipitation, and demonstrate extreme interannual variability from year to year, leading not only to variation in water levels but also salinity (Jassby et al. 1995; Dettinger et al. 2016).

The Delta consists of a crisscrossing network of sloughs and river channels, in which “islands” are formed between the channels. Formerly, these were marshlands, but today they are diked and primarily used for agriculture (Whipple et al. 2012). Superimposed on this hydrologically variable habitat is the legacy of hydraulic gold mining, which generated a massive sediment supply starting in the mid-1800s. Suspended-sediment delivery from the Central Valley rivers to the Delta has declined as a result of multiple factors, including sediment retention in reservoirs behind mid-20th-century dams, deposition within flood bypasses, and structural modification of river channels (Wright and Schoellhamer 2004; Stern et al. 2016).

Sediment deposition continues in the Delta, but at a reduced rate compared to pre-impoundment conditions, largely driven by erosion (Schoellhamer et al. 2012). Legacy sediment deposits as well as most current sediment inputs predominantly comprise fine sediments, which are continually re-suspended with the tides and currents (Schoellhamer and Wright 2003; Ganju et al. 2008). Re-suspension of sediments constitutes

the principal mechanism of light attenuation in the water column, thereby constraining photosynthetic activity and primary production across the Delta and San Francisco Bay (Cloern 1987; Alpine and Cloern 1988; Jassby et al. 2002; Strong et al. 2021). As a result, the biomass of phytoplankton in Delta waterways is relatively low. Moreover, two invasive filter-feeding Asian clams were introduced to the Bay-Delta—*Corbicula fluminea* (in the 1940s) and *Potamocorbula amurensis* (in the 1980s) which further depressed phytoplankton biomass as a result of increased grazing pressures (Alpine and Cloern 1992; Crauder et al. 2016; Hammock et al. 2019; Mussen et al. 2024).

Agricultural run-off and tailwaters contribute substantial loads of nutrients to Delta waterways (Jassby and Cloern 2000; Preece et al., this issue; Saleh and Domalgaski 2015). In addition, contributions of nutrients from sources such as wastewater discharges and urban stormwater runoff add to the load (Senn and Novick 2014; Novick et al. 2015). Although some upgrades to wastewater treatment plants (WWTPs) have reduced inorganic nitrogen inputs (Saleh and Domalgaski 2021), nutrient enrichment in the Delta persists from legacy phosphorus pools and ongoing anthropogenic inputs. As a result of relatively low phytoplankton biomass, inputs of nutrients to Delta waterways are mostly in excess of phytoplankton demand, leading to variable degrees of unused residual nutrients in the water column (Jassby 2008). Taken together, the abovementioned variations of physical, hydrological, chemical, and biological factors have led to a complex mosaic of habitats in the Delta.

In tandem with anthropogenic modifications and climate change, the Delta has been plagued by cyanobacterial harmful algal bloom (CHAB) events. Delta CHAB events are typically dominated by the potentially toxin-producing genus *Microcystis*, which was first reported in 1920 but was not observed in colonial form until 1999 (Lehman et al. 2005). Since 1999, *Microcystis* blooms have been occurring annually in the Delta (Lehman et al. 2017, 2022). Other common

cyanobacteria which have also been observed in some portions of the Delta include genera such as *Aphanizomenon*, *Planktothrix*, *Dolichospermum*, *Pseudanabaena*, and *Planktolyngbia* (Lehman et al. 2008, 2017, 2022; Spier et al. 2013; Perry et al. 2025, 2025; Bouma–Gregson et al. 2024).

Given the diversity and complexity of habitats, CHABs do not occur uniformly across the Delta. Visual observations as well as sporadic special studies indicate that certain regions are more prone to CHAB events, both in frequency and intensity (Lehman et al. 2017; Bouma–Gregson et al. 2024; Preece, Otten, and Cooke 2024). In addition to the Delta’s natural complexity, numerous jurisdictional boundaries and varying perspectives on the goals and priorities for monitoring may confer challenges for CHAB monitoring (Kudela et al. 2023). To date, monitoring and assessments of CHABs in the Delta have relied on special studies, intermittent monitoring, and leveraging parts of established water-quality programs (Lehman et al. 2005, 2013, 2022). Because of the short-lived nature of many of these studies—especially where the most severe CHABs are known to occur—it is not known whether CHAB events are increasing in severity and frequency or whether they have reached an equilibrium.

In response to the lack of formal monitoring for CHABs, Delta natural resource agencies have developed a framework for future collaborative monitoring and management of CHABs in the Delta (Delta CHAB Monitoring Strategy; Preece, Berg, et al. 2024). Building on the Delta CHAB Monitoring Strategy, our two-part paper leverages the initial data analysis to advance understanding and management of CHABs. First, in this paper we synthesize water-quality data derived from a number of different water-quality monitoring programs to assess spatial and temporal patterns of key environmental drivers (e.g., flow, temperature, salinity, turbidity, nutrients) that potentially enhance or limit the growth of CHABs across the Delta. In the second paper we synthesize CHAB monitoring parameters (e.g., chlorophyll, the *Microcystis* visual index, *Microcystis* detected by microscopy,

Microcystis detected by quantitative polymerase chain reaction, microcystins in water grab samples, and *Microcystis* seedstock). Collectively, the information used in these papers can be used to inform recommendations to incorporate into future Delta monitoring.

STUDY DESIGN AND METHODS

As mentioned above, CHAB occurrences vary across the Delta. To facilitate our analysis of CHAB occurrences, and synthesis of potential drivers linked to the occurrences, the Delta was divided into seven geographic regions: the Cache Slough Complex (CSC), the lower Sacramento River (LSR), the Central Delta (CD), the lower San Joaquin River (LSJR), the upper San Joaquin River (USJR), the South Delta (SD), and the East Delta (ED) (Figure 1). These regions were delineated based on existing knowledge of Delta CHABs and previous studies that have divided the Delta into regions for ecological comparisons (Bouma–Gregson et al. 2024; Hartman et al. 2024).

Several ongoing Delta monitoring efforts collect continuous as well as discrete environmental data that are available from public data portals (Table 1). Agencies that manage continuous and discrete water-quality monitoring stations include the California Department of Water Resources (CDWR), California Department of Fish and Wildlife (CDFW), US Bureau of Reclamation (Reclamation), and the US Geological Survey (USGS). While these monitoring programs were not designed to collect information on CHAB drivers, they provide useful data for better understanding CHABs across the Delta.

The Eulerian monitoring approach, which captures water-column properties as they flow past fixed monitoring points, provides an effective basis for studying long-term trends and detecting changes in environmental conditions over time. Since these monitoring programs have been in place for several decades, there exists a cache of environmental data that can be used in calibrating ecological models as well as for interpreting drivers of CHAB events. Below, we summarize water-quality constituent data

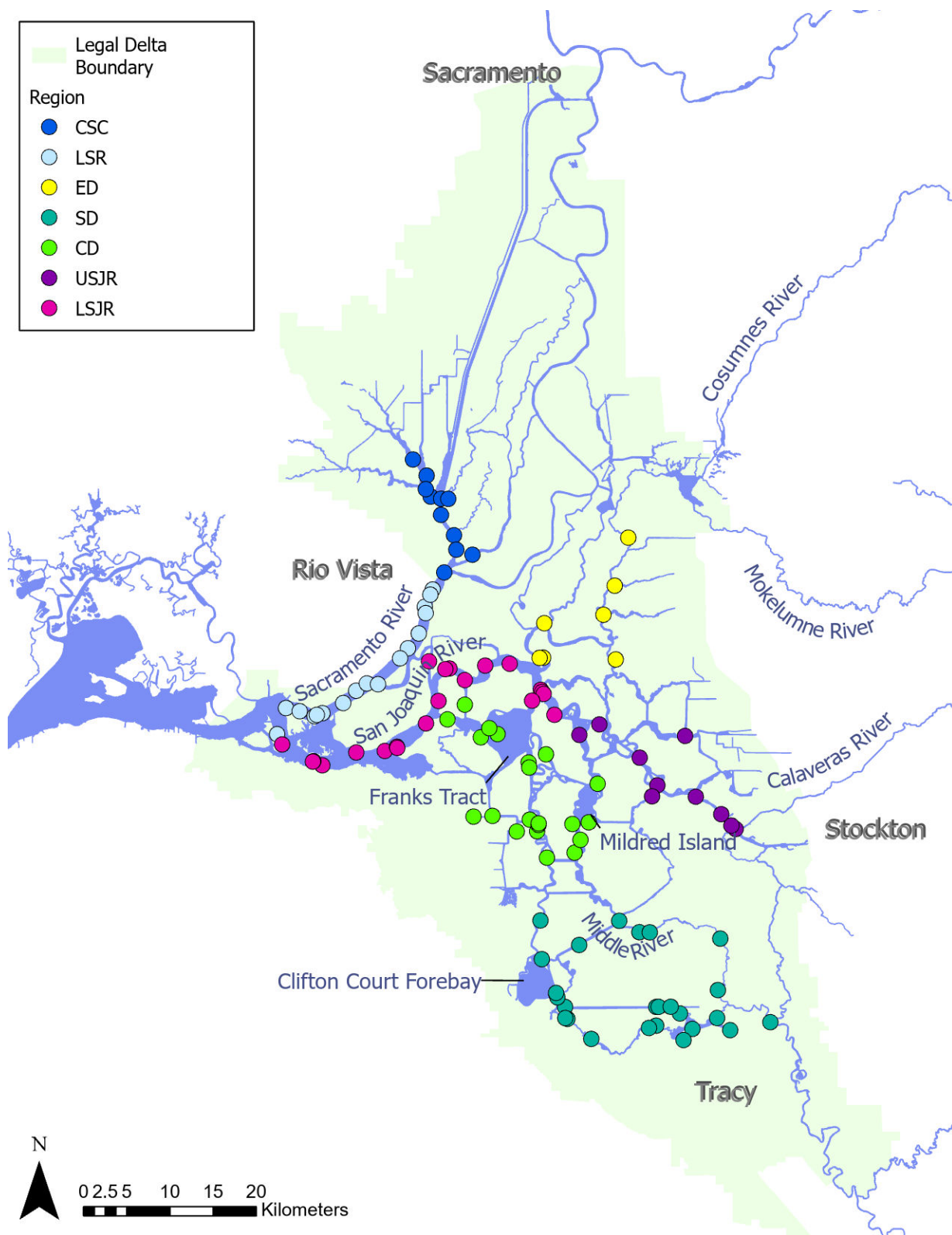


Figure 1 Map of the Sacramento-San Joaquin Delta showing the seven different regions used for the study analysis. Each *circle* represents an individual station, and *colors* are used to designate each region. CSC = Cache Slough Complex, LSR = lower Sacramento River, CD = Central Delta, LSJR = lower San Joaquin River, USJR = upper San Joaquin River, SD = South Delta, and ED = East Delta.

Table 1 Temporal and spatial information about existing programs that monitor environmental drivers relevant to CHABs. The spatial scope describes the general areas the monitoring program oversees. Individual monitoring sites may have been added, removed, or moved by programs over time. Monitoring frequency may also have changed over time. CDWR = California Department of Water Resources, CDFW = California Department of Fish and Wildlife, USGS = United States Geological Survey.

Agency	Program	Spatial scope	Monitoring frequency	Environmental drivers	Monitoring time-span
CDWR	Environmental Monitoring Program	San Pablo Bay, Suisun Bay, Suisun Marsh, Montezuma Slough, Sacramento River, San Joaquin River, Old and Middle rivers	At least monthly	nutrients, water temperature, turbidity, conductivity, pH, dissolved oxygen	1975–present
CDWR	Yolo Bypass Fish Monitoring Program	Yolo Bypass, Cache Slough Complex, Sacramento River	variable, roughly monthly, typically December/January through June	water temperature, turbidity, conductivity, pH, dissolved oxygen	1998–present
CDWR	Water Quality Evaluation Section	South Delta, Central Delta, North Delta	monthly	water temperature, turbidity, conductivity, pH, dissolved oxygen	1999–present
CDFW	Fish Restoration Program Effectiveness Monitoring Team	Cache Slough Complex, Lower Sacramento River, Confluence, Suisun Bay, Suisun Marsh	spring, summer, and fall	nutrients, water temperature, turbidity, conductivity, pH, dissolved oxygen	2016–present
USGS	California Water Science Center Biogeochemistry Group	Delta-wide during mapping surveys (30 sites), currently ~12 fixed stations, but amount of sampling depends on funded projects	monthly, spring, summer, fall	nutrients, water temperature, turbidity, conductivity, pH, dissolved oxygen	1971–present
USGS	SFB Research and Monitoring Program	San Francisco Bay, San Pablo Bay, Suisun Bay, and lower Sacramento River	every 2 weeks, monthly, year-round	nutrients, water temperature, turbidity, conductivity, pH, dissolved oxygen	1969–present

from these programs consolidated from the Environmental Data Initiative (EDI) Delta Water Quality Integrated Dataset Package (Bashevkin et al. 2022), and through personal communication with individual monitoring programs.

Robust water-quality data exist for a number of environmental drivers previously demonstrated to play important roles in CHAB occurrences in the Delta, including streamflow, water temperature, salinity, turbidity (and by extension light availability), and nutrient concentrations (e.g., Lehman et al. 2013, 2017; Berg and Sutula 2015). For the current analyses, we retrieved turbidity, salinity, water temperature, nitrate + nitrite, and orthophosphate) concentration data from the CDWR’s Environmental Monitoring Program (EMP) and North Central Regional Office (NCRO) (CDWR 2024) as well as from Battey and Perry (2023), the CDWR (2025), and the California Department of Fish and Wildlife (CDFW) (Bashevkin et al. 2022). When possible,

we used all available datasets to show how these drivers may affect cyanobacteria in different regions of the Delta. Data were available from 115 fixed stations; however, data availability varied across stations and drivers. For example, no data were available for nutrient concentrations in the ED. Likewise, the nitrogen analysis was limited to nitrate and nitrite because more than half of the ammonia measurements were below detection limits.

Data from each dataset were summarized from 2008 to 2022, except for nutrient data: only limited nutrient data were available before 2014. Nutrient data were summarized from 2014 to 2022, except in the SD where they were only summarized from 2017 to 2022. From 2007 to 2019, turbidity was reported in nephelometric turbidity units (NTUs). From 2019 to present, turbidity was reported in formazin nephelometric units (FNUs). While the values produced by each of these measures can vary slightly, and exact comparability depends on

the specific instruments used, for this analysis the data are treated as comparable, though potential differences cannot be ruled out (Matos et al. 2024).

Although streamflow and residence times are important for understanding environmental conditions that support CHAB, synthesizing sub-regional flow was beyond the scope of our study. Instead, we rely on past studies that have thoroughly analyzed flow dynamics and how water-quality constituents move within the Delta (e.g., MacWilliams et al. 2016; Schoellhamer et al. 2016; Hutton et al. 2019). We incorporated flow data into our analysis by examining flow over time in the Sacramento and San Joaquin rivers at locations near the outer boundaries of the Delta. The CDWR operates a fixed water-quality station at the San Joaquin River at Vernalis and in the Sacramento River at Freeport (CDWR 2026). These stations provide a representative measure of total upstream San Joaquin River and Sacramento River inflows and were more appropriate to analyze then looking at discrete flow measurements across the different regions. Water-quality station records were acquired through the California Water Data Library by querying the database for flow from 2008 to 2022 (CDWR 2026). Flow data were processed using a cosine Lanczos filter to remove the tidal component of the time-series, leaving only the net advection. The Sacramento and San Joaquin Valley Hydrologic Classification Index was used to classify water year types (CDEC 2025). This index classifies water years as wet, above normal, below normal, dry, and critical, based on measured unimpaired runoff. For the purposes of this analysis, dry and critical years were grouped together since both are considered drought years. Below normal and above normal years are also grouped, because these are hydrologically similar.

All available data for the calendar year were included in the data interpretation and in statistical models. April through October was selected as the period for regional analysis section based on the typical seasonal onset of water temperatures reaching 19 °C, the temperature associated with the initial appearance of cyanobacteria in Delta waters

(Lehman et al. 2013). Although cyanobacteria and cyanotoxins may persist into November or even December in some areas, their presence typically tapers off by October (Preece et al., this issue). As such, the focus of the regional analysis is April through October.

Data Analysis

To evaluate temporal trends in turbidity, salinity, water temperature, and nutrient concentrations, data from all monitoring sites within each region were aggregated to compute monthly mean values for each calendar year. These regional monthly means served as the basis for trend analysis over time (i.e., by year). Medians were also calculated and are included in Appendix A (see Tables A1 through A5).

Generalized Additive Mixed Models (GAMMs) were then used to model annual temporal variation in five water-quality parameter response variables (temperature, conductivity, salinity, turbidity, nitrate + nitrite, and orthophosphate) across the seven Delta regions, following procedures outlined by Zuur et al. (2009). For some variables, fewer regions were modeled because insufficient data were available. Turbidity data was natural logarithmic transformed to meet the assumption of normality. GAMMs were chosen to account for the non-linear nature of the environmental variables while also accounting for spatial and temporal autocorrelation. Generalized additive models essentially model subsets of predictor variables using first-, second-, or third-order polynomials that are stitched together to form non-linear patterns (Zuur et al. 2009). The variables were modeled as:

$$y_{jk[i]} = \beta_0 + s(\text{day of year}) + a_j + a_k + \varepsilon_{jk[i]}$$

$$a_j \sim N(0, \theta^2 a_j) \text{ for } j = 1 \dots J_{\text{station}}$$

$$a_k \sim N(0, \theta^2 a_k) \text{ for } k = 1 \dots K_{\text{year}}$$

$$\varepsilon \sim N(0, \sigma_\varepsilon^2)$$

where $y_{jk[i]}$ was the expected environmental response value at station j in year k , β_0 was the intercept, $s(\text{day of year})$ was the smoothing environmental response variable over day of year

using a cyclic cubic spline regression smoothing function, a_j was the random effect for station, a_k was the random effect for year, and $\varepsilon_{jk[i]}$ was the residual error for each year and station. An autoregressive correlation structure was used to account for autocorrelation between day of year and stations. The random effects a_j and a_k were assumed to be normal with a mean of 0 and variance of $\sigma_{a_j}^2$ and $\sigma_{a_k}^2$ for each station and year, respectively. $\varepsilon_{jk[i]}$ was assumed to be normal with a mean of 0 and variance of σ_{ε}^2 . We conducted our statistical modeling with the ‘mgcv’ package version 1.9-3 (Wood 2004) in R version 4.5.0 (R Core Team 2025). R values for each model can be found in Table 2, and regional smoothing term p -values can be found in Appendix A.

We used a mixed-effects model to simulate temperature, salinity, turbidity, nitrate + nitrite, and orthophosphate as a function of region, with random intercepts for the month (from April to October) nested within water year and for sampling stations. The model was fit using the restricted maximum likelihood method. Post-hoc Tukey pairwise comparisons were used to determine significant differences to a 95% confidence level between regions. Model performance statistics can be found in Appendix A.

Finally, we employed principal component analysis (PCA) to compare patterns between discrete water-quality data (temperature, salinity, turbidity, nitrate + nitrite, orthophosphate, and Secchi depth) and to visualize differences in water quality between six of the seven regions. No nutrient data were available for the ED, so this region was omitted from the PCA analysis. The PCA used monthly mean values (April to October) for each region from 2014 to 2022 as model inputs. Secchi depth measurements were not available for April and May in the CSC, so the mean Secchi depth from June through October was used as inputs for those months. The PCA was conducted using the ‘factoextra’ package (Kassambara and Mundt 2020) in R version 4.5.0 (R Core Team 2025). To verify the PCA results and test the significance of clustering between years, a permutational multivariate analysis of variance (PERMANOVA)

Table 2 R^2 values from Generalized Additive Mixed Models (GAMMs) used to characterize annual temporal variation in environmental response variables across regions of the Delta

Response variable	R
Temperature	0.92
Salinity	0.20
Turbidity	0.26
Nitrate	0.36
Orthophosphate	0.23

based on Euclidean distance matrices was performed with 999 permutations using the ‘vegan’ package (Anderson 2017). Euclidean distance matrices were utilized because the PCA was calculated with Euclidean geometry. A pairwise comparison using Euclidean distance and the Holm correction was used to determine significant differences between regions.

ENVIRONMENTAL DRIVERS OF DELTA CHABS

CHABs in the Delta are promoted by a combination of environmental, climatic, and anthropogenic factors. Environmental drivers known to create favorable conditions for CHABs in the Delta include areas with long residence times and low streamflow, sufficient light availability, warm water temperatures, and expansive freshwater areas with low salinity. Each of these drivers is analyzed and discussed in detail below.

While the word “driver” suggests a positive effect in terms of growth of CHAB species, each driver can have either a positive or negative effect, depending on its range relative to specific growth thresholds. For example, water temperatures below 19 °C may limit growth rates of *Microcystis* and formation of blooms (Lehman et al. 2013) while temperatures above 19 °C—and particularly above 25 °C—may promote blooms (e.g., You et al. 2018). Similarly, relatively high turbidities and water column mixing have been demonstrated to act as negative drivers, while decreased mixing and clear water act as positive drivers and promote CHAB blooms in the Delta (Lehman et al. 2017). Salinity, which may limit the distribution of

a CHAB event to the freshwater and low-salinity reaches of the Delta, mainly acts as a negative driver on its spread and distribution. While not covered here, biotic factors such as allelopathic compounds, infections, and grazing are also recognized as factors that can limit cyanobacteria growth or cause blooms to disappear (Harris et al. 2024).

Streamflow and Turbulence

Background

Blooms of cyanobacteria and CHAB species are sensitive to stream flow, which controls water column mixing (turbulence) and water residence time (i.e., the average time it takes to exchange the volume of water within a certain region). For cyanobacterial cells or colonies to accumulate and a bloom to occur, the growth rate of the CHAB species needs to be shorter than the residence time of the water (Paerl 2008). Areas with short residence times typically cannot produce high enough biomass to form a bloom because the cells that are produced are flushed downstream before they have a chance to accumulate. Conversely, areas with low channel velocities and high hydraulic residence times are more likely to promote cell accumulation, and aggregation in the case of *Microcystis* cells, which is a factor that contributes to high biomass and occurrence of blooms.

Delta-Specific Analysis

Inflow is driven by the combined streamflow in the Sacramento and San Joaquin rivers, with the Sacramento River comprising approximately 84% of the total from these two sources (Arthur et al. 1996; Cloern and Jassby 2012). Outflow from the Delta consists primarily of the difference between inflow and water diversions to the state (State Water Project) and federal (Central Valley Project) pumping projects, with additional losses to evapotranspiration and groundwater seepage, and typically represents around 70% of inflow annually (Kimmerer 2004; Cloern and Jassby 2012).

Inflow to the Delta varies substantially with precipitation and drought (Figures 2 and 3), with

wet years greatly reducing residence time in many areas of the San Francisco Estuary during the winter and spring months (Jassby et al. 1995; Kimmerer 2004). Conversely, in dry winters and springs, residence times increase along the Sacramento and San Joaquin rivers (Lucas and Thompson, 2012; Glibert et al. 2014; Hammock et al. 2019). During low inflow periods, residence times in the central and southern Delta are strongly influenced by agricultural diversions and exports through the State Water Project and Central Valley Project, which reduce residence time along the San Joaquin River (Hammock et al. 2019). During drought conditions when Delta inflow and outflow are reduced, management actions including salinity barriers and operation of gates such as the Delta Cross Channel, may influence residence time in localized regions (Kimmerer et al. 2019; Bouma-Gregson et al. 2024). Tides and geometric features of Delta waterways—including bends, junctions, shallow water areas, and levees—also influence water residence times (Healey 2008; Schoellhamer et al. 2016), particularly at smaller, regional scales (Gross et al. 2019).

Summertime algal blooms in the Delta can comprise green algae, cryptophytes, dinoflagellates miscellaneous flagellates, diatoms, or filamentous or colonial cyanobacteria (Lehman et al. 2017). Cyanobacteria are less competitive under strong mixing, which instead favors eukaryotic algae (Ibelings et al. 1994; Huisman et al. 1999). Thus, different taxa dominate under different hydrodynamic conditions. Compared to main channels, areas such as dead-end sloughs, marinas, and edge habitats experience lower flow and water exchange (Downing et al. 2016; Lenocho et al. 2021). High-velocity flows in main channels maintain shorter residence times and higher flushing rates, limiting phytoplankton accumulation (Jassby et al. 2002, 2008). In contrast, dead-end sloughs, floodplains, and marinas with limited water exchange experience elevated chlorophyll-*a* concentrations during summer, underscoring the importance of residence time in the accumulation of phytoplankton, including cyanobacteria

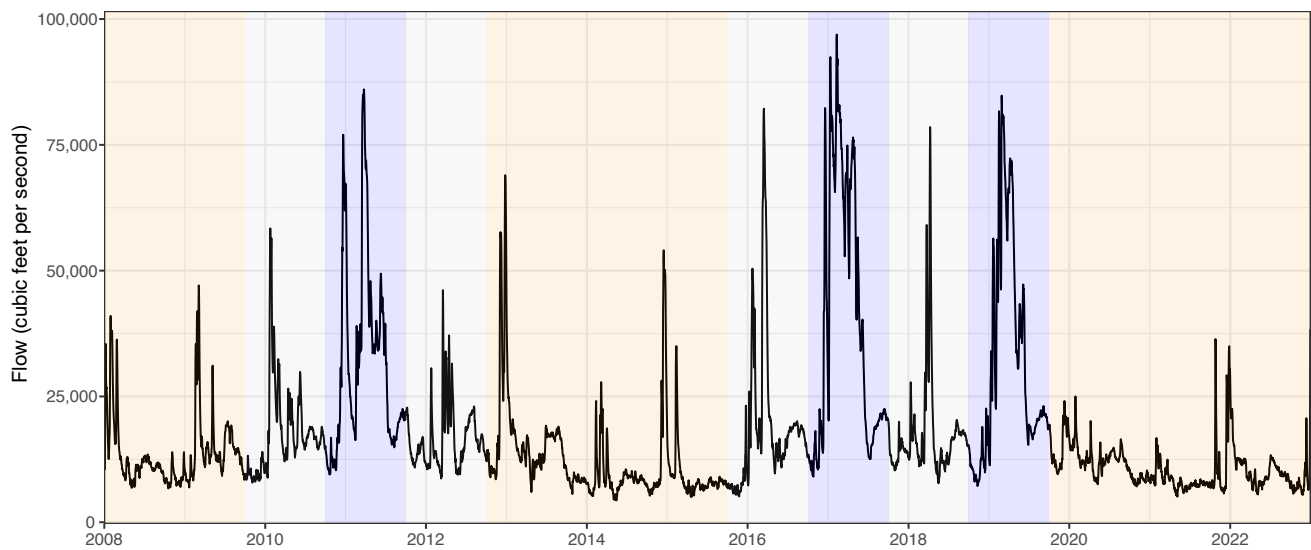


Figure 2 Flow in the Sacramento River at Freeport from 2008 to 2022. *Orange columns* represent dry/critical years, *grey columns* represent above normal/below normal years, and *blue columns* represent wet years.

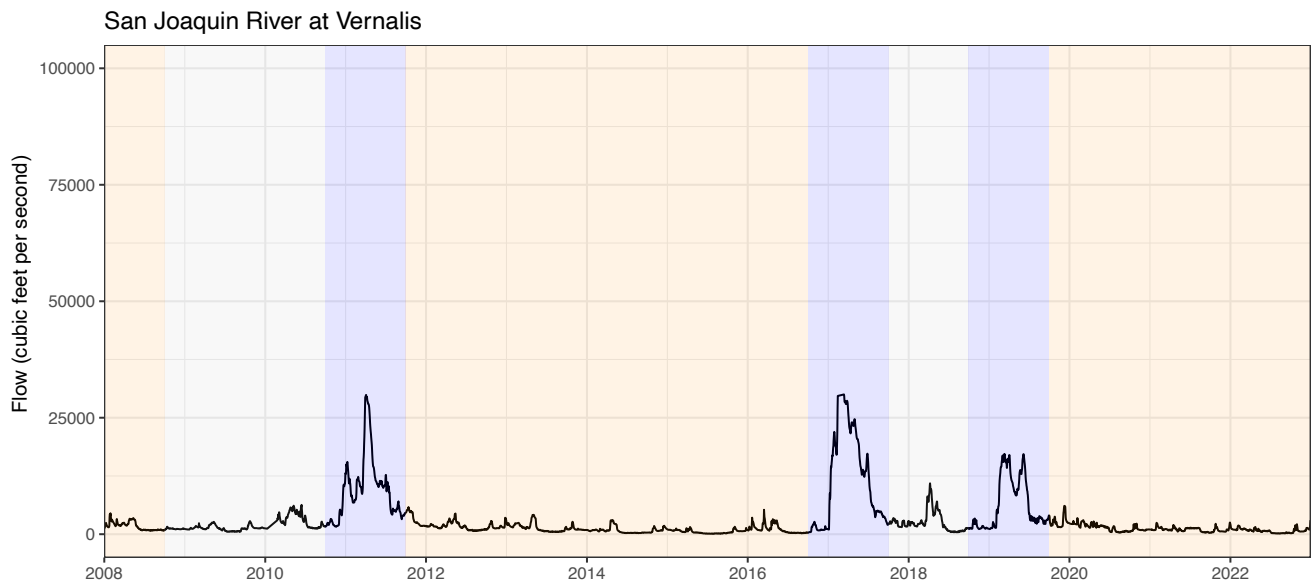


Figure 3 Flow in the San Joaquin River at Vernalis from 2008 to 2022. *Orange columns* represent dry/critical years, *grey columns* represent above normal/below normal years, and *blue columns* represent wet years.

(Schemel et al. 2004; Lehman et al. 2008; Downing et al. 2016; Loken et al. 2022; Preece, Otten, and Cooke 2024).

Sediment Re-Suspension and Water Column Light Availability

Background

Cyanobacterial dominance and succession are affected by numerous abiotic and biotic factors including light requirements (Wang et al. 2021). For CHAB species such as *Microcystis* that have

low photosynthetic efficiencies (e.g., Wu et al. 2009) and require exposure to continuous light to reach maximal growth rates (Mitrovic et al. 2003), their growth is restricted by mixing out of the euphotic zone and being exposed to fluctuating light (Visser et al. 2016). Because suspended sediments rapidly attenuate light with depth, suspended sediment concentrations strongly affect the depth of the euphotic zone. As concentrations increase, the depth of the euphotic zone—where light is sufficient for photosynthesis to occur—decreases. In general, productivity of phytoplankton, including CHAB species, decreases the more time phytoplankton spend below the euphotic zone (Cloern 1987; Alpine and Cloern 1988; Lucas and Cloern 2002; Mussen et al. 2023). Therefore, in a well-mixed water column, relatively high suspended sediment concentrations may affect CHAB species by limiting the light available for photosynthesis and growth (Visser et al. 2016).

In addition to growth requirements, light and photosynthesis are important for cyanobacteria to regulate their buoyancy through production and accumulation of carbohydrates within their cells, known as ballast (Thomas and Walsby 1985). Because cyanobacteria produce gas vesicles that render them positively buoyant, production of ballast enables them to counterbalance the effect of the gas vesicles and optimize their position in the water column, depending on temperature and light conditions (Ma et al. 2015; Yang et al. 2024). For example, over shorter time-scales *Microcystis* sp. undertake diel vertical migration. Over longer time-scales, the amount of ballast stored in the cell has been demonstrated to inversely correlate with growth rate and temperature in *Microcystis* sp. (Yang et al. 2012; Wang et al. 2013; Samudra 2023).

Delta-Specific Analysis

A persistent feature of the San Francisco Estuary, including the Delta, is the intense mixing of the water column as the result of winds, currents, and tidal oscillations (Cloern 1991; Kimmerer 2004). High-energy tidal forcing combined with riverine sediment loading (i.e., McDonald and Cheng 1997; Schoellhamer et al. 2012) leads to relatively high

suspended sediment concentrations and turbidity (Cloern 1987; May et al. 2003). Consequently, mixing and sediment re-suspension act as key negative controls on CHAB development in the Delta, likely restricting severe CHAB events to localized “hot spots” where mixing and turbidity are reduced (Preece, Otten, and Cooke 2024). Long-term monitoring data indicate a decline in turbidity since 1975, suggesting a shift toward more favorable conditions for cyanobacterial growth and CHAB formation (Hestir et al. 2016).

Turbidity is variable across the Delta during the summer and fall seasons, ranging from a monthly mean of 2 to 30 NTU depending on region (Figure 4). Though the turbidity dataset is very limited for the LSR and CSC, these regions have the highest turbidity relative to the other regions (Figures 4 and 5). Secchi depth measurements—available for much of the study period and used to assess water clarity—indicate that the LSR has lower clarity than the other regions, while the CSC’s clarity is also relatively low and comparable to that of the LSJR and SD (Figure 6). Elevated turbidity in the CSC has been previously identified as a key factor contributing to its suitability as habitat for species such as the endangered Delta Smelt (Nobriga et al. 2005). This is largely the result of the region’s bathymetry, wind fetch, and hydrodynamic conditions, which promote sediment retention through a combination of low freshwater inflow during the dry season, flood tide dominance, and limited tidal excursion (Schoellhamer et al. 2016). During the April through October period, the USJR and ED have the lowest turbidity while the CD, LSJR and SD have turbidity concentrations that are in between the high- and low-turbidity regions (Figures 4 and 5). Although part of the same river, summer turbidity in the LSJR region is approximately twice that occurring in the USJR region. This also holds true for Secchi depth measurements that show much higher water clarity in the USJR compared to the LSJR (Figure 6).

In particular, the regions diverge on turbidity during the month of August—a primary month for CHAB events—when turbidity is greatest in the SD region and lowest in the ED and USJR

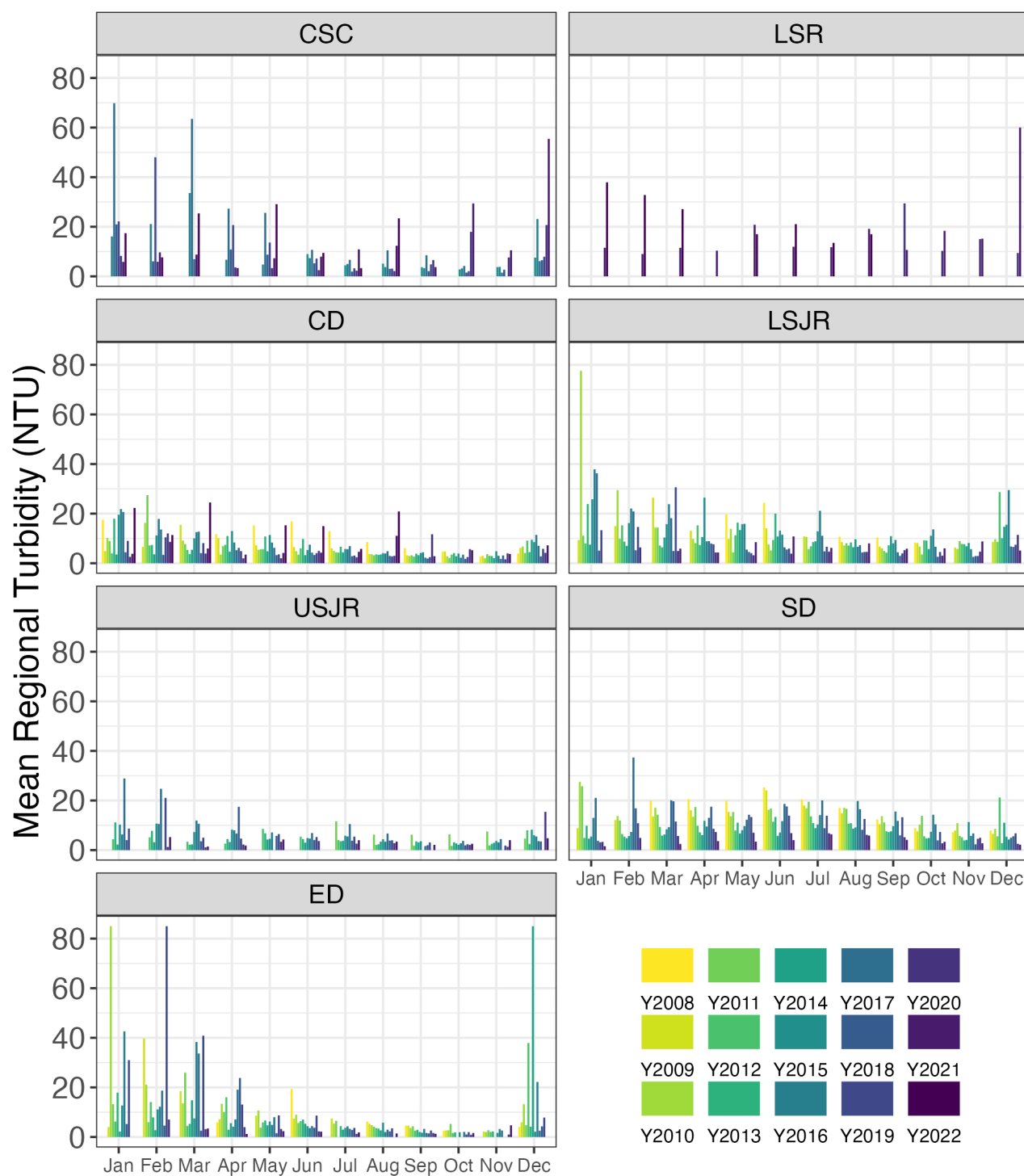


Figure 4 Mean turbidity in the seven Delta regions by month. CSC = Cache Slough Complex, LSR = lower Sacramento River, CD = Central Delta, LSJR = lower San Joaquin River, USJR = upper San Joaquin River, SD = South Delta, ED = East Delta.

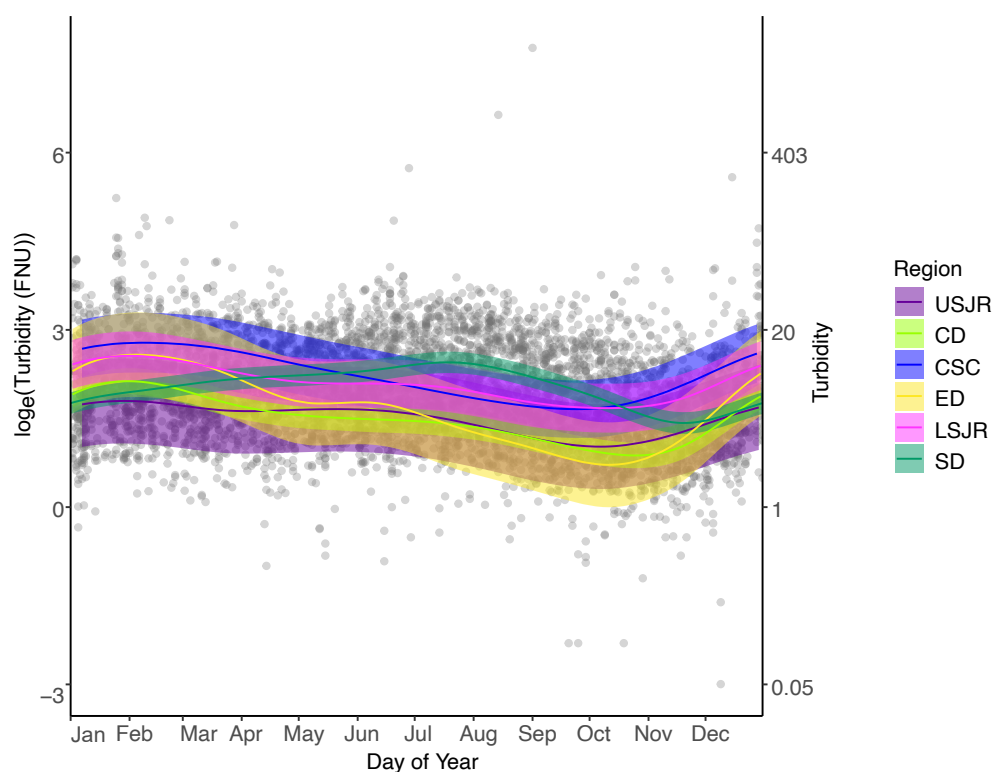


Figure 5 Observed log (turbidity [FNU]) across the calendar year (transparent gray points) shown with Generalized Additive Mixed Models (GAMMs) predicted Delta turbidity per region (colored lines). Shown with 95% confidence intervals (shaded areas). Right y-axis denotes back-transformed turbidity (FNU). CSC = Cache Slough Complex, CD = Central Delta, LSJR = lower San Joaquin River, USJR = upper San Joaquin River, SD = South Delta, ED = East Delta. The LSR = lower Sacramento River was removed from the analysis as a result of low data density.

region (Figure 5). During this month, the mean turbidity in the SD typically ranges from 6 to 20 FNU, while the mean turbidity ranges from 1 to 6 FNU in the ED and 2 to 7 in the USJR (Figure 4). For the entire dataset, the August median in the SD is 11.4 FNU, 3.5 in the ED, and 3.9 in the USJR (Table A2). The relatively high summertime turbidity in the SD has also been observed in other studies and attributed to the area having a high trap efficiency, which means that a high fraction of incoming sediment is deposited in the area (Schoellhamer et al. 2016). Slow advection of sediment southward also increases turbidity in the SD. This contrasts with the northern Delta that generally has a high load of incoming sediment, but low trap efficiency and higher advection. However, elevated summer turbidity in the SD may result primarily from high phytoplankton biomass in the water column rather than sediment re-suspension (Yuan 2021).

Temperature

Background

Temperature is recognized as one of the strongest positive drivers of CHAB events around the world (Paerl and Huisman 2008; Carey et al. 2012; Lehman et al. 2022). One reason is that cyanobacteria—compared with other phytoplankton groups—achieve higher growth rates at warmer temperatures (Berg and Sutula 2015). For example, You et al. (2018) found the optimal growth rate for *Microcystis* in the laboratory is 27.5 °C. In a survey of eight cyanobacteria, the growth optima of two *M. aeruginosa* strains were 30 to 32.5 °C and that of *Aphanizomenon gracile* was 32.5 °C. Lower growth temperature optima were observed in *Cynlindrospermopsis raciborskii* and *Planktothrix agardhii*, both 27.5 °C, while *Dolichospermum* had an optimum of 25 °C (Lüring et al. 2013). In another survey of six *Microcystis* strains, their temperature growth optima varied from 31 to 37 °C (Bui et al. 2018). *Microcystis* is notable for its ability to rapidly accelerate growth rates

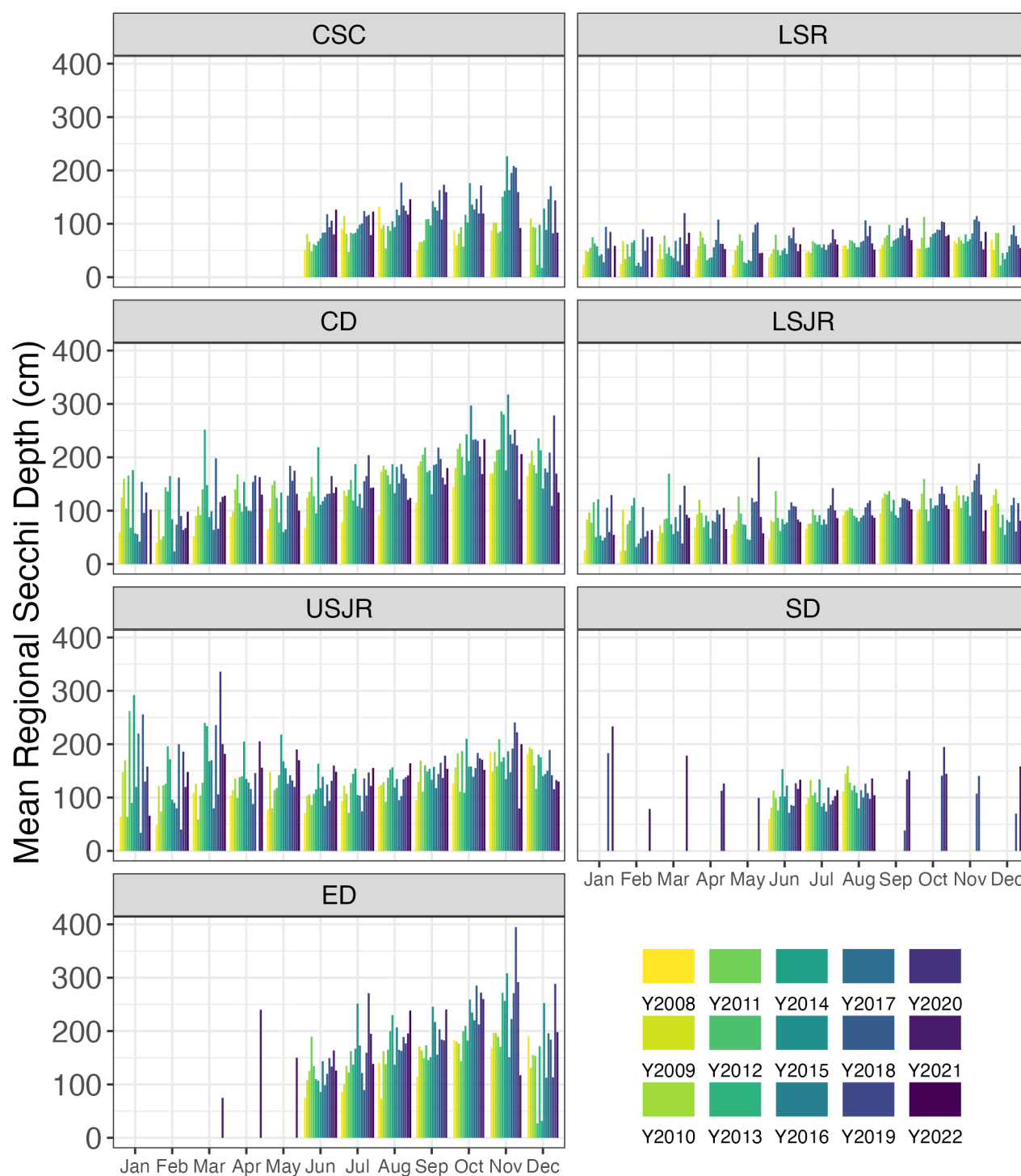


Figure 6 Mean regional Secchi Depth in the seven Delta regions by month for the period 2014 to 2022. CSC = Cache Slough Complex, LSR = lower Sacramento River, CD = Central Delta, LSJR = lower San Joaquin River, USJR = upper San Joaquin River, SD = South Delta, ED = East Delta.

with increasing temperature (Reynolds 2006; Carey et al. 2012). While the acceleration of growth rate per 10 °C increase in temperature (Q10) for cyanobacteria generally ranges from 1 to 4, it ranges from 4 to 9 for *Microcystis*, the highest recorded for any phytoplankton species, prokaryotic or eukaryotic (Reynolds 2006).

Delta-Specific Analysis

Initiation of *Microcystis* blooms in the Delta typically occurs when water temperatures reach approximately 19 °C (Lehman et al. 2013). Across most Delta regions this temperature is first reached in April, though in the LSR, the LSJR, and in most years within the ED, it does not occur until at least May or even June (Figures 7 and 8). Mean surface water temperatures recorded in the Delta during the summer are usually not as high as the growth optima of the various CHAB species mentioned above (Figure 7). However, water temperatures commonly exceed 23 °C in the main channels of the Delta during July–September, the period of peak CHAB abundance (Lehman et al. 2013; Figure 7). In contrast with our dataset from the main channels where high flushing rates may limit surface water temperatures, dead-end sloughs and marinas with lower rates of water column mixing and flushing are more susceptible to higher absolute temperatures (Preece et al., this issue). In these locations, surface water temperatures from July–September may range from 25 to 28 °C or warmer (Preece, Otten, and Cooke 2024) and could provide ideal conditions for CHAB species to out-compete other phytoplankton groups that have lower growth temperature optima (Berg and Sutula 2015 and references therein). Although these locations appear to have warmer temperatures, routine monitoring is almost entirely restricted to the main channels, and the limited data available from dead-end sloughs and marinas makes it difficult to evaluate temperature changes and trends.

Throughout the Delta, mean monthly surface water temperatures typically peak in July, but the absolute July temperature varies substantially by region (Figure 7). The regions with the lowest mean July surface water temperatures are in the

northern portion and include the LSR region (20.6–22.8 °C) and CSC region (20.6–23.2 °C), while the highest temperatures occur in the USJR region where they vary from 23.6 °C to 26.8 °C, followed by the SD region where they vary from 22.8 °C to 26.1 °C (Figure 7). Mean July surface water temperatures in the CD are in between the low and high regions, varying from 22.8 to 24.6 °C (Figure 7). For the entire dataset, the largest difference in temperature among regions occurs in the month of August (Figure 7). During this month, the highest temperature occurs in the USJR, followed by the SD and the CD regions (Figures 7 and 8). The overall median August temperature is 24.9 °C in the USJR, 24.2 °C in the SD, and 23.7 °C in the CD regions (Table A1).

Perhaps the most interesting month in terms of temperature changes over time in the Delta appears to be June. While at the beginning of the record presented in Figure 7 (2008), average June surface-water temperatures varied around 19–20 °C, the temperature hypothesized to promote the emergence of *Microcystis* from the sediments into the water column (Lehman et al. 2017). Since then, June temperatures have increased significantly and linearly across several regions. The steepest change has been in the ED with a rise of 0.20 °C per year, followed by the LSJR at 0.17 °C per year, and the central Delta at 0.09 °C per year (Table 3). An increase of 0.1 °C per year in the LSR is also notable though not significant (Table 3). In both the USJR and SD regions, surface-water temperatures are high relative to the other regions and do not appear to be increasing in the summer months as in the other regions (Table 3). For example, in the SD, June surface-water temperatures have not increased significantly, varying between 22.4 and 22.7 °C over the 2008–2022 time-period (Table 3, Figure 7).

Mean surface-water temperatures have also increased for May and October, extending the potential bloom season for *Microcystis* (e.g., Lehman et al. 2017), in several Delta locations (Figure 7). Previous studies suggest that *Microcystis* can persist in surface waters for 8 months or longer if temperatures in the

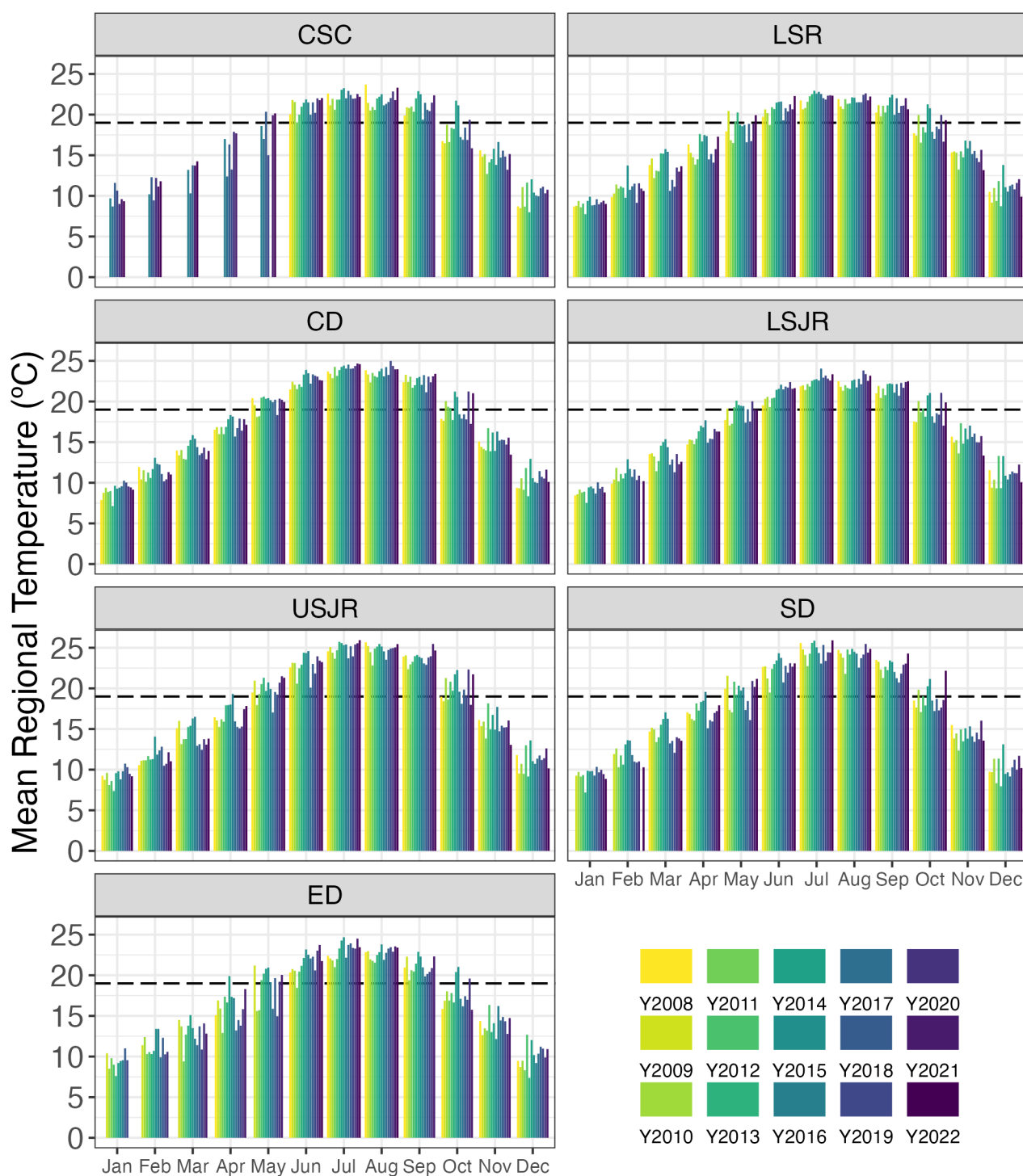


Figure 7 Mean regional temperature in the seven Delta regions by month. The *dashed horizontal line* shows the 19 °C temperature associated with the initial appearance of cyanobacteria in Delta waters. CSC = Cache Slough Complex, LSR = lower Sacramento River, CD = Central Delta, LSJR = lower San Joaquin River, USJR = upper San Joaquin River, SD = South Delta, ED = East Delta.

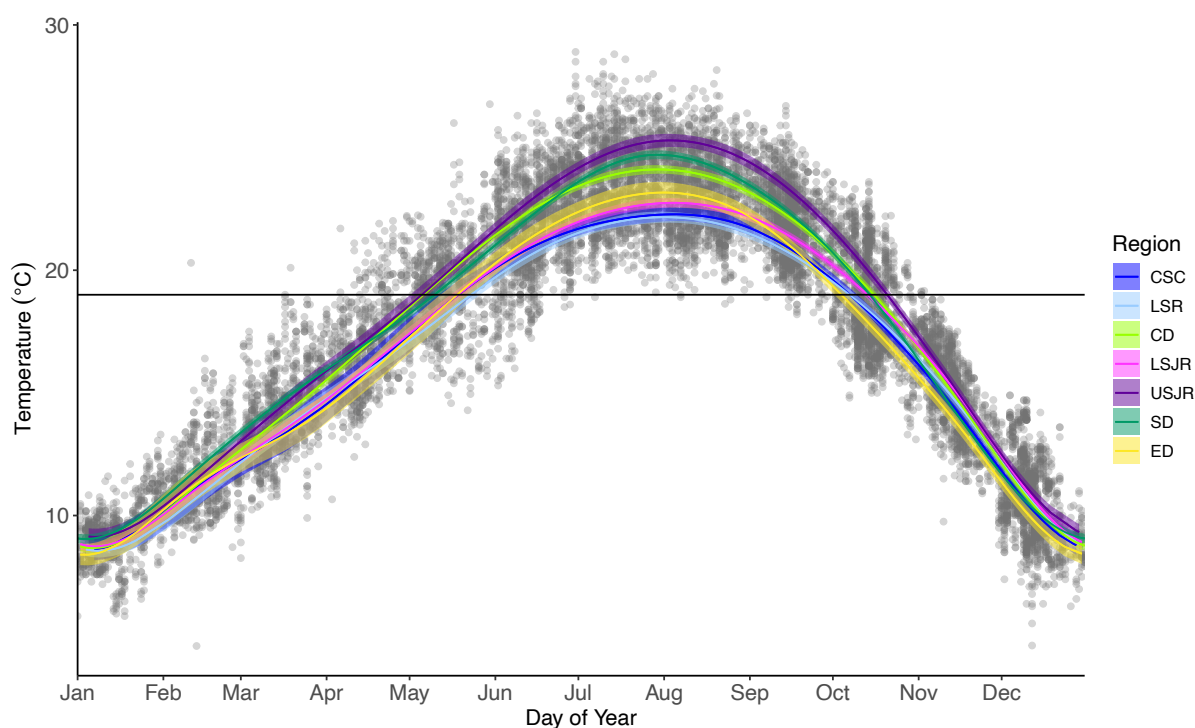


Figure 8 Observed temperature across the calendar year (transparent gray points) shown with Generalized Additive Mixed Models (GAMMs) predicted Delta temperature per region (colored lines). Shown with 95% confidence intervals (shaded areas). Solid black horizontal line shows the 19 °C temperature associated with the initial appearance of cyanobacteria in Delta waters LSR = Lower Sacramento River, USJR = Upper San Joaquin River, CD = Central Delta, CSC = Cache Slough Complex, ED = East Delta, LSJR = Lower San Joaquin River, SD = South Delta.

Table 3 Regressions of mean June surface-water temperatures (°C) as a function of year (2008–2022; $n = 15$) in seven separate regions of the Delta. CSC = Cache Slough Complex, LSR = lower Sacramento River, CD = Central Delta, LSJR = lower San Joaquin River, USJR = upper San Joaquin River, SD = South Delta, ED = East Delta. Significant slopes in **bold** and *light blue* shaded cells.

Region	Slope (Temp~Year)	Probability	<i>R</i>
CSC	0.083	0.145	0.16
LSR	0.096	0.085	0.21
CD	0.090	0.038	0.29
LSJR	0.171	0.000	0.69
USJR	0.041	0.617	0.02
SD	0.067	0.378	0.06
ED	0.201	0.008	0.43

later months of the year are warmer than 15 °C (Lehman et al. 2017; Preece, Otten, and Cooke 2024).

Salinity

Background

Most freshwater cyanobacteria cannot survive for extended periods in saline waters and therefore salinity can act as barrier to—and negative driver of—cyanobacteria blooms (e.g., Sellner et al. 1988; Hagemann 2013). Nevertheless, some genera have a relatively high salt tolerance (Patiño et al. 2023) and *Microcystis* cells have been shown to grow in a range of salinities (Otsuka et al. 1999; Tonk et al. 2007; Zhang et al. 2013; Qiu et al. 2022). Optimal salinities for *Microcystis* growth vary based on the system, strain, or different physiological statuses of individual colonies (Bormans et al. 2023). Salinity data is typically reported as either ppt and psu, with one part ppt considered equal to one psu. For consistency, we report all data as ppt.

Wang et al. (2022) reports optimal *Microcystis* growth occurred at a salinity of 0 ppt in the

coastal Yuniao River, China, and as salinity increased closer to the coast the relative abundance of *Microcystis* decreased. In contrast, a laboratory study found *Microcystis* growth was higher at 4 and 7 ppt than in the control of 1 ppt (Qiu et al. 2022). The authors suggested these higher salinities promoted *Microcystis* growth during the early stage of culture, partly because it facilitated photosynthesis. The same study found that a salinity of 10 ppt inhibited *Microcystis* growth and caused irreversible damage to the organism.

As *Microcystis* is transported through estuarine systems from freshwater to more saline environments it can cause cells to undergo a salt shock. This immediately decreases photosynthetic activity, resulting in decreased growth (Georges de Aulnois et al. 2020). However, when cells are gradually exposed to increasing salinities, they can acclimate or adapt and continue growing even if the cells originated in a lower-salinity environment (Melero-Jimenez et al. 2019). Interestingly, salinities of 5 ppt are associated with higher microcystin production because of the up-regulation of microcystin production genes (Qiu et al. 2022). Thus, *Microcystis* with higher salt tolerance have more intracellular toxins than those in lower-salinity environments (Li et al. 2024). Increased salinity also results in higher osmotic pressures that cause *Microcystis* cells to lyse and release toxins into the surrounding waters (Preece et al. 2017).

In general, literature reports agree that *Microcystis* has a salt tolerance of around ≤ 10 ppt (Preece et al. 2017). The adaptability or acclimation of some *Microcystis* strains to higher salinities allows cells to persist in more saline environments. This is exemplified in a study by Miller et al. (2010) that showed survival in seawater (average salinity of 35 ppt) for up to 48 hours. Fewer studies have addressed the salt tolerances of other cyanobacteria species. Based on the available literature, it appears that the salinity tolerance of *Dolichospermum* and *Anabaenopsis* is similar to that of *Microcystis* (Moisander et al. 2002; Kemp and John 2006; Tolar 2014).

Delta-Specific Analysis

The principal factors that influence Delta salinity are tidal intrusion of Pacific Ocean saltwater and freshwater inflows from the watershed. Management of these freshwater flows ensures that most of the Delta remains fresh year-round. Mean salinities in the Delta regions where *Microcystis* tends to bloom remain below 2 ppt during the spring and summer growing season (Figure 9). However, colonial *Microcystis* embedded in mucilage, as commonly observed in the Delta, may tolerate elevated salinity (e.g., up to salinity of 20) and persist even when active growth is limited (Bormans et al. 2023). This may explain why *Microcystis* has been documented at salinities up to 18 ppt in the San Francisco Estuary just downstream of the Delta, despite likely being stressed and not actively multiplying under these conditions (Lehman et al. 2005). If up-regulation of toxin genes associated with higher salinities holds true for the Delta, issues with increased toxin production and cell lysis would be of greater concern in more saline waters that occur downstream of the Delta.

Salinity throughout most of the Delta is well below the 10 ppt salt tolerance threshold for *Microcystis* (Figure 9). As expected, salinity is highest in the LSR region, in the western Delta (Figures 9 and 10). The CSC, also in the western Delta, has much lower salinity than the LSR, mainly because its source of water is the upper Sacramento River, rather than the LSR. Through tidal exchange, the LSR region supplies saline water to the LSJR and to a lesser degree the USJR and the CD regions (Figure 9). The regions with the lowest salinity include the ED and CSC (Figures 9 and 10). The CD, USJR, and SD also maintain salinities well below 1 ppt.

Nutrients

Background

Concentrations of the macronutrients nitrogen (N) and phosphorus (P) are important positive drivers that influence the magnitude and duration of CHAB events (Ibelings et al. 2021). Globally, there has been an increase in blooms of CHAB species in concert with increased loads

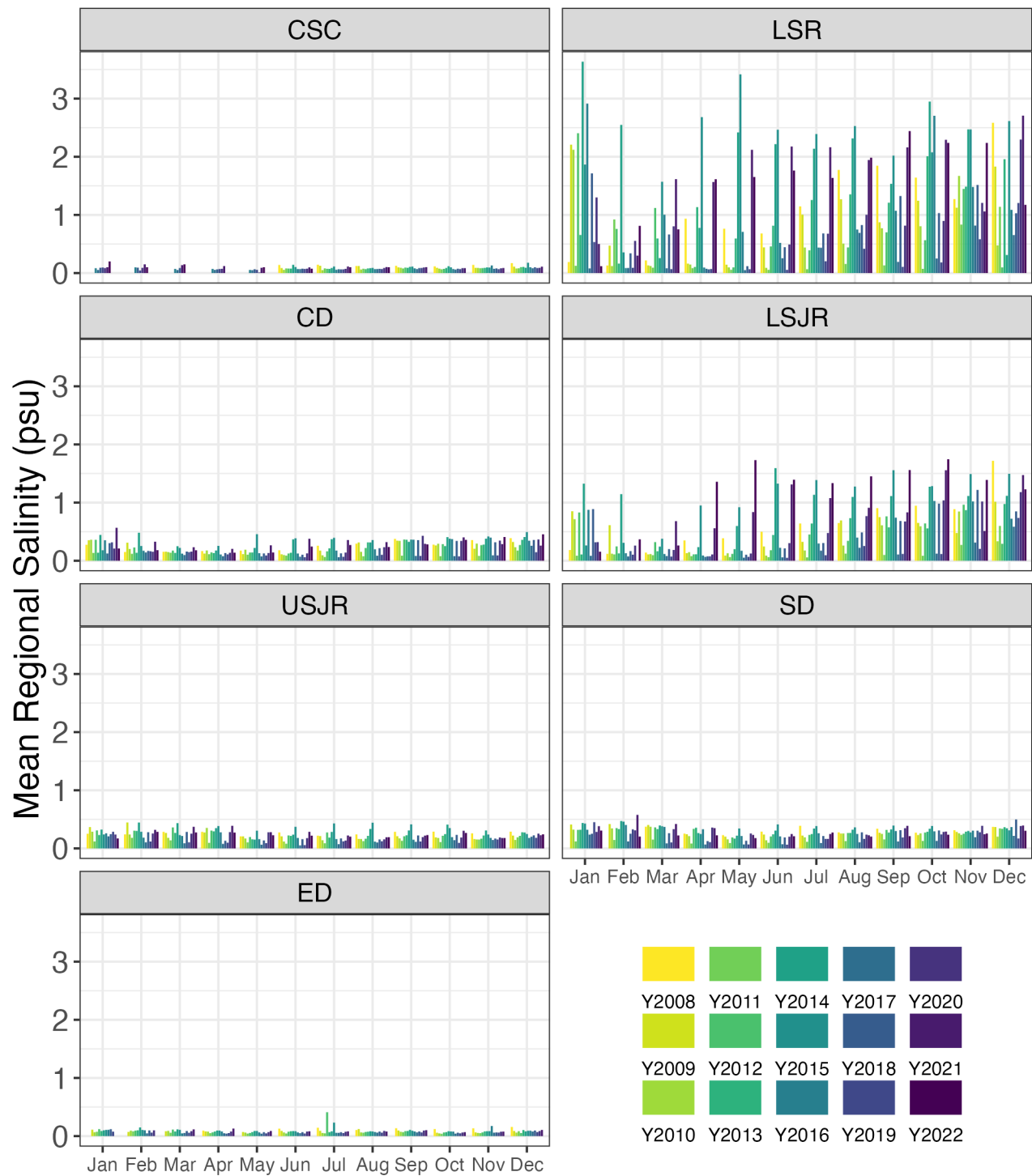


Figure 9 Mean regional salinity in the seven Delta regions by month. CSC = Cache Slough Complex, LSR = lower Sacramento River, CD = Central Delta, LSJR = lower San Joaquin River, USJR = upper San Joaquin River, SD = South Delta, ED = East Delta.

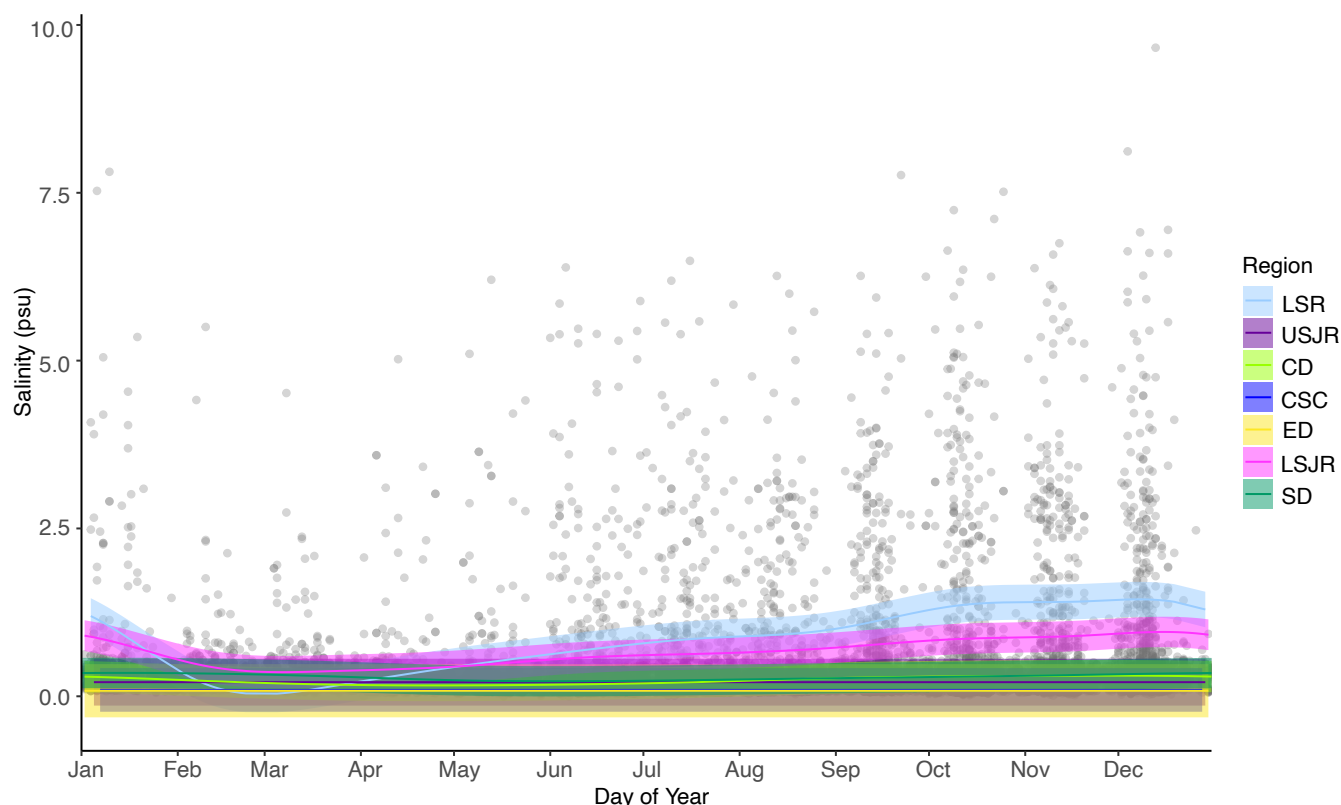


Figure 10 Observed salinity across the calendar year (transparent gray points) shown with Generalized Additive Mixed Models (GAMMs) predicted Delta salinity per region (colored lines). Shown with 95% confidence intervals (shaded areas). LSR = lower Sacramento River, USJR = upper San Joaquin River, CD = Central Delta, CSC = Cache Slough Complex, ED = East Delta, LSJR = lower San Joaquin River, SD = South Delta.

of nutrients (e.g., Paerl 2008; Lehman et al. 2017; Wang and Zhang 2020; Phlips et al. 2025). While increases in biomass of cyanobacteria in freshwater systems have traditionally been associated with increased P (Schindler et al. 1977; Elmgren and Larsson 2001; Schindler et al. 2008), and in estuarine systems with increased N (Paerl 2008; Conley et al. 2009; Ahn 2011), both point and non-point source nutrient contributions—such as wastewater discharge and agricultural run-off—tend to increase N and P concentrations simultaneously (Paerl and Paul 2012; Paerl, Hall, et al. 2014). Studies of hyper-eutrophic Lake Taihu in China have demonstrated that when cyanobacteria biomass is at its maximum, and nutrient concentrations at their minimum, N and P exert equal control over biomass (Paerl, Xu, et al. 2014). In other words, both N and P are needed to sustain blooms of cyanobacteria. In Lake Taihu and other systems world-wide, increased

nutrient loadings in tandem with increased water temperatures have led to changes in community composition away from being diatom-dominated to becoming dominated by CHAB species such as *Microcystis* sp., *Planktothrix* sp. and *Cylindrospermopsis* sp. (Burford and Donahue 2006; Qin et al. 2010; Paerl, Xu et al. 2014). Increasing dominance of cyanobacteria relative to diatoms and green algae is considered to negatively affect food web dynamics because the latter are generally considered more nutritious to grazers and higher trophic levels as a result of their greater N and polyunsaturated fatty acid (PUFA) contents (Kjørboe 1989; Frost and Elser 2002; Sommer et al. 2012).

Delta-Specific Analysis

Extensive studies of the effect of nutrients (e.g., Jassby et al. 2002; Dugdale et al. 2007; Jassby 2008; Cloern and Jassby 2012; Kraus et al. 2017;

Strong et al. 2021) have been completed in the Delta. Two principal sources of nutrients to the Delta are point-source discharges from publicly owned treatment works (POTWs) and agricultural discharges in the form of irrigation return flows and other non-point discharges associated with agriculture (Kratzer et al. 2011; Saleh and Domalgaski 2015; Dahm et al. 2016). The two primary vehicles for loading nutrients into the Delta are the Sacramento River, which contributes nutrients largely from POTWs, and the San Joaquin River, which delivers nutrients primarily from agricultural return flows (Kratzer et al. 2011; Novick et al. 2015).

Concentrations of both dissolved N and P are relatively high across all regions in the Delta year-round (e.g., Jassby et al. 2002). Focusing on April through October, monthly mean nitrate + nitrite concentrations were greatest in the USJR region (Figures 11 and 12). In this region, concentrations typically vary from 0.30–2.10 mg L⁻¹ (21–148 µmol L⁻¹) in April and decrease gradually to reach a minimum, varying from 0.15–0.65 mg L⁻¹ (11–46 µmol L⁻¹) in August, before increasing again in the fall (Figure 11). This pattern of decrease in nitrate + nitrite concentration from spring to summer suggests that maximum phytoplankton biomass is reached during the month of August in the USJR region; although, at lower absolute concentrations, nitrate + nitrite followed a similar pattern in the SD, LSJR, and CD regions, with minimum concentrations reached during the month of August (Figures 11 and 12). Concentrations of nitrate + nitrite are significantly higher in the USJR region compared with the other regions (Table A6) as evidenced by elevated concentrations in spring and fall outside the phytoplankton growth window (Figures 11 and 12).

In contrast with the aforementioned regions, nitrate + nitrite concentrations in the LSR and CSC regions did not decrease appreciably from spring to summer, varying from 0.24–0.76 mg L⁻¹ (17–54 µmol L⁻¹) in April to 0.20–0.62 mg L⁻¹ (14–44 µmol L⁻¹) in August (Figure 11). This suggests that phytoplankton biomass accumulation in these two regions is generally not sufficient

to draw down nitrate + nitrite in a detectable manner.

The same was true for orthophosphate, which did not vary appreciably from spring to summer in any of the regions across the Delta (Figures 13 and 14). This suggests that orthophosphate concentrations, mainly varying between 0.05 and 0.10 mg L⁻¹ (1.6–3.2 µmol L⁻¹) from April through October, are greater than phytoplankton demand. Therefore, the uptake of orthophosphate is generally not detectable as a decrease in concentration. The lack of change in concentration across the growing season could be aided by rapid regeneration of orthophosphate from organically bound phosphate as well (e.g., Ammerman and Azam 1985; Labry et al. 2016).

The USJR region represented an exception to the lack of change in orthophosphate concentrations in other regions. Water exports that divert much of the lower San Joaquin River water, may limit the effects of these nutrients across other Delta regions (Schlegel and Domagalski 2015). In the USJR region, orthophosphate concentrations were up to 3-fold greater compared with the other regions (Figures 13 and 14). In addition, orthophosphate concentrations appear on the increase, with notably higher concentrations recorded for April through June in the years 2021 and 2022 (Figure 13), indicating a unique pattern in nutrient accumulation in the USJR region. Moreover, a decrease in concentration from June to August was notable for these 2 latter years (Figure 13), suggesting a greater accumulation of phytoplankton biomass and/or productivity in this region that was sufficient to decrease phosphate in a detectable manner. Increasing orthophosphate concentrations in the USJR may reflect the influence of extended drought periods, specifically 2012–2016 and 2020–2022, the latter being California's driest 3-year span on record (CDWR 2023). Previous research has shown that prolonged drought conditions appear to be a key driver of nutrient enrichment, promoting the internal regeneration of legacy nutrients stored in sediments (Bosworth et al. 2024; Preece, Paerl et al. 2025).

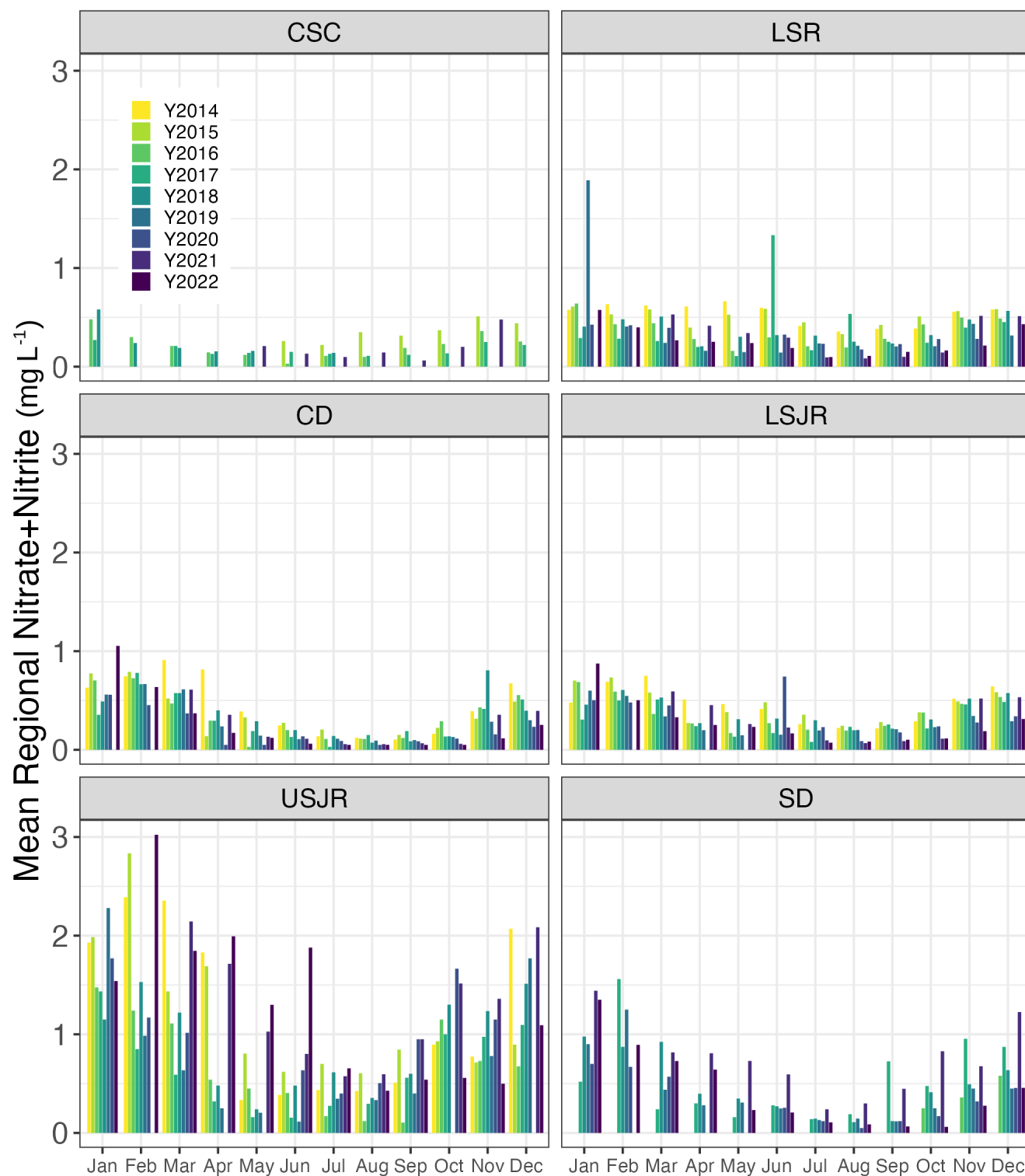


Figure 11 Mean regional nitrate + nitrite concentrations in six Delta regions by month for the period 2014–2022. CSC = Cache Slough Complex, LSR = lower Sacramento River, CD = Central Delta, LSJR = lower San Joaquin River, USJR = upper San Joaquin River, SD = South Delta, No data available for ED = East Delta.

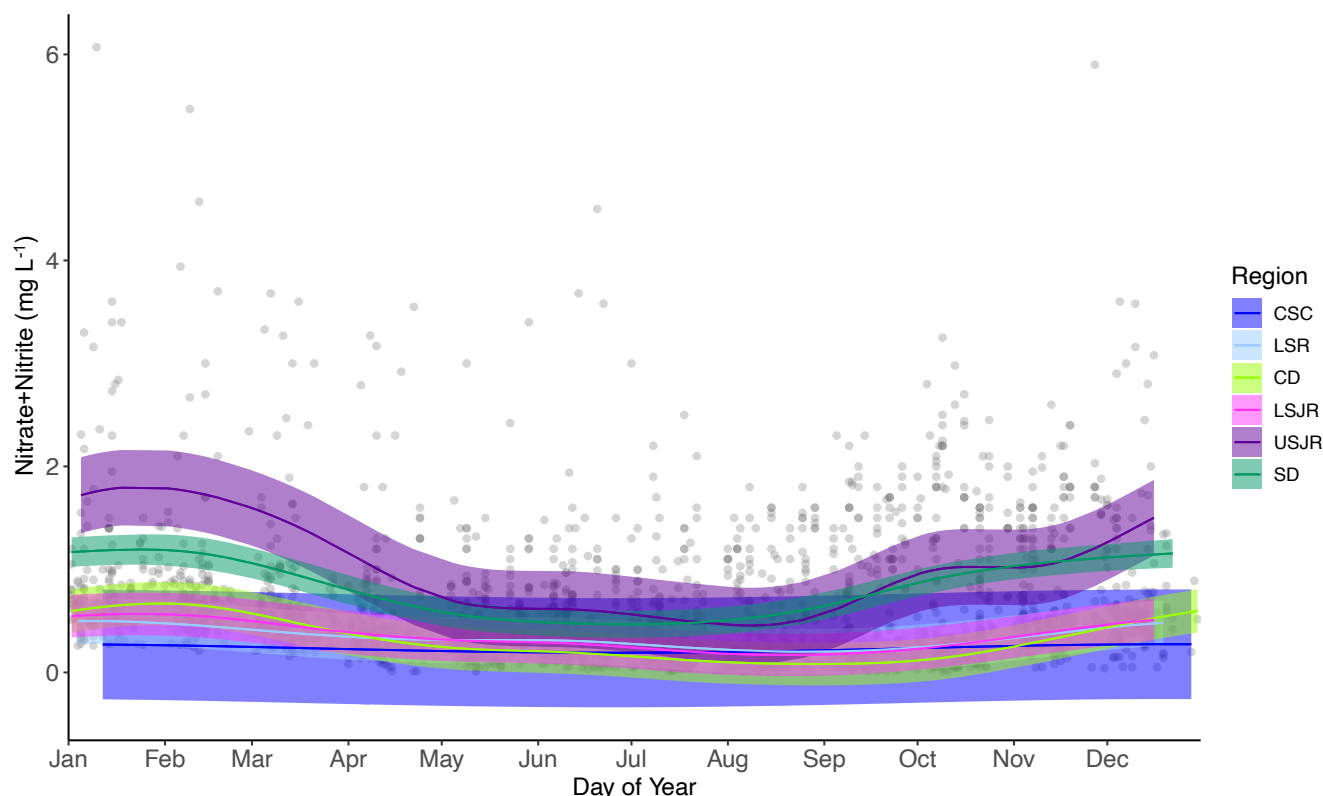


Figure 12 Observed nitrate + nitrite concentrations across the calendar year (*transparent gray points*) shown with Generalized Additive Mixed Models (GAMMs) predicted Delta nitrate concentration per region (*colored lines*). Shown with 95% confidence intervals (*shaded areas*). LSR = lower Sacramento River, USJR = upper San Joaquin River, CD = Central Delta, CSC = Cache Slough Complex, LSJR = lower San Joaquin River, SD = South Delta. No data available for ED = East Delta.

Our dataset ends in 2022, but between 2019 and 2021, the EchoWater Resource Recovery Facility (Jassby 2008; Novick et al. 2015; Saleh and Domagalski 2015), a major Delta point-source discharger, was upgraded to meet its National Pollutant Discharge Elimination System (NPDES) permit. By 2022, after the upgrade, ammonium loading decreased, resulting in lower dissolved inorganic nitrogen (ammonium + nitrate) inputs to the Delta. However, in the LSJR, agricultural discharges continue to contribute high nitrogen loads (Richardson et al. 2025). Orthophosphate reductions were also observed downstream of the facility and along the Sacramento River into Suisun Bay, but similar declines were not evident elsewhere in the Delta (Richardson et al. 2025).

In our analysis, nitrate + nitrite concentrations across the growing season in Delta waterways

notably decreased, but the residual nitrate + nitrite concentration—i.e., that left over when phytoplankton biomass has reached a maximum—was relatively high (varying from 10–30 $\mu\text{mol N L}^{-1}$) across all the regions. This suggests that phytoplankton biomass could accumulate to a substantially greater extent across all the Delta regions even with the facility upgrade discussed above (see Preece et al., this issue). This may be especially important in the USJR region where there are high concentrations of orthophosphate. Moving into a warmer and hydrologically uncertain future, this large and unused nutrient pool may present an increasing risk for CHAB events.

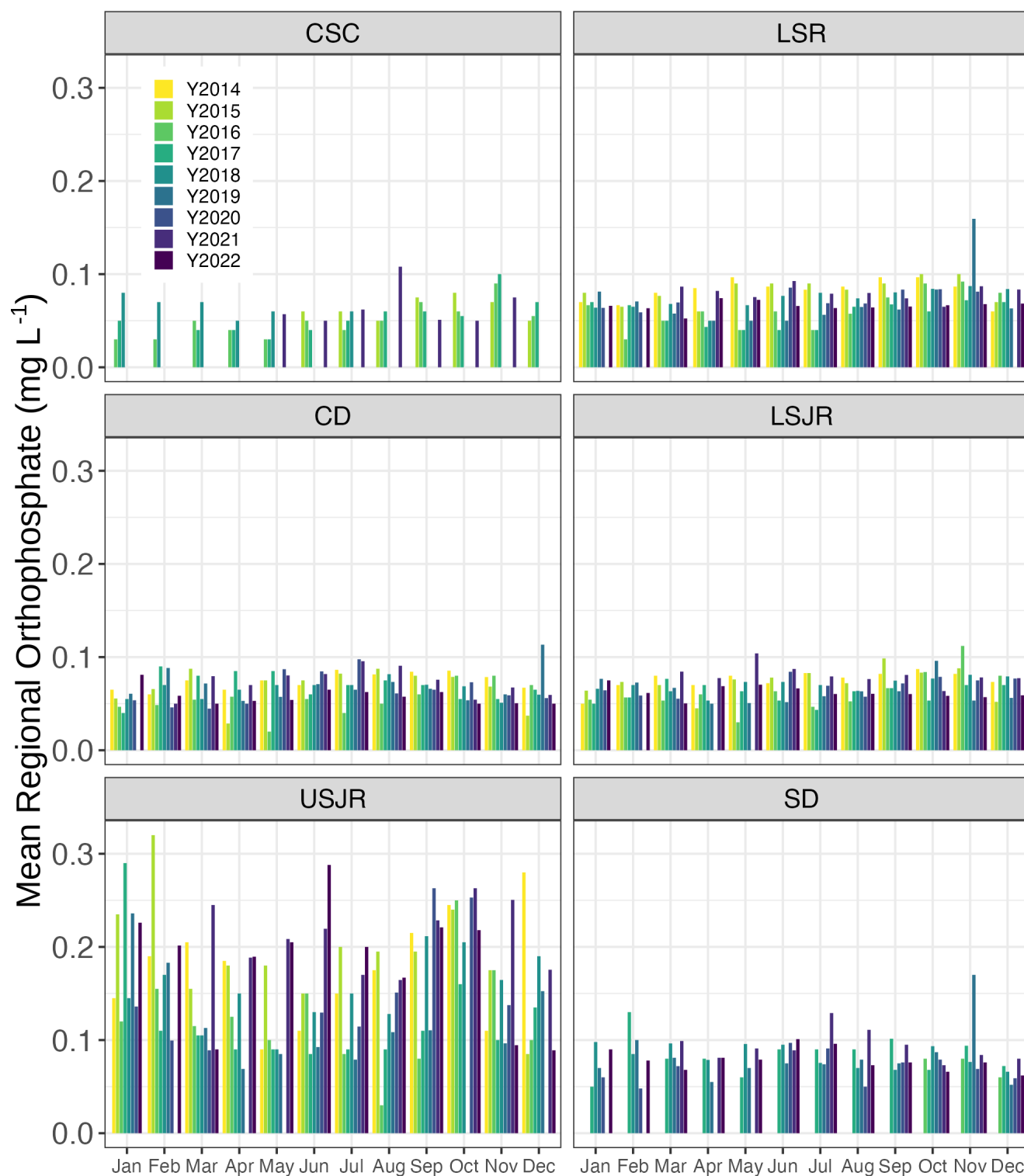


Figure 13 Mean regional orthophosphate in six Delta regions by month for the period 2014–2022. CSC = Cache Slough Complex, LSR = lower Sacramento River, CD = Central Delta, LSJR = lower San Joaquin River, USJR = upper San Joaquin River, SD = South Delta. No data available for ED = East Delta.

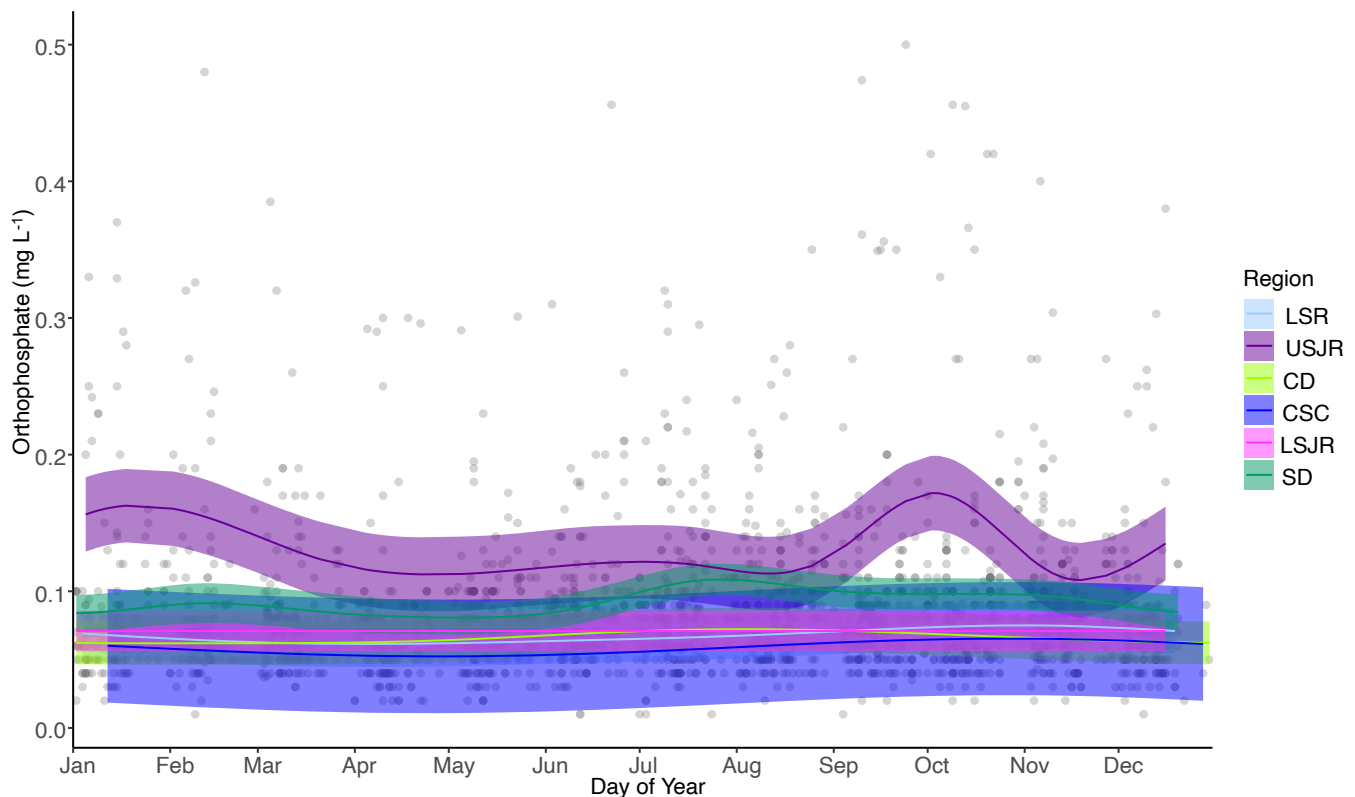


Figure 14 Observed orthophosphate concentration across the calendar year (*transparent gray points*) shown with Generalized Additive Mixed Models (GAMMs) predicted Delta orthophosphate concentration per region (*colored lines*). Shown with 95% confidence intervals (*shaded areas*). LSR = lower Sacramento River, USJR = upper San Joaquin River, CD = Central Delta, CSC = Cache Slough Complex, LSJR = lower San Joaquin River, SD = South Delta. No data available for ED = East Delta.

REGIONAL ANALYSES

In addition to the GAMM analyses above, we used PCA to visualize differences in environmental drivers across the regions. Colors were assigned to each of the six regions, and 95% confidence ellipses were drawn around clusters the PCA calculations identified. The ED was not included in the analysis because it lacked sufficient nutrient data. To demonstrate statistically significant differences between regions, a PERMANOVA test was used. The first two principal components captured 71.3 % of the variance ([Figure 15](#)). Principal component 3 (not shown) accounted for an additional 17.0% of the variance. The PERMANOVA test confirmed significant differences between the PCA ellipses ($p < 0.001$), suggesting that the regions are ecologically distinct. Pairwise comparisons show the regions were all significantly different

from one another ($p = 0.015\text{--}0.024$). The primary axis (PC1) separates USJR from LSR along orthophosphate and turbidity and, to a lesser extent, nutrients and salinity. The secondary axis (PC2) largely separates temperature and nutrients from salinity and turbidity. Secchi depth also separates from turbidity in the analysis, which reflects the inverse relationship between the two, with higher turbidity values corresponding to lower Secchi depths. Temperature is negatively correlated with PC2 and positively correlated with PC1, suggesting warmer regions are associated with high nutrients but lower salinity and turbidity. Overall, these results suggest that nutrient enrichment and salinity and turbidity gradients are the main regional differences in CHAB drivers.

While the PCA highlights overall patterns in how regions cluster based on water-quality characteristics, the heat-map provides a more detailed view of how individual analytes vary among regions (Figure 16). The LSR and USJR regions frequently represented either the lowest or highest values in the measured range of the different environmental parameters, in essence bookending the other regions (Figure 16). This was especially true during the July through September period when CHABs are most problematic in the Delta.

During the summer CHAB season, the USJR region was on the lowest end of values within the measured range for turbidity, the highest end of values within the measured range of water temperature, and the highest end of values within the measured range for phosphate concentrations; the region also had some of the highest nitrate + nitrite concentrations (Figure 16). Although the GAMM model predicts higher overall nitrate + nitrite in the USJR compared to the SD, there is a period from July through August where the SD is modeled to have higher nitrate + nitrite than the USJR. Measured median nitrate + nitrite concentrations are similar between the two regions. Though slightly cooler than the USJR, the CD and SD also had relatively high mean water temperatures (Figure 7). In contrast, the LSR region was at the highest end of the range for turbidity and salinity, and the lowest for water temperature (Figure 16). While the CSC region was similar to the LSR region, it differed significantly for salinity, generally having less saline waters than the LSR. The LSJR was also like the LSR, with nearly overlapping lines on the GAMM plots, and close to the LSR ellipse on the PCA biplot. The most notable difference is that the LSJR has slightly warmer summer water temperatures than the LSR (Figure 7, Figure 8)

CHAB MONITORING CONSIDERATIONS

Based on the long-term discrete data analyzed here, we have demonstrated significant differences among regions in terms of environmental drivers and have identified regions that are undergoing environmental

changes. The USJR consistently exhibits higher summer water temperatures compared to other Delta regions. Nutrients, although occurring at high concentrations across all Delta regions, are particularly high in the USJR region while turbidity is relatively low. Collectively, these factors provide some of the best conditions in the Delta for CHAB proliferation. This area has previously been recognized as one of the areas in the Delta most prone to CHAB events (Lehman et al. 2017; Preece, Paerl, et al. 2025). Long-term nutrient controls are broadly recognized as the most effective strategy for reducing CHABs (e.g., Paerl et al. 2018; Paerl et al. 2024). Our results indicate that such reductions in both N and P may be particularly necessary in the USJR region, given that climate change is projected to intensify the severity and duration of droughts that promote nutrient enrichment (Preece, Paerl et al. 2025).

Although the SD was not quite as warm as the USJR, the region also has many of the characteristics needed to support CHABs, including warm summer water temperatures, low salinity, and high nutrients. This area has also been identified as an area of the Delta (along with the CD and LSJR) that is expected to be the driest and warmest under future climate conditions (He 2022), increasing the risk of CHABs. One notable difference from the USJR is that during summer months turbidity in the SD was significantly higher (Table A6). Despite relatively high turbidity, this region remains susceptible to CHAB events (Lehman et al. 2017). Yet, the SD also has high clam densities and extensive submerged aquatic vegetation, which can inhibit phytoplankton production (Alpine and Cloern 1992; Crauder et al. 2016; Durand 2017; Hammock et al. 2019; Mussen et al. 2024). Nevertheless, this is an area that will require monitoring for CHABs in the future because, overall, the region is well suited to support CHABs.

An example of a region that appears to be undergoing change is the ED region, where temperatures appear to be rising faster than the other study regions. Our analysis shows temperatures are increasing at an annual rate

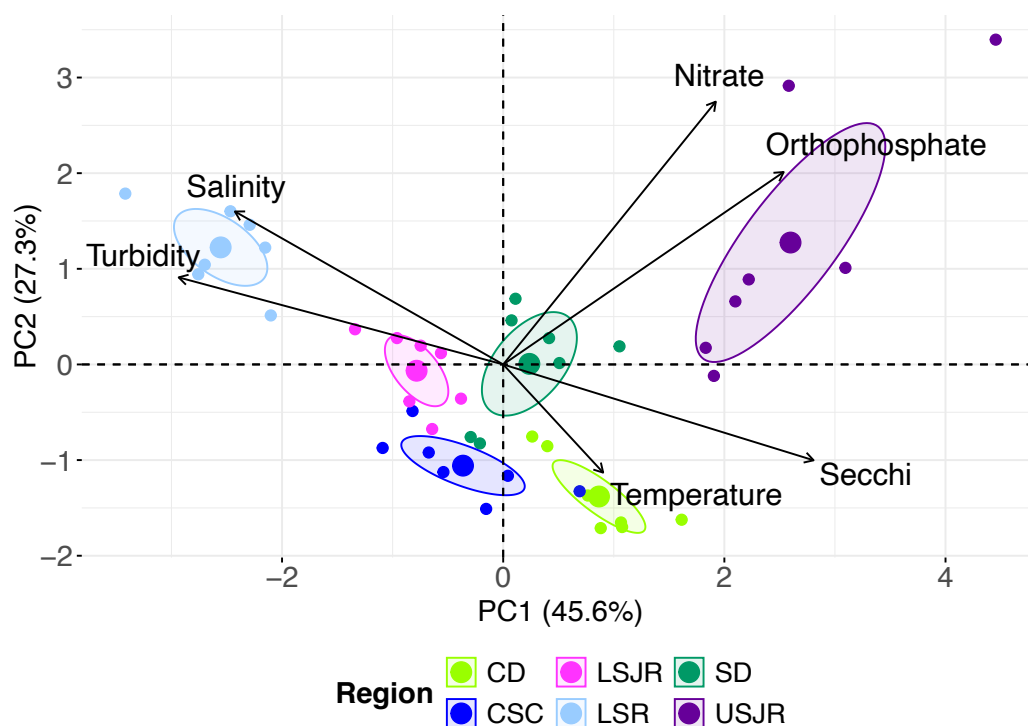


Figure 15 Principal component biplot for the first two principal components. The *arrows* originating from the central point of the PCA biplot indicate positive or negative correlations of different variables. The closeness of arrows indicates correlation strength between variables. To facilitate visual identification of patterns, 95% confidence *ellipses* were constructed around clusters for each of the six regions used for the analysis. CD = Central Delta, LSJR = lower San Joaquin River, SD = South Delta, CSC = Cache Slough Complex, LSR = lower Sacramento River, USJR = upper San Joaquin River. No data available for East Delta (ED).

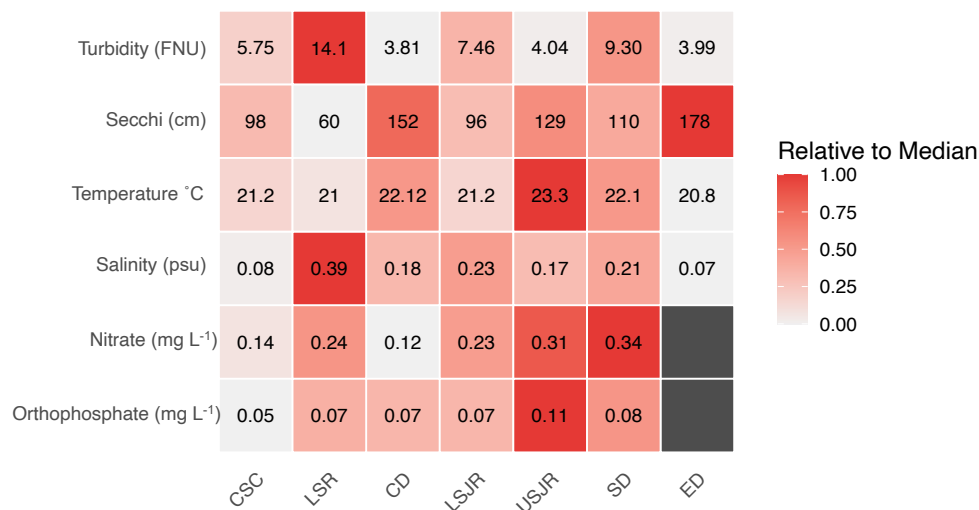


Figure 16 Median concentrations of turbidity, Secchi, temperature, salinity, orthophosphate, and nitrate + nitrite between April and October. Colors are scaled relative to the maximum value within each analyte, allowing comparison of relative levels among regions; however, colors are not directly comparable between analytes. *Light grey* indicates the lowest value for that analyte, and *dark red* indicates the highest, while *dark grey* represents missing data. Numbers inside the tiles show the actual median values. Temperature, turbidity, and salinity data is from 2008 to 2022. Turbidity data in the lower Sacramento River (LSR) is limited to 2021 and 2022, and Cache Slough Complex (CSC) is limited to 2017 to 2022. Nutrient data is from 2014 to 2022 except for the South Delta (SD) which is from 2017 to 2022. CSC = Cache Slough Complex, LSR = lower Sacramento River, CD = Central Delta, LSJR = lower San Joaquin River, USJR = upper San Joaquin River, SD = South, and ED = East Delta. *Dark grey cells* indicate no nutrient data available for the ED.

of 0.2 °C in June within the ED. This is also the least studied region in our analysis, with stations limited to the Mokelumne River, the south fork of the Mokelumne River, and Little Potato Slough. The seven ED stations had temperature, turbidity, and salinity data, but no nutrient data. Special studies in the ED using boat-based mapping have found that N and P concentrations are generally very low in the Mokelumne River, except in 2018 when the Delta Cross Channel was open, which allowed effluent derived nutrient-rich Sacramento River water to flow into the ED (Richardson et al. 2025). Upgrades to the EchoWater Resource Recovery Facility have reduced nutrient inputs, reducing the likelihood that future Delta Cross Channel openings will elevate nutrient levels in the ED. Although this suggests that nutrients may be relatively low in this area of the Delta, several dead-end sloughs off the south fork of the Mokelumne River could serve as cyanobacteria habitat, especially if temperatures warm sufficiently in that area. Increases of dissolved organic carbon have been detected in the dead-end sloughs, which were attributed to longer residence times (Richardson et al. 2025). These dead-end channels may contain legacy P in the sediments, but additional monitoring is needed to confirm this. Routine nutrient monitoring would improve understanding of nutrient dynamics in both the main channels and dead-end sloughs of the ED. Further monitoring in this region, especially in the dead-end slough areas will be important to better understand the potential for these areas to support cyanobacteria in the future. Future work could explore how projected changes in water temperature—alongside other drivers such as flow regime and nutrient dynamics—may influence the duration of the bloom window under different climate scenarios.

The dataset in this paper had several limitations. First, we used only discrete environmental data. Continuous monitoring stations across the Delta collect additional environmental data that could be used to support the analysis provided herein. Depending on the station, continuous sensors may collect temperature, turbidity, salinity, dissolved oxygen, flow, and/or other data at 15-minute increments. Though there are fewer continuous

monitoring stations than discrete data-collection efforts, that continuous monitoring station data provides another set of information that can be used to study how different regions may support CHABs.

A second limitation is that all our data was collected in areas of the Delta known as “main channel” sites. These locations are characterized as having strong stream flow, high rate of flushing, tidal forcing, continuous vertical mixing (i.e., no change in temperature with depth), a high degree of sediment re-suspension, and a relatively deep water column (Preece et al., this issue). These locations have less cyanobacteria than other areas of the Delta, such as the peripheral areas that are shallower, warmer, and have less flushing. There are known CHABs hot spots in the Delta including Discovery Bay, Big Break, and the Stockton waterfront where there is only limited environmental monitoring (Preece, Cooke et al. 2024; Preece, Otten, Cooke, et al. 2025; Preece, Paerl, et al. 2025). Key to gaining insight into the occurrence of CHAB events is determining the difference in environmental parameters between hot-spot and non-hot spot (i.e., main channel) locations. For example, basic information, such as whether nutrients are greater at hot-spot locations compared with other locations, is not well studied. Understanding these types of differences and characterizing the rate of change in parameters in the main channels of the Delta, may tell us how rapidly dense CHAB events could spread from isolated spots to cover larger areas in the future.

Another limitation is the relatively short temporal extent of the dataset (2014–2022). Although this period spans a range of water-year types—from very wet to multi-year drought conditions—most years were classified as dry or critical, with relatively few wet or above- or below-normal years. Thus, the dataset may not fully capture longer-term variability in hydrologic regimes. As a result, it may be biased toward drought conditions, and the extent to which these findings represent longer-term hydrologic variability remains uncertain. However, climate projections indicate increasing hydrologic variability

in the Delta, including declining dry-season precipitation, rising temperatures, and more extreme precipitation events, which suggests that this period may broadly inform future conditions (He 2022). In Part 2 of this paper (see Preece et al., this issue), we build from the work presented here. Specifically, we further examine the different habitat types that support Delta CHABs and synthesize existing data on monitoring parameters used to quantify CHABs. Collectively, the work presented in this paper and Part 2 can be used to inform future monitoring needs for CHABs in the Delta.

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