Hydroclimate Impacts on Phytoplankton Community Composition and Abundance in the Lower Sacramento-San Joaquin River Delta, 2008-2022

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ABSTRACT

Phytoplankton, as the base of the trophic food web, plays a crucial role in supporting the freshwater ecosystem in the lower Sacramento-San Joaquin River (Delta). However, hydroclimatic fluctuations alongside altered water systems in the Delta waters have influenced phytoplankton dynamics. Studying spatiotemporal variation of phytoplankton communities in different hydrological settings was necessary to understand its productivity. I examined the long-term trends in the composition and abundance of six major phytoplankton taxa, the seasonal variations in the species density during both wet and dry water years, and the impact of hydrological parameters (conductance, salinity, temperature, turbidity, and velocity) on the population across three distinct water bodies (saline, brackish, and fresh). For the time series analysis of the phytoplankton communities and hypothesis testing, I used two datasets, phytoplankton (2008-2022) and hydrological parameters (2010-2022), to apply in the multivariate autoregressive model. I found that the extreme abundance of Cyanophyceae disrupted community diversity, while the other five taxa–Bacillariophyceae, Chlorophyceae, Coscinodiscophyceae, Cryptophyceae, and Fragilariophyceae–remained low in abundance across all sites. Phytoplankton generally flourished more in wet seasons during wet and dry water years. Conductance followed by salinity were the most critical drivers for the variations in community; each had the lowest AICc values with 663.15 and 666.18 respectively. These results suggest freshwater inflow and water quality management is impactful in regulating both the density and the diversity of phytoplankton within the Delta ecosystem, in light of anticipated hydroclimate anomalies.

KEYWORDS

multivariate autoregressive model, population dynamics, primary productivity, spatiotemporal trends, time series analysis

INTRODUCTION

Climate change poses numerous challenges for the freshwater ecosystems, including elevated water temperatures, frequent and prolonged droughts, and seasonal discharge anomalies (Bennett. 2019). Freshwater variability affects physical properties and biological responses within the Sacramento-San Joaquin River Delta (Delta) (Kimmerer et al 2018). The Delta is the upstream part of the hydrologically complex San Francisco estuary, exporting a quarter of the total water inflow for the state's water demand (Cloern et al. 2014, WRCB 2023). The Delta undergoes continuous water alterations (e.g., canals, channels, levees, reservoirs, and dams) to accommodate the needs of various stakeholders (Lund et al. 2010). These hydrological disruptions lead to reduced water flow, stratified water columns, and extended water residence times, which exacerbate the production of the freshwater ecosystem (Conrad et al. 2016, Mussen et al. 2023). Globally, the net production of most estuaries is positive (Cloern et al. 2014). Yet the primary productivity of the Delta ecosystem has declined since the 1980s due to the concentration of nutrients and organic carbon induced from land (Parker et al. 2012, Strong et al. 2021). The hydrological and biogeochemical complexity of the estuary influences primary productivity across all trophic levels, including phytoplankton (Behrenfeld et al. 2021).

Phytoplankton encompasses both prokaryotic and eukaryotic autotrophs that inhabit the open waters of oceans, lakes, ponds and rivers. Regardless of their diverse origins and phenological traits, their unifying ecological role as primary producers classifies them under the group of phytoplankton (Raynalds 2006). They capture sunlight energy and convert it into organic carbon through photosynthesis. Most of phytoplankton production (~90%) contributes to the local metabolism of higher trophic levels unlike the fractional use of macrophyte production (24-44%) (Cloern et al. 2014, Henson et al. 2021). Thus, the collective decline of the pelagic community, zooplankton and fish species along the Delta often finds an explanation from the decreased phytoplankton, based on "bottom-up effects" theory (Jassby 2008, Kimmerer et al. 2018, Mussen et al. 2023). Since the onset of cyanobacteria harmful algal blooms (CHABs) in 1999, there has been a noticeable shift in species diversity and community composition within the Delta (Lehman et al. 2020). These potentially harmful cyanobacteria outperforms diatoms in nutrient absorption and thrive in stratified water systems, particularly under warm temperatures ranging from 20°C to 27°C (68°F to 80.6°F) (Santos et al. 2011; WRCB 2023). Because both cyanobacteria and other phytoplankton species compete for the same energy source—light and nutrients, the superior performance of cyanobacteria poses a threat to the greater ecosystem beyond the phytoplankton community (Van Nes et al. 2007). A massive cyanobacterial bloom can significantly degrade water quality by altering chemistry (pH, dissolved oxygen), and generating noxious compounds. Toxins from some species can cause animals death and human disease (Blaha et al. 2009). They also disrupt ecosystem functioning by altering light availability and oxygen concentration levels (Lehman et al 2021). Consequently, concerns about the diversity and stability of phytoplankton communities have grown in the interest of maintaining a healthy Delta ecosystem.

Given the crucial role as bioindicators in freshwater ecosystems, researchers have extensively studied temporal trends in phytoplankton populations. A longitudinal study conducted between 1996 and 2005 reported positive trends of phytoplankton biomass in the two upper estuaries while the trend in Suisun Bay remained neutral (Jassby, 2008). Several short-term studies over the past decade have reported a significant decrease in Chl-a, a proxy for phytoplankton, from the upstream to the downstream areas of the lower Sacramento River (Parker et al. 2012, Gilbert et al. 2015, Kraus et al. 2017, Mussen et al 2023). Despite numerous studies, the longitudinal change of phytoplankton communities in different hydrological settings remain less explored.

The purpose of this study is to investigate the influence of hydroclimate variables on the phytoplankton community across three distinct water bodies in the Delta. To gain a better understanding, I examined the long-term (2008-2022) trends in phytoplankton abundance and taxonomic composition in saline, brackish, fresh water bodies. I compared the difference in phytoplankton succession between wet water years (October 2016-September 2017) and dry water years (October 2020-September 2021). I analyzed which hydrological drivers (conductance, salinity, temperature, turbidity, velocity) influence the phytoplankton population most over the 12 year period (2010-2022). My hypotheses were as follows: 1) I hypothesized a declining trend in the total annual phytoplankton biomass, particularly diatoms, and a potential outgrowth trend in Cyanophyceae during the summer dry season due to warmer water temperatures. 2) I expected a lower phytoplankton biomass during the wet season in both wet and dry years due to increased turbulence and rising turbidity, which can disrupt the stability required for their growth. 3) I predicted a stronger impact of water turbidity on the phytoplankton population because a declining water quality from nutrient inflow can inhibit light penetration.

METHODS

Study area

The Sacramento-San Joaquin River Delta (Delta) is a complex network of rivers, channels, wetlands, and floodplains (Lund et al. 2010). The depth of its water varies, ranging from a few meters in shallow flooded islands to 13 m in the heart of major river channels. The Delta's tides can reach 2 m in height with velocities up to 30 cm s^{-1} and can extend 10 km or more during tidal excursion (Lehman 2021). The Delta's volume is significantly reduced by extensive water export, as the river supplies 80% of California's freshwater (DWR n.d.b., Jassby 2008). Furthermore, the water flow often fluctuates in response to seasonal climatic patterns between wet season (October–March) and dry season (April–September) (Liberto 2017, DWR n.d.a.).

I selected three study sites within an approximate 45 mile range from the lower Sacramento River to Suisun Bay to see how the phytoplankton communities respond differently in hydrologically distinct environments of fresh, brackish and saline water bodies (Figure 1). Although the Chipps Island site in Suisun Bay falls under the broader category of brackish water, I have classified it as a saline water body for this study, based on the relative differences among the three sites (Figure 2).

Freshwater: Hood site (38.36771, -121.5205) is situated in Sacramento County, approximately 15 miles south of the city of Sacramento. The surrounding Sacramento River exhibits a uniform and stable bathymetry, characterizing it as a relatively freshwater body with a salinity level of 0.0-0.1 ppt. Currently, the Delta Tunnel project, a 40 mile tunnel that would divert water from Hood, is approved for the state water projects (DWR n.d.b.).

Brackish water: Decker Island site (38.08453, -121.7391) is located 3.53 miles north of the confluence of the Sacramento and San Joaquin rivers in the estuarine limnetic zone, which has a salinity level of 0-0.5 ppt. Although the water body is primarily freshwater, it can exhibit a temporary increase in salinity up to 3 ppt. The bathymetry is relatively uniform, shallow, and weak in lateral mixing (Benette and Burau 2015).

Saline water: Chipps Island site (38.0463, -121.9183) is located at the legally defined boundary between the Delta and Suisun Bay. The salinity of this site fluctuates between 0 and 8 (µS cm^{-1}) during the study period (2010-2022). Despite being highly subject to tidal current impact, it falls within the limnetic and oligohaline zones with a salinity of 0.5-5 ppt. during median flow conditions (Jassby 2008). Its interannual and intra-annual salinity vary; the salinity can drop to near zero under high seasonal tide periods in spring outflows and can spike up to 8 μS cm^{-1} in the summer season (Figure 1).

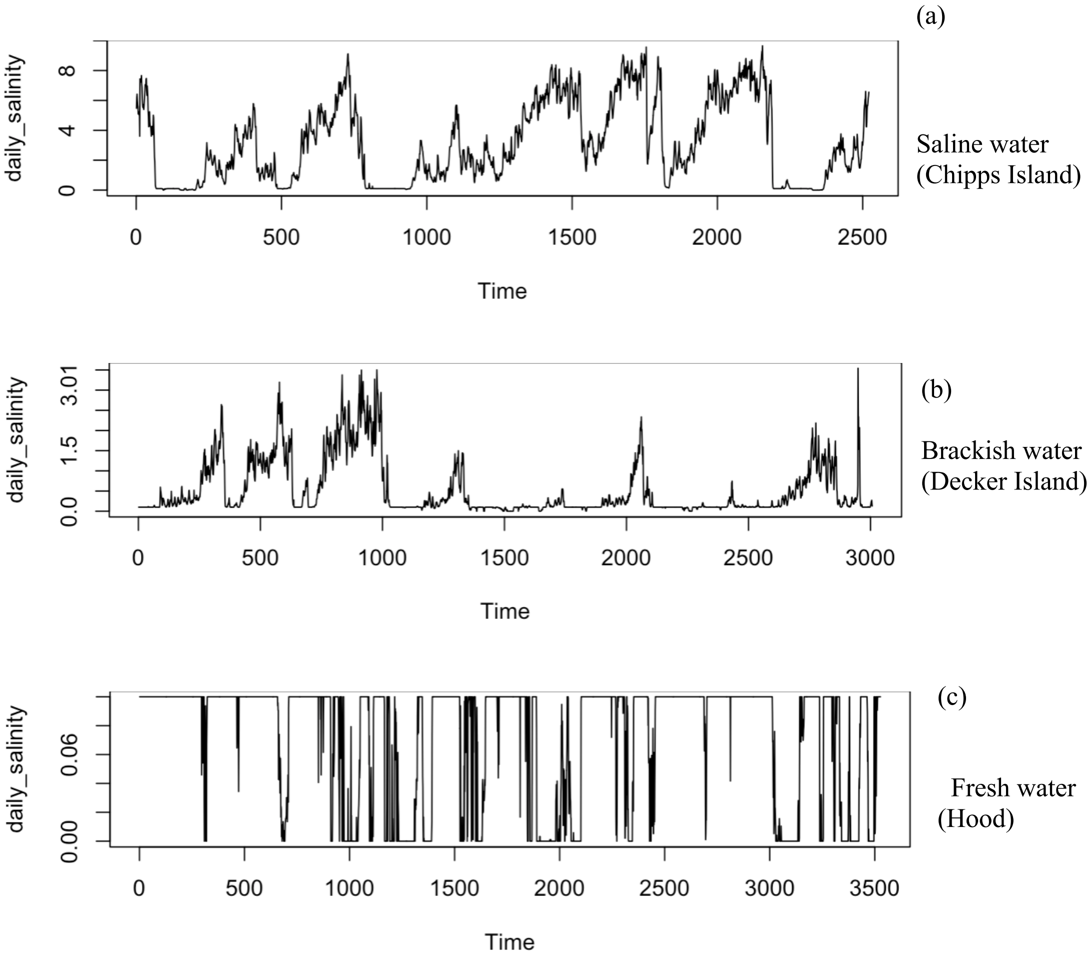


Figure 1. Daily means of salinity level across three study sites. Salinity level is on the x-axis (January 2010 - December 2022**).** Salinity level (μS cm^{-1}): (a) 0.03–7.85 (b) 0.02-2.49 (c) 0.0-0.10.

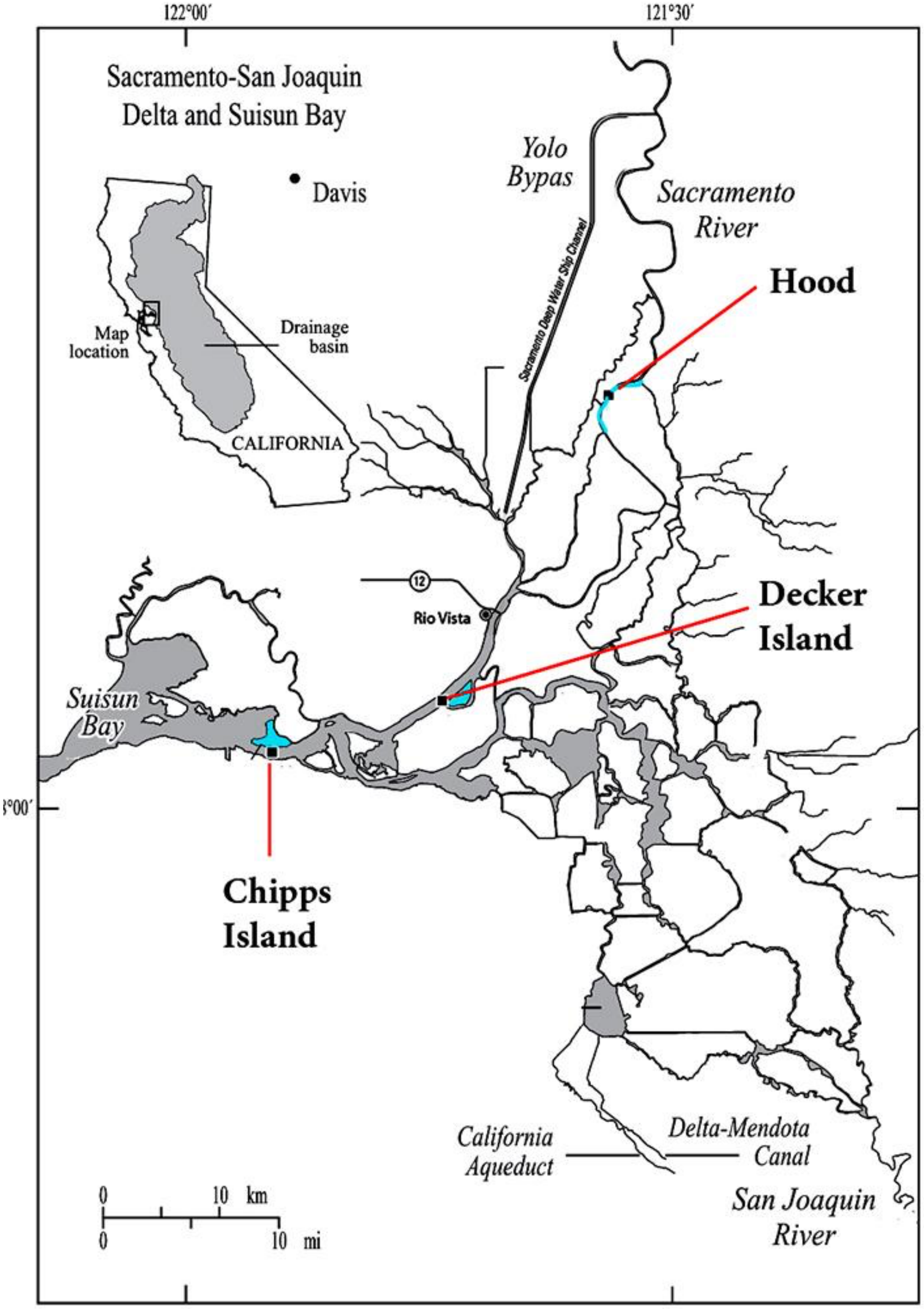


Figure 2. **The Sacramento-San Joaquin River Delta Map.** Study sites are colored in blue. From the top, Hood (freshwater), Decker Island (brackish water), Chipps Island (originally brackish water but named based on the relatively higher salinity among three sites). Map courtesy of CDWR.

Data collection

Dataset description

Phytoplankton (variate) data. To observe the change in longitudinal abundance trend and species composition, I retrieved the phytoplankton dataset (2008–2022) from the Environmental Data Initiative data portal, which was collected by the Interagency Environmental Monitoring Program (Battey and Perry 2023). To represent Decker Island, I combined data from nearby stations, including “Sacramento River at Emmaton,” “San Joaquin River at Twitchell Island,” “Sacramento River above Point Sacramento,” and "Sacramento River below Rio Vista Bridge.” From a total of 1,089 unique dates, I extracted 180 monthly observations for analysis. These were then reorganized into monthly averages, representing the average cells per mL per present taxonomic class for every month from January 2008 to December 2022.

Water (covariate) data. I collected 13 years (2010-2022) of water parameter data (conductance, salinity, temperature, turbidity, velocity) from the US Geological Survey (USGS) national water database (www.waterdata.usgs.gov) to examine the impact of hydrological factors on phytoplankton species. All water sampling has been continuously recorded at 15-minute intervals at a fixed USGS streamflow gauge monitoring station. For the longitudinal analysis, I reorganized the 15-minute interval records from 4,120 dates into monthly averages to match against the phytoplankton (variate) observation data. The velocity data in saline water (Chipps Island) including nearby sites in the Suisun Bay was not available during the study time period. Thus, the model for “the velocity in saline water” was dropped (Table 6).

Data analysis

Trends of phytoplankton composition and abundance in different hydrological settings

I compared the abundance of six major phytoplankton taxonomic groups over a 15-year period to observe if each taxon exhibited distinct trends across three sites. I utilized the “ggplot2” package in R to visualize the population trends and identify any cyclical patterns (R Core Team

2023). Additionally, I applied the autocorrelation function (ACF) to measure the similarity between observations of phytoplankton abundance at different time lags. The ACF quantifies the correlation of a value with its past values, which helps in reducing the autocorrelation structure (Hampton et al. 2013).

Temporal variability in the abundance of phytoplankton between dry and wet years

To investigate the seasonal and interannual variability of phytoplankton between dry and wet water years across three sites, I utilized non-metric multidimensional scaling (NMDS). I selected the wettest (2016-2017) and driest (2020-2021) years over the study period based on the water year report from the Department of Water Resource (2023). I converted the biovolume means of the phytoplankton taxonomic group into a community matrix for comparison, taking into account the dry/wet seasons and the dry/wet years. I created a table containing each Class, Year Month, average of that Month, Site, and Season. I calculated the average of each class to contribute to an overarching average for the respective dry and wet seasons. The irregular time series data was condensed into a general average over the seasons. The biovolume dataset was log-transformed. Based on the Bray-Curtis distance matrix, I visualized differences in phytoplankton composition at each site based on season and year predictor variables. All analyses were performed in R, using the “vegan” package to run NMDS (R Core Team 2023).

The effect of hydrological drivers on species survival

Multivariate autoregressive model. To quantify the impact of hydrological drivers on phytoplankton abundance, I utilized the multivariate autoregressive model (MAR). I selected MAR models due to their effectiveness in quantifying ecological dynamics for time series data with stochasticity including process and observation errors (Ward et al. 2010). In this research, stochasticity includes intra-annual and inter-annual fluctuations in hydroclimatic conditions, which are influenced by flooding and drought that affect population estimates. I modeled the dynamics of phytoplankton communities based on linear relationships with covariates, specifically abundance against hydrological factors. For the variates, I selected six phytoplankton subspecies that are constantly present in the region, collectively constituting more than 99% of the population

(Table 1). For the covariates, I extracted the annual mean value of each water parameter over a 13-year period (Table 3). Prior to incorporating all covariates into the time series models, I normalized the Z-score and conducted correlation tests.

Table 1. Variables used in the multivariate autoregressive modeling. Phytoplankton data were downloaded from the Environmental Data Initiative data portal and hydrological data were extracted from the US Geological Survey national water database.

Variables	Class (Taxonomic Group)	Algal Group	Years	Definition
Variates (Response Variables)	Bacillariophyceae	Diatom	2008–2022	mean biomass (µm³/l)
	Chlorophyceae	Green algae	2008–2022	mean biomass (µm³/l)
	Coscinodiscophyceae	Centric Diatom	2008–2022	mean biomass (µm³/l)
	Cryptophyceae	Cryptophytes	2008–2022	mean biomass (µm³/l)
	Cyanophyceae	Cyanobacteria	2008–2022	mean biomass (µm³/l)
	Fragilariophyceae	Diatom	2008–2022	mean biomass (µm³/l)
Covariates (Continuous Predictor Variables)	**Class**	**Units**	**Years**	**Definition**
	Conductance	(μS cm^{-1})	2010–2022	monthly mean water temperature
	Salinity	(μS cm^{-1})	2013–2022	monthly mean water quality
	Temperature	(°C)	2010–2022	monthly mean water temperature
	Turbidity	(NTU)	2013–2022	monthly mean water turbidity
	Velocity	(ft/s)	2013–2022	monthly mean water velocity
	Site Type	**Location**	**Years**	
	Brackish Water	Decker Island	2010–2022	
	Fresh Water	Hood	2010–2022	
	Saline Water	Chipps Island	2010–2022	

To determine which covariates most effectively explained the variation in the population density of phytoplankton, I employed MAR modeling as follows:

$$x_t = Bx_{t-1} + U + Cc_t + w_t, \qquad \text{where } w_t \sim MVN\ (Q)$$

In this model, $\mathbf{x}_t$ is the natural log density of the phytoplankton species, which is an **N** x 1 vector of **N** observations ("variates") at time *t*. **B** is the interaction matrix that represents the strength of density dependence. The population growth rate matrix **U** was fixed to zero by default as "unequal" because all **U**s are naturally different without a long-term trend in the data. **C** is the matrix that describes the effect of each covariate on each species. $\mathbf{c}_t$ is an **M** x 1 vector of **M** covariates (driving factors affecting the time series), and **C** is an **N** x **M** matrix describing how each covariate in $\mathbf{c}_t$ affects each variate. $\mathbf{w}_t$ is the process error at time ***t*** that represents random deviations or white noise, resulting from environmental or demographic stochasticity. **N** represents the number of discrete study sites, and **M** represents the number of water parameters. **c** represents how strongly (positively or negatively) ***u*** affects log-abundance. $\mathbf{w}_t$ is white noise from the multivariate norm of **Q**. **Q** is the process error matrix which describes how much variance each of the **N** states has.

I combined a MAR model with an observation model using the MARSS model:

$$y_t = Zx_{t-1} + v_t \; v_t \qquad \text{where} \sim \text{MVN}(0, R)$$

Throughout the simulations, the **Z**, **B**, **U**, **R**, **A** parameters were made consistent. The **Z** matrix was specified to default identity so that each class corresponds to its own state in the **x** matrix. The **B** interaction matrix being an identity matrix assumes none of the states had any interactions with each other. The observation error matrix, **R**, was set zero because the covariate and variate data were collected at stations from consistent survey agencies. The **A** was a zero matrix, all data is centered around 0 after standardizing values through z-scores. The covariate **c** matrix is numerical monthly average data of four covariates.

To identify the best model for each location, I computed the covariate effect **C** which is an **M** x **N** or 3 x 5 matrix. Before transposing the matrices, I aligned the monthly values so that both the covariate and variate matrices had the same number of **T** columns, with entries values positioned in corresponding dates. The **Z** and **C** matrix do not attribute the location sites as the effect. Instead, the variate effects for each site were calculated independently and analyzed after obtaining results. To ascertain whether **Q**, the process errors, should be different across classes versus connected, I ran a model with species-specific variance (without covariance) as well as a single-variance (with single-covariance). Although an **R** matrix of “diagonal and equal” passed the convergence test, I used MAR with the zero **R** matrix and an identity **Z** matrix. The zero **R** matrix implies that all data was collected the same manner, indicating similar levels of uncertainty across the data.

To determine the most effective combination of covariates, I employed changes in corrected Akaike's Information Criterion values (ΔAICc). The best-fitting model is the one with the lowest ΔAICc value. Differences in AICc relative to the best model (ΔAICc) are shown for each driver metric. Here, ΔAICc value of 0 indicates the model that has the strongest support (Table 6). For the top-performing models, I evaluated the significance of covariate effects by examining the 95% confidence intervals, which were obtained after bootstrapping 5,209 samples. All MAR analyses were performed using ‘MARSS’ R-package (Holmes et al. 2023; R Core Team 2023).

RESULTS

Trends of phytoplankton composition and abundance in different hydrological settings

I found significant spatiotemporal differences in the composition and abundance of phytoplankton communities among the saline, brackish, and fresh waters. All water types experienced a surge in Chlorophyceae and Cyanophyceae between 2015-2020. The freshwater site (Hood) had a more distinguished downward trend in overall phytoplankton volume compared to brackish and saline water sites (Figure 4). Despite the downward trend, Hood still ranked the highest in mean diatom biomass over 10 years. (Table 2). Notably, an explosive growth of diatoms (Fragilariophyceae and Bacillariophyceae) occurred exclusively at the Hood site between 2009 and 2013 (Figure 4). Fragilariophyceae reached the highest volume at 161,987.85 cells/mL and Bacillariophyceae recorded 64,931.83 cells/mL in December 2010.

I observed the highest abundance of Cyanophyceae in the saline water. I found no seasonal pattern in Cyanophyceae abundance in either the saline or brackish water since their presence was dominant throughout the year (Table 4). Particularly, mean total Cyanophyceae concentrations were significantly greater in 2017 across water body types (Figure 3, Table 2). Cyanophyceae class showed a significant upward trend until early 2019. The other five taxa are graphed separately due to Cyanophyceae's significant prominence (Figure 4). In 2017, Chlorophyceae exhibited a similar surge alongside Cyanophyceae at all sites. Over the 15-year study period, Chlorophyceae was the second dominant class in both the saline and brackish waters and the third at the freshwater site. Fragilariophyceae outperformed Chlorophyceae only at the freshwater site. A relatively synchronized growth trend was observed between Chlorophyceae and Cyanophyceae across all three sites (Table 2).

The autocorrelation function (ACF) graph on Cyanophyceae at the saline water site showed a growing and tapering pattern in correlation as the lag increases (Figure 3). The autocorrelation values range from 0.1 to 0.7 while many spikes are above the confidence interval lines. This suggests that the abundance of phytoplankton is somewhat correlated with its abundance in the distant past. The autocorrelation values ranged from 0.01 to 0.4 at the brackish water while all of the spikes are within the confidence interval lines close to zero, indicating that any observed correlation is likely due to random chance rather than an underlying pattern in the data. At the freshwater, autocorrelation values range from 0.1 to 0.5 and its graph shows a sharp decline in correlation as the lag increases, indicating less correlation (Figure 3). This suggests that the abundance of phytoplankton does not depend strongly on its abundance in the distant past, but rather is more influenced by recent conditions. The ACF graphs for the other five taxa show that there was no significant autocorrelation for the "CellsPermL " data at different lags; all bars are within the confidence interval and data points were further apart in time, indicating less correlation with each other. (Figure 4).

The scattergram, which illustrates the mean monthly abundance of the five phytoplankton classes, shows greater variability at the freshwater site compared to the other sites (Figure 5). Cyanophyceae and Chlorophyceae exhibited similar spike patterns in both the saline and brackish water sites, while the abundance of other taxa remained notably low. Interestingly, there were significant spikes in Fragilariophyceae at the freshwater site during the early years of the study period, specifically from 2008 to 2013.

Table 2. Mean abundance of each phytoplankton class in each study site. Results are for all data combined from the period from January 2008 to December 2022.

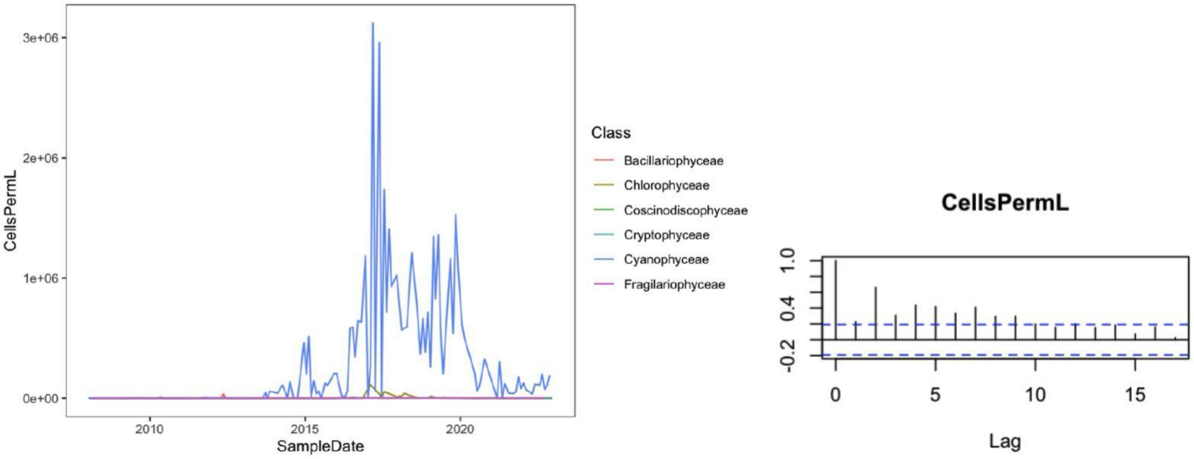
	Class	**Mean**	**Max**	**Min**	**Std**
Saline water	Bacillariophyceae	556.64	33125.71	0.46	3036.35
(Chipps Island)	Chlorophyceae	4980.77	111706.64	1.31	15073.22
	Coscinodiscophyceae	528.09	10551.43	0.11	1206.73
	Cryptophyceae	586.09	8896.00	0.30	1234.712
	Cyanophyceae	374379.10	3122380.80	0.10	557415.60
	Fragilariophyceae	206.55	2573.88	0.16	473.04
Brackish water	Bacillariophyceae	269.47	4721.71	1.13	582.28
(Decker Island)	Chlorophyceae	3399.88	34232.68	1.28	6954.20
	Coscinodiscophyceae	651.15	10009.56	0.73	1341.37
	Cryptophyceae	419.39	3800.51	4.09	626.42
	Cyanophyceae	265003.50	3043105.11	7.20	451116.80
	Fragilariophyceae	260.78	1801.72	0.91	455.85
Freshwater	Bacillariophyceae	2836.16	85503.39	2.89	9357.23
(Hood)	Chlorophyceae	3631.61	110383.48	4.73	12404.92
	Coscinodiscophyceae	2397.00	39865.00	4.10	5801.07
	Cryptophyceae	774.63	12986.37	1.00	1871.71
	Cyanophyceae	174670.70	3040457.10	17.60	393597.60
	Fragilariophyceae	9250.28	161987.85	0.13	24850.55

During the study period (2010-2022), there was notable spatial variability in hydrological variance across the three water bodies. I found that the saline water site (Chipps Island) within the estuary showed the highest mean values for conductance, salinity and turbidity. Additionally, it showed the greatest variability in conductance and salinity. Conversely, the freshwater recorded the highest temperature, accompanied by the most significant variability in temperature, turbidity and velocity. The difference in average conductance between saline and brackish waters was significantly larger than the difference in average salinity (Table 3).

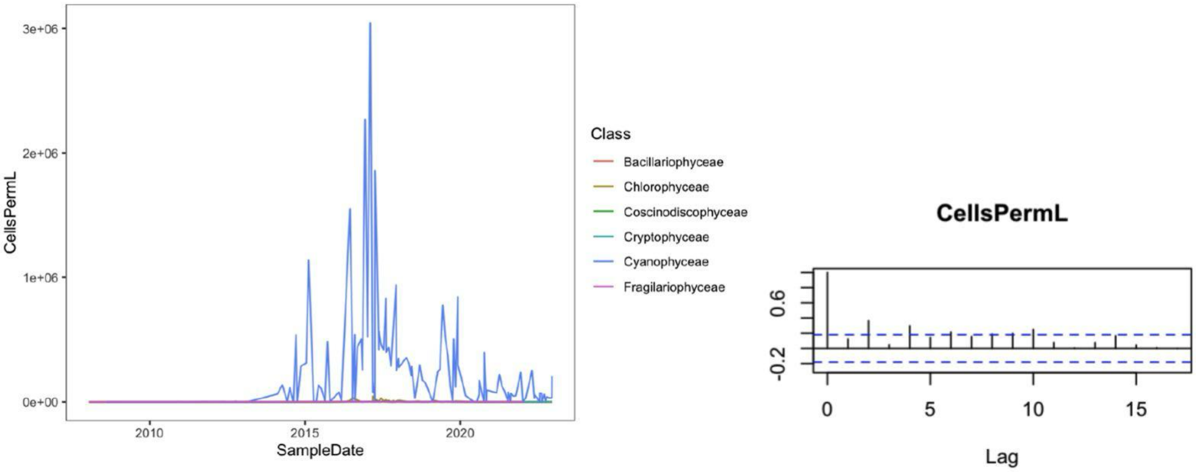
Table 3. Annually averaged daily values and max-min envelopes of water parameters from 2010 to 2022. Saline water–Chipps Island, brackish water–Decker Island, and freshwater–Hood.

	Site Type	**Mean**	**Max**	**Min**	**Std**
Conductance ($\mu S\ cm^{-1}$)	Saline	5564.60	13610.50	118.60	4414.05
	Brackish	255.90	1165.90	113.20	200.96
	Freshwater	143.58	232.09	75.44	31.31
Salinity ($\mu S\ cm^{-1}$)	Saline	3.15	7.85	0.03	2.56
	Brackish	0.53	2.49	0.02	0.62
	Freshwater	0.07	0.10	0.00	0.04
Temperature(°C)	Saline	15.87	23.90	6.96	4.66
	Brackish	16.07	23.22	7.62	4.64
	Freshwater	16.39	24.73	8.06	4.84
Turbidity (NTU)	Saline	25.56	125.39	5.13	11.75
	Brackish	19.86	88.78	6.58	13.74
	Freshwater	13.38	93.36	1.16	15.78
Velocity (ft./s)	Saline	n/a	n/a	n/a	n/a
	Brackish	0.42	3.03	-0.35	0.35
	Freshwater	1.21	3.56	0.36	0.75

(a) Saline (Chipps Island)



(b) Brackish (Decker Island)



(c) Freshwater (Hood)

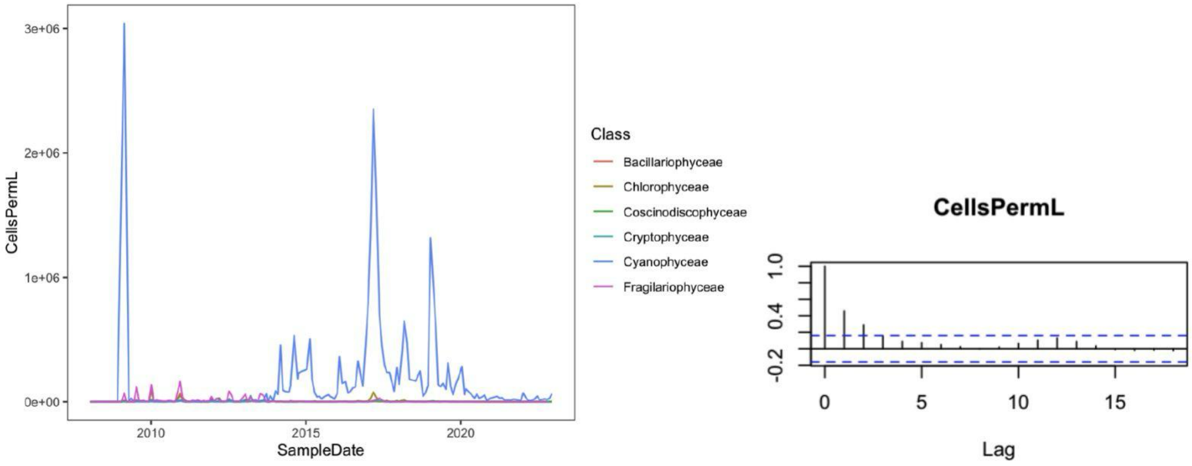
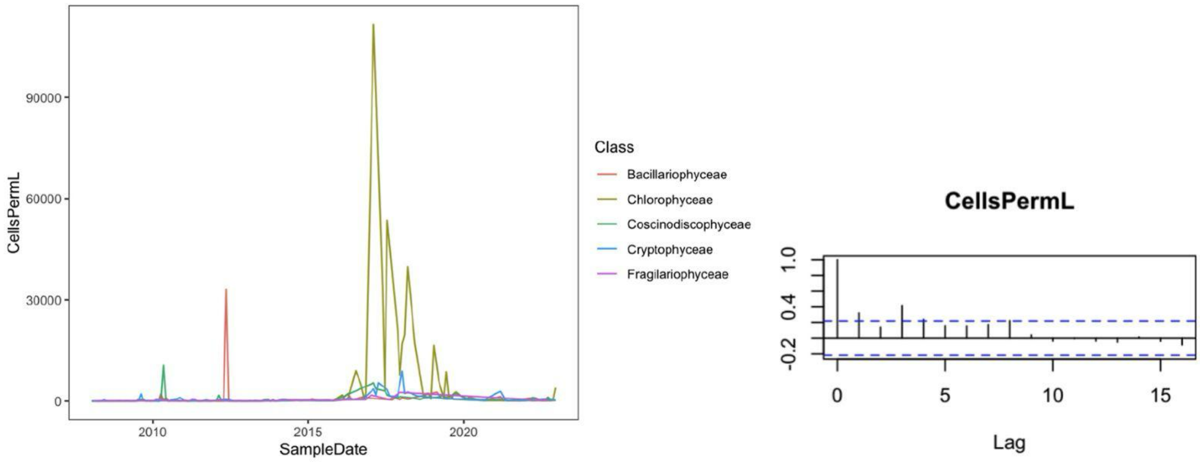
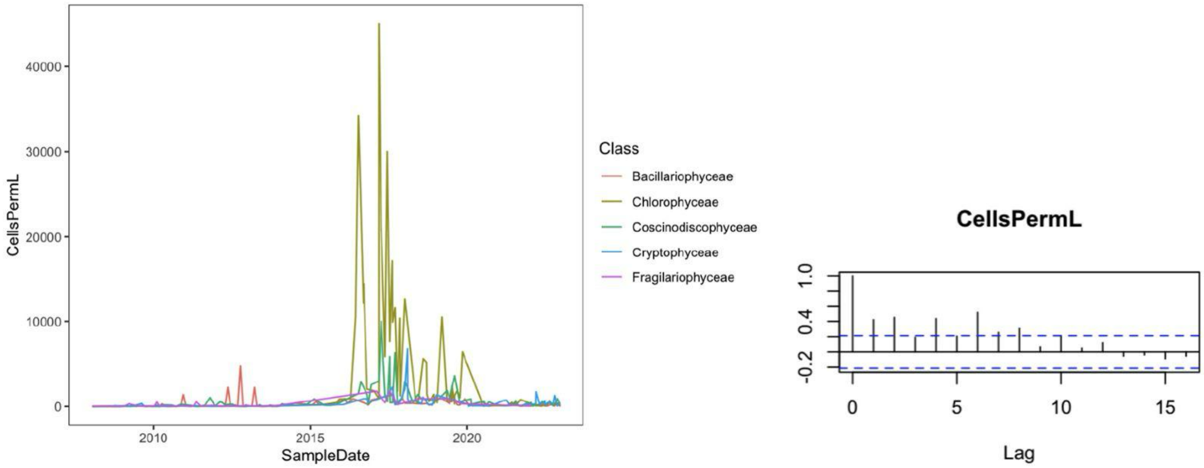


Figure 3. Mean monthly abundance of 6 phytoplankton taxa over a 15-year time series (2008-2022) (left) and the autocorrelation function (ACF) graph of the Cyanophyceae abundance (right). The X-axis represents lag in years, and the y-axis represents the correlation coefficient on the ACF graph.

(a) Saline (Chipps Island)



(b)Brackish (Decker Island)



(c) Freshwater (Hood)

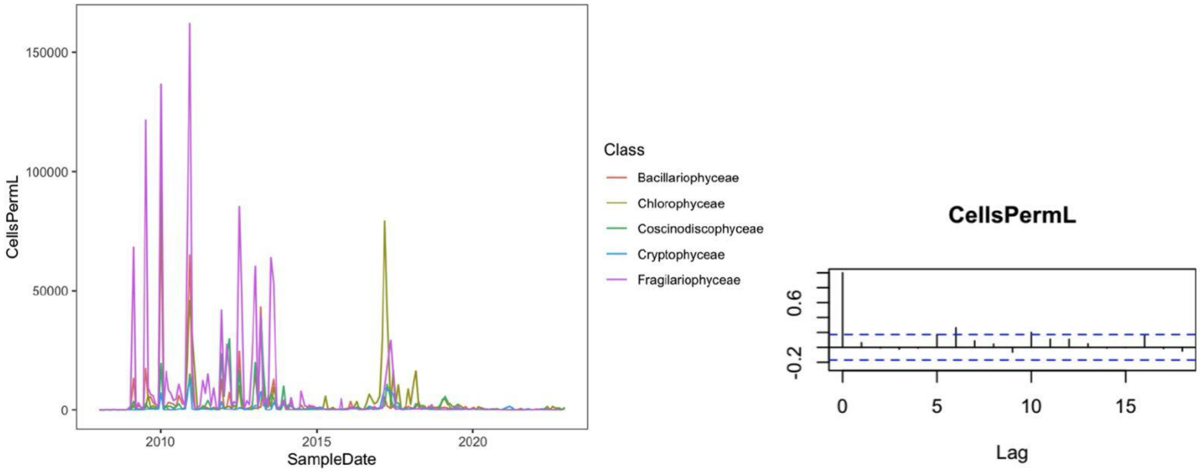


Figure 4. Mean monthly abundance of 5 phytoplankton taxa over a 15-year time-series (2008-2022) excluding Cyanophyceae (left) and the autocorrelation function (ACF) graph (right). X-axis represents lag in years, y-axis represents the correlation coefficient on the ACF graph.

Table 4. Anomalies in time series data of major phytoplankton taxa abundance over a 15-year period. Data for the months and years with the top 20 highest and lowest abundances are presented to observe the seasonal patterns across the sites.

	Highest Abundance Month			**Lowest Abundance Month**		
Site Type	**Fragilariophyceae**	**Chlorophyceae**	**Cyanophyceae**	**Fragilariophyceae**	**Chlorophyceae**	**Cyanophyceae**
	Diatoms	Green Algae	Blue-green Algae	Diatoms	Green Algae	Blue-green Algae
Saline water (Chipps Island)	2017. 1, 8, 12 2011. 1, 3-5 2016. 3, 11 2014. 3, 11	2017. 2, 5, 7, 11 2018. 1-3, 6 2019. 1,3, 4, 6,10 2016. 7, 9, 11	2017. 3,5,7-12 2019. 2-4, 9-12 2018. 5-6, 8,10,12 2016. 12	2008. 1-4, 7, 11,12 2012. 3,9,11 2011. 2-3,7,11 2013. 4, 5, 7	2010. 1- 7, 10-12 2011. 4-11 2013. 2,6 2015. 10	2008. 1-4, 6, 1 2010. 3, 6 ,9 2012. 7, 9 2013. 8. 10
Brackish water (Decker Island)	2017. 2, 5, 7, 11 2018. 5, 6 2019. 5, 11 2010. 2,4, 6-8	2017. 3–11 2016. 6, 7-10 2018. 1, 8, 9 2019. 3, 9, 11	2017. 1-9, 12 2016. 6, 9, 10, 12 2019. 6-9, 12 2015. 2, 9	2010. 3,6,7,9 2012. 3,9,11-12, 2013. 5,10 2011. 2-3	2010. 1, 3, 9 2011. 4,6 2012. 7 2013. 4	2008. 8 2010. 7~9 2014. 6, 8, 10 2015. 4, 5, 8, 10
Freshwater (Hood)	2010. 1, 12, 2009. 2, 7 2013. 1, 3, 7, 8 2019. 1, 3, 7, 12	2017. 2-8, 12 2018. 1-3. 6, 11 2019. 1, 3-6, 10 2016. 7, 9, 11	2017. 1-6, 2019. 1-3, 8 2018. 2-4 2016. 2, 9, 12	2008. 1~4, 8 2021. 8 2022. 10-11 2021. 8,7,9,3,12	2008. 1-10 2021. 4-6 2011. 3, 11 2020. 2, 12	2008. 2~12 2011. 4, 6, 8 2010. 7, 10 2009. 6, 12

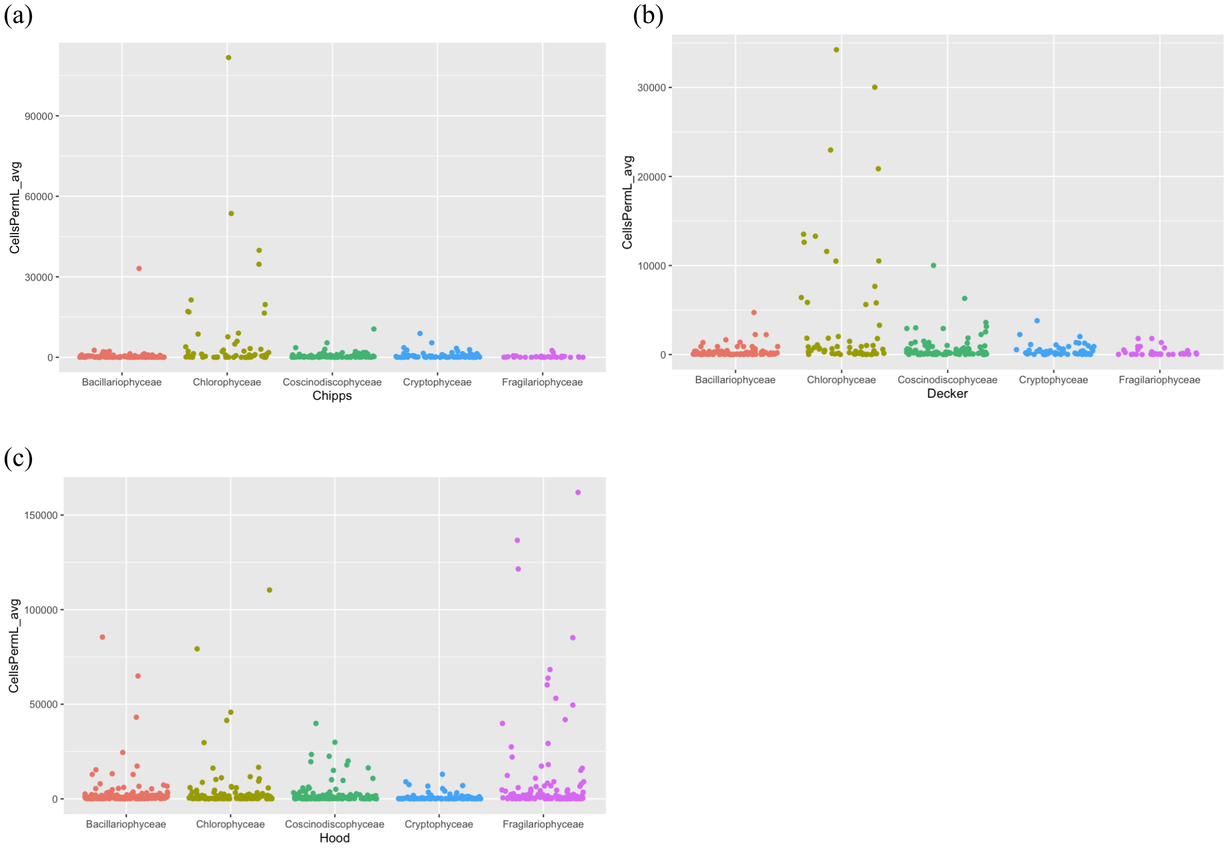


Figure 5. Scattergram for mean monthly abundance of 5 phytoplankton classes over a 15-year time-series (2008-2022) excluding Cyanophyceae.

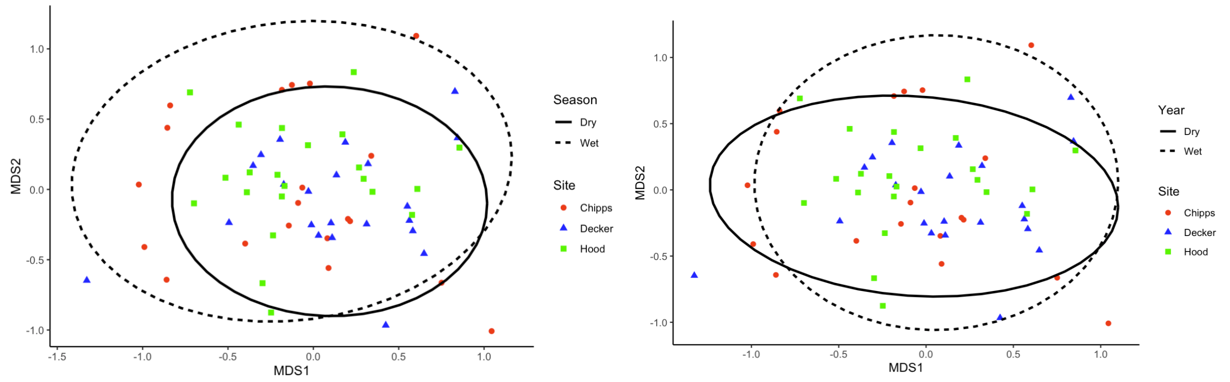
Temporal variability in the abundance of phytoplankton between dry and wet years

I found a significant difference in the mean abundance in response to hydroclimatic changes between dry years and wet years for every taxonomic class. The average phytoplankton volume during the wet season in wet water years (2016-2017) was about 15 times higher than the wet season in dry water years' average (2020-2021). The interannual difference of the dry season abundance was on average, 26 times greater in the wet water years than the dry water years. The higher abundance during the wet season in the wet year was apparent at brackish and freshwater, but Cyanophyceae showed a slightly better performance in the following dry season in wet year (Table 5). During the dry water year, the whole community outperformed during the wet season, particularly at saline water. The Saline water site showed the highest abundance peaks across all taxa, while the Freshwater site displayed the lowest abundance but the greatest seasonal variability between dry and wet water years.

Table 5. Mean abundance comparison of phytoplankton between wet year and dry year. The classifications were based on the water year cycle: the wet water year (October 2016–September 2017) and dry water year (October 2020–September 2021). Cyanophyceae abundance was separated from five phytoplankton taxa (Bacillariophyceae, Chlorophyceae, Coscinodiscophyceae, Cryptophyceae, and Fragilariophyceae).

		Wet Water Year (2016-2017)		Dry Water Year (2020-2021)	
Site Type	**Taxa**	**Wet Season Oct 2016-Mar 2017**	**Dry Season Apr 2017-Sept 2017**	**Wet Season Oct 2020-Mar 2021**	**Dry Season Apr 2021-Sep 2021**
Saline water	Cyanophyceae	1,046,439.00	1,148,621.00	161,959.80	100,969.10
(Chipps Island)	5 taxa group	9429.00	7364.52	1046.25	190.24
Brackish water	Cyano	1,118,718.00	560,441.80	106,278.70	92,204.80
(Decker Island)	5 taxa group	2724.43	4343.98	228.10	266.98
Freshwater	Cyano	882,016.40	618,192.50	33,264.66	21,105.02
(Hood)	5 taxa group	6034.27	6043.17	244.04	102.66

The NMDS (Non-metric multidimensional scaling) graph showed much similarity across all water sites during dry seasons. Brackish and freshwater sites demonstrated dissimilarity during wet seasons, while saline water maintained relatively consistent similarity. Overall, the wet season population variability was much greater than dry season variability. In contrast, sites are more dispersed along both NMDS axes, indicating greater variability. During wet years, the grouping is tighter, suggesting more consistent abundance. Brackish and freshwater sites showed stronger associations during wet years whereas saline water exhibited less distinct seasonal separation (Figure 6).


(a) Sites grouped by dry/wet seasons

(b) Sites grouped by dry/wet years

Figure 6. NMDS ordination plot for the phytoplankton abundance across seasons (a) and years (b). Each plot shows the same ordination (stress = 0.19), with 95% confidence interval ellipses plotted for each level of the predictor variable.

The effect of hydrological factors on species survival

By fitting the MARSS model to 13 year time series data of phytoplankton abundances, I found that the "conductance" metric showed the highest association with abundance of phytoplankton at the saline water site out of the 14 models (Table 6). The predictor variable combination of site type "saline water", and the interaction of site type "saline water" and the water parameter "conductance" best explained the variation in phytoplankton abundance. Salinity factor showed the second lowest AICc values across fresh, brackish and saline water bodies, indicating the strong association with species survival.

Both the saline water and freshwater sites showed the best interaction strength with conductivity. Salinity was also highly correlated with the decline of phytoplankton population biomass throughout every type of waterbody and the velocity of water is also a negative influence on phytoplankton growth particularly in freshwater streams. The MAR models with "equalvarcov" Q matrices had lower AICc values at freshwater, as opposed to brackish and saline water sites which preferred species-specific "diagonal and unequal" Q-matrices. Accounting for a lack of covariance netted a significantly worse model at freshwater.

Most models from the C matrices exhibited confidence intervals containing zero, making them non-significant. Each phytoplankton class is relatively more impacted by conductance and salinity than temperature, turbidity, or velocity. Because cyanophyceae (cyanobacteria) was the predominantly major Class (Figure 3), I ran another model but with an adjusted x_t matrix (5 x T) that omitted cyanobacteria (Figure 4). The AICc for every model reduced from around 20% through 30%.

Table 6. MAR model performance for phytoplankton species. The models are ordered from highest to lowest support based on AICc within each site with Q matrix set to 'diagonal and unequal' (without covariance) and 'equalvarcov' (with covariance). The model for "the velocity in saline water" was dropped due to the missing data.

Model		**Without Covariance**		**With Covariance**	
Sites	Water parameter	**AICc**	**ΔAIC**	**AICc**	**ΔAIC**
Saline water (Chipps Island)	Conductivity	663.15	0	703.58	0
	Salinity	666.18	3.03	707.886	8
	Turbidity	1244.97	581.22	1291.27	587.6912
	Temperature	1586.13	922.98	1636.13	932.5452
	Velocity	n/a	n/a	n/a	n/a
Backish Water (Decker Island)	Salinity	999.33	0	994.55	0
	Conductivity	1190.93	191.6	1199.55	205.0007
	Velocity	1326.58	327.22	1335.28	340.7377
	Temperature	1331.48	332.12	1339.00	344.4607
	Turbidity	1359.39	360.06	1370.09	375.5407
Freshwater (Hood)	Conductivity	1459.36	0	1403.66	0
	Salinity	1475.33	15.97	1422.02	18.36
	Velocity	1852.56	393.20	1463.03	59.35
	Temperature	2035.05	575.69	1691.80	288.14
	Turbidity	2197.59	722.27	1845.83	442.17

DISCUSSION

In this study, I found significant interannual, seasonal, and spatial variability in phytoplankton composition and biomass across the Delta. These variabilities most likely coincided with the effects of conductivity and salinity across three distinct water bodies. The interannual variation of phytoplankton density was notably larger than the intra-annual seasonal variation for each taxon across the sites. The biomass of diatom, which supports the food web, was significantly lower compared to Cyanophyceae. While the abundance of Cyanophyceae disrupted community diversity, Chlorophyceae displayed a trend of abundance that was synchronized with Cyanophyceae. Given the higher phytoplankton abundance observed in the wet season during both wet and dry water years across all taxa, these findings suggest that freshwater inflow plays a significant role in governing hydrological structure and function of stream ecosystems that boosts phytoplankton productivity.

Trends of phytoplankton composition and abundance in different hydrological settings

The result exhibited distinct seasonal differences and even more pronounced yearly differences in the abundance of the six taxa across the sites. As the abundance of phytoplankton has fluctuated significantly over the years, the community diversity has also declined. The decreasing trend of total annual phytoplankton biomass, particularly diatoms (Bacillariophyceae, Fragilariophyceae), was aligned with my hypothesis. This result corroborates with the other research that observed the decreased Chl-a concentration between 1989 and 2019 in the 38-mile stretch of the lower Sacramento River from the confluence (IEP 2020). Declining pattern was more distinct at the freshwater body than brackish and saline water bodies. Although the mean abundance of six taxa of the 15-year period was significantly high (Table 3), the recent mean abundance data from the wet water year (2016-2017) and the dry water year (2020-2021) shows the significant decline at the freshwater site (Table 5). Phytoplankton biomass is usually higher in fresh water than in low-salinity water (Kimmerer and Thompson 2014). However, this result shows the deviations from typical phytoplankton abundance patterns, which suggests the ecological changes occurring in the Delta freshwaters affected by increased temperature, nutrients, and decreased freshwater inflow (Dodds and Smith 2014, Kimmerer et al. 2018). Additionally, the brackish water sites displayed the least productivity across most taxa, potentially indicating unfavorable hydrologic conditions such as relatively shallow bathymetry, weak lateral mixing, and lingering particles due to tidal effect (Benette and Burau 2015).

Cyanophyceae class demonstrated a significant upward trend until early 2019 with the year-round presence across the sites. Contrary to my prediction of its bloom during the summer season, Cyanophyceae flourished throughout the year across the sites (Figure 3, Table 4). Microcystis blooms typically occur in the summer and fall, but the bloom season extends during drought years (Lehman et al. 2017). My findings show that the year-round Cyanophyceae bloom occurred following the severe drought years from 2012 to 2016 (DWR n.d.a). Cyanobacterial abundance in both dry and rainy periods was also observed in the lentic mediterranean lake Koronia in Greece (Michaloudi et al. 2009) and tropical reservoir in Brazil (Moura et al. 2021). Year-round presence of Cyanophyceae suggests that their dominant population might have caused diatom declines because Cyanophyceae outgrowth boost internal nutrient loading (Sevindik et al.2022). Cyanophyceae outgrowth can shift the ratio of nitrogen (N) to phosphorus (P) as much as 10:1 (Michaloudi et al. 2009). This chemical rebalancing can lead to the decrease of the Cyanophyceae bloom, followed by the increase of other phytoplankton taxonomic groups. In the brackish water site, I observed a potential alternating succession cycle between diatoms and Cyanophyceae. Fragilariophyceae bloomed a month earlier than Cyanophyceae in the year when their highest abundance overlapped. Even though their years of highest abundance did not overlap, there was a one-month lag in the bloom period during the year of highest abundance that did overlap in the brackish water site (Table 4). For instance, following the bloom of Fragilariophyceae in November of 2017 and 2019, Cyanophyceae flourished in December of 2017 and 2019, respectively. This seasonal succession pattern between Cyanobacteria and diatoms (Bacillariophyceae) was also observed in another study, which demonstrated the alternating pattern of the dominant class during the summer (Kim et al. 2019). Meanwhile, there was a relatively synchronized trend of the population spike between Chlorophyceae and Cyanophyceae across all three sites. Their peak abundance months and years from 2016 to 2019 largely overlapped, unlike Bacillariophyceae or Fragilariophyceae (Table 4). The co-occurrence of Chlorophyceae and Cyanophyceae can be attributed to their shared characteristics, such as a higher affinity in brackish waters (Michaloudi et al. 2009), and a great productivity in nutrient-rich polluted water (Geradi and Lytle. 2015). Chlorophyceae and Cyanophyceae thrived over diatoms in eutrophic water that has a high concentration of $NH4^+$ in other studies (Gilbert et al. 2015). These studies suggest the divergent growth trends in phytoplankton assemblages which impedes the diversity of the species in degraded hydrological environments of the Delta.

Interannual difference of phytoplankton abundance between wet and dry water years

The result indicates a higher rate of phytoplankton succession throughout the wet water year. I initially hypothesized lower phytoplankton biomass during the wet season (October-March) in the wet water year due to increased water turbulence and turbidity, which can inhibit light resources and stability necessary for their growth. However, only five taxa groups at the brackish water site showed slightly more abundance during the dry season in both the wet and dry water years in line with my hypothesis (Table 5). The productivity at the brackish water site, which is influenced by tidal fluctuation, might be boosted by the stable hydrological conditions during the dry season (Benette and Burau 2015). Contrary to my expectations, the abundance of most phytoplankton taxa was greater during the wet season in the wet water year (Table 4). It's possible that the elevated nutrient levels during the wet season, resulting from runoff, could have stimulated phytoplankton growth and promoted their widespread distribution (Quigg et al. 2023). Although a single intense flash flooding can decimate the phytoplankton community, a temporal succession follows immediately after the event (Abdel-Meguid et al. 2018). Research conducted in the Nile river-delta region demonstrated that the biomass returned to its pre-flooding levels by the fifth day post-flood. Yet, another study for the Galveston Bay at Texas showed a decrease in biomass and productivity despite high nutrient concentrations following Hurricane Harvey (Quigg et al. 2023). The ability of phytoplankton communities to revert to their pre-flooding status can depend on the magnitude and the severity of the hydrological changes. Also, Cyanophyceae demonstrated year-round abundance in the wet year due to its exceptional tolerance to nutrient-rich waters (Strong et al. 2021, Sevindik et al. 2022). However, in 2017, diatoms (Bacillariophyceae) did not reach their peak abundance concurrently with Chlorophyceae and Cyanophyceae (Table 4). This observation supports the theory that successions typically culminate in a dynamic climax state, where the species best adapted to competition survive at the expense of their competitors (Raynolds, 2006).

The most significant seasonal fluctuations in phytoplankton biomass between wet and dry water years were observed at the freshwater site (Hood). This result suggests a significant role of freshwater inflow in governing the hydrological structure and function of stream ecosystems. Considering the higher abundance observed in the wet season across the taxa as well as increased population during the wet season in the dry water year (Table 4), these findings underscores the importance of freshwater inflow volume in supporting phytoplankton productivity (Lehman et al. 2021, Papry et al 2021). Furthermore, past research has noted a surge in chlorophyll concentration in the fall of 2012, following a cycle of dry years from 2007 to 2010 and a wet year in 2011 (Kimmerer et al. 2018). This pattern aligns with my findings, which show a peak in abundance throughout 2017 after a series of dry years from 2012 to 2016.

The long-term effect of hydrological factors on species abundance

Phytoplankton abundance showed the highest sensitivity to conductivity and salinity, underscoring the importance of water quality. Given the inherent salinity in the estuarine environment, I had anticipated that an increase in water turbidity might negatively have affected the phytoplankton population by inhibiting light penetration and phytoplankton distribution (Lehman 2021). However, contrary to my hypothesis, conductivity was the most crucial parameter in determining the phytoplankton abundance in the Delta. Conductivity measures the ability of a solution to conduct electricity. Conductivity values depend on the ionic strength of the solution, the ions present, and the ion concentration. Elevated conductivity indicates poor water quality of the Delta, which increases with organic and inorganic substances, chemicals, minerals, and pollutants (Kraus; et al. 2017). Herbicides have been the most frequently detected contaminant type in California water bodies (Orlando et al. 2014). Upon the increase of aquatic invasive plants along the Delta, herbicides have been directly applied to water bodies of the Delta from March through November (Khanna et al 2023). Additionally, urban and agricultural runoff can increase conductivity by adding ions such as chloride, phosphate, and nitrate Considering the surrounding environment of the Delta, which includes oil refineries and plants, the levels of electrical conductivity, and dissolved oxygen may have risen to a point that limits phytoplankton growth.

Salinity is another critical factor in shifting phytoplankton distribution. Increased salinity has been a recognized problem by the state, which caused by imported salts in irrigated water, and land-derived salts from agricultural and wetland discharge (Minasian 2005) In addition to the natural cause of higher salt water density, the Delta experiences significant salinity intrusion occurrence nearly every year. This is due to dredged water channels by freshwater diversion and groundwater extraction, which disrupt the balance between freshwater and saline water in estuarine environments (CCW 2010). Other studies on Mediterranean coastal waters have found that changes in salinity significantly impact the microbial biodiversity, biomass and resource use efficiency (Stefanidou et al. 2018). Moreover, the continuous exposure to salinity fluctuation showed the consequence of the harmful algal blooms, whichI discussed earlier about the strong survivability of Cyanobacteria (Stefanidou et al. 2020). Increasing salinity in riverine water indicates the depletion of freshwater, suggesting the significance of keeping freshwater inflow. The influence of other water parameters, such as warmer water temperature and increased turbidity resulting from nutrient inputs from urban and agricultural runoff, should also be considered. These factors contribute to the low abundance of phytoplankton, as other researchers have found a negative impact in the San Francisco Estuary (Kimmerer & Thompson, 2014).

Limitations and future directions

This research focuses on hydroclimate impact on the phytoplankton community structure and distribution, however there are multiple variables such as multivariate environmental drivers and inter-specific dynamics within species that can interfere temporal changes in phytoplankton communities. As the phytoplankton and hydrological data came from two different databases in widely different time and spatial coordinates, the study scope was downsized while compiling datasets to match the study period and sites. As the ACF result showed, the abundance of phytoplankton does not depend heavily on its abundance in the distant past, but rather is more influenced by recent environmental conditions (Figure 3 and 4). While other biogeochemical factors play a significant role, the lack of long-term datasets led to the exclusion of many key factors such as nutrients and water gauges from my analysis. Besides, Hood was selected for freshwater due to the accessibility of both phytoplankton and hydrological data. Yet, its proximity to the Sacramento Regional Wastewater Treatment Plant (SRWTP), located 6 miles upstream to the north, potentially compromises its adequacy as a representative site for freshwater bodies in the Delta. The higher nitrogen(N) and ammonium (NH_4^+) inputs from wastewater treatment plants have been identified as a major factor affecting phytoplankton in the many large rivers and estuaries in urban areas (Parker et al. 2012). SRWTP is known to be the single largest point source of N to the Delta by discharging approximately 15,000 kg of NH_4^+ (Strong et al. 2021). Although this study encompasses methodical limitations, this long-term trend research framework can be applied to other riverine environments to detect the deviation from normal phytoplankton biomass range which can elucidate the management direction to maintain the productivity of freshwater ecosystems.

Future research can incorporate more comprehensive environmental drivers and additional sites, particularly freshwater bodies along the Delta. My study demonstrated the highest association between conductivity and the presence of phytoplankton, however, more environmental drivers might better explain spatiotemporal effects on the species and the complex patterns of the species dynamics in the future studies. As the ACF result showed, the abundance of phytoplankton does not depend heavily on its abundance in the distant past, but rather is more influenced by recent conditions (Figure 3 and 4). Hence, factors like water discharge, level, Total-N and P, and dissolved oxygen, along with biotic drivers such as non-native aquatic vegetation and zooplankton, which significantly impact phytoplankton productivity and trophic food-web changes would provide a clearer understanding of phytoplankton population dynamics (Kimmer et al. 2018, Khanna et al. 2023). Various water quantity and quality variables would better elucidate the effect on phytoplankton population change. Additionally, the year 2023 was one of the record-high wet years followed by the prior three driest years (2020–2022). Future research on this could help understand how freshwater ecosystems respond to flow-regime changes post heavy rainfall. While this study focused on taxonomic groups, examining phytoplankton based on functional groups, which share similar environmental adaptabilities, could reveal different trends or succession patterns (Kim et al. 2019, Sevindik et al. 2022).

Broader implications

Climate change and increasing water demands are projected to reduce freshwater inflow to the estuaries, thereby modifying the scale and timing of flow as well as biological responses to these changes (Kimmerer et al. 2018). There have been substantial alterations to rivers and streams, resulting in hydrologic shifts including changes in the volume and velocity of runoff and sediment, the size and frequency of floods, and the recharge and discharge of groundwater (Kozlowski et al.2016). Alongside these hydrological changes, the eutrophic condition of the Delta affects structure and density of the phytoplankton community (Strong et al. 2021). This study showed a divergent trend in the phytoplankton community, marked by a decrease in diatoms and a surge in cyanobacteria, in response to the fluctuating hydrological environment. The results suggest a loss of diversity and resilience within the phytoplankton community due to hydroclimate anomalies, which could potentially lead to instability in the Delta's freshwater ecosystem.

The collective results of this study highlight the impact of river flow conditions on the phytoplankton community's survival and underscore the significance of freshwater management. My findings on the abundance of phytoplankton, specifically Cyanophyceae, peaking immediately after a wet year that followed several successive drought years, could indicate a cyclical pattern. Moreover, other findings related to the effect of conductivity and salinity on population changes suggest a degradation in water quality due to a reduced freshwater volume. Various stakeholders in the Delta can apply these insights in ecological water management while preparing for potential Cyanophyceae bloom. The Delta Conveyance Project is under way for both water export and storm water storage (CDWR 2024). The new 44 mile-channel construction may enhance water quality by acting as a buffer against salt water intrusion or exacerbate salinity and water retention issues due to a loss in water volume. In light of expected hydrological changes from anthropogenic and climatic perturbations, it becomes increasingly crucial to understand spatiotemporal patterns of phytoplankton abundance and composition because identifying shifts within their community is vital for the preservation of the Delta ecosystem.

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