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Influence of Flow Regulation on Phytoplankton Biomass and Composition Along the Salinity Ecocline: Caloosahatchee River Estuary, Florida, USA

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ABSTRACT

The Caloosahatchee River Estuary (CRE; Florida, USA) is a flow-regulated ecosystem receiving discharges from eutrophic Lake Okeechobee and surrounding watersheds via the C-43 Canal. These discharges alter the estuary's salinity ecoclines, water residence times, and nutrient fluxes, but it remains unclear how changes in discharge volume drive changes in the phytoplankton dynamics and harmful algal bloom (HAB) risk. To address this gap, we compared three sampling periods with distinct discharge patterns (2009/2010, 2018/2019, 2021–2024) to determine the effects of different discharge regimes on phytoplankton composition and biomass. In the first two periods, low to moderate discharge coincided with major blooms of the euryhaline dinoflagellate *Akashiwo sanguinea* in the oligohaline to mesohaline upper estuary, whereas high discharge was followed by toxic *Karenia brevis* in the lower estuary and nearshore, including a major 2018 red tide. The third period had consistent moderate to high discharge rates that extended freshwater and oligohaline conditions downstream. The upper estuary became dominated by filamentous and colonial freshwater cyanobacteria typical of the Canal and Lake

Okeechobee, euryhaline diatoms (*Skeletonema costatum* cf., *Coscinodiscus* sp.) dominated the oligohaline–mesohaline mid and lower estuary, and dinoflagellates (*Peridinium quadridentatum*, *K. brevis*) bloomed under polyhaline–euhaline conditions, including a *K. brevis* red tide coinciding with Hurricane Ian in the fall of 2022. Overall, regulating C-43 Canal discharges could help mitigate HAB intensity and duration in the CRE and adjacent nearshore waters by modifying salinity ecoclines, limiting water residence times, and altering nutrient inputs.

INTRODUCTION

Estuaries associated with major freshwater inflows are characterized by high spatial and temporal variability in phytoplankton composition and biomass (Cloern and Jassby, 2008; Fugate and Andresen, 2020; Monbet, 1992). The character of phytoplankton communities in estuaries and nearshore regions can be affected by freshwater inflows in a range of ways, such as alterations in salinity gradients, nutrient levels, water residence times, flushing rates, stratification, and water clarity (Burford et al., 2012; Fugate and Andresen, 2020; Muyllaert et al., 2009). Globally, river discharges from developed coastal watersheds have raised nutrient loads in many estuaries (Eyre, 2000; Glibert, 2020; O’Neil et al., 2012; Palmer, 2004; Smith, 2003). However, the responses of phytoplankton composition and biomass to the inputs vary across ecosystems due to other factors, such as changes in climatic conditions, light availability, hydrologic conditions, grazing losses, and disease (Belgrano et al., 2004; Cheng et al., 2026; Medina et al., 2020; Medina-Sánchez et al., 2013; Quinlan et al., 2007). Nutrient-rich inflows to an estuary can stimulate phytoplankton growth, sometimes leading to harmful algal blooms (HABs) (Gillanders and Kingsford, 2002; Mallin et al., 1998; Medina et al., 2022), but depending on the geomorphology of the estuary, high discharges can also lower water residence times, reducing the degree of phytoplankton biomass accumulation (Cloern et al., 1989; Lucas et al., 1999; Paerl et al., 2006; Phlips et al., 2004, 2011, 2020). Conversely, given sufficient local nutrient sources, prolonged periods of low discharge to an estuary can enhance phytoplankton bloom formation due to increased residence time (Burford et al., 2012; Fugate and Andresen, 2020; Hall et al., 2008; Paerl et al., 2006; Ralston et al., 2015). In estuaries associated with freshwater inflows from eutrophic sources, there is also potential for allochthonous introductions of freshwater HABs (Phlips et al., 2012, 2020, 2025; Preece and Hartman, 2024; Sun et al., 2022;). Freshwater inflows can also limit phytoplankton growth more directly by carrying high concentrations of humic substances or suspended matter, reducing light penetration and

constraining primary production regardless of nutrient supply (Paczkowska et al., 2020; Reynolds, 2006).

The effects of freshwater discharges on estuarine phytoplankton communities are further complicated when freshwater inflows are regulated by water control structures, sometimes becoming partially disconnected from the natural wet/dry rainfall cycles for a region (Kim et al., 2021; Mitrovic et al., 2003, 2011; Ruan et al., 2024; Sin et al., 2013; Sin and Jeong, 2015) In Florida, one of the most prominent examples of a flow-regulated ecosystem is the Okeechobee Waterway that connects the large eutrophic Lake Okeechobee to the Caloosahatchee River Estuary (CRE) on the central west coast of Florida via the C-43 Canal, and the St. Lucie Estuary on the east coast via the C-44 Canal. Both canals contain multiple water control structures (i.e. dams and locks). Water releases from the structures are regulated by the U.S. Army Corps of Engineers, in collaboration with the South Florida Water Management District, based on the Lake Okeechobee System Operation Manual (LOSOM). LOSOM is designed to satisfy multiple objectives, including flood control, water supply for agriculture, urban uses, navigational demands, and maintaining the health of the downstream estuaries and adjacent coastal environments (Alber, 2002; Chilton et al., 2021; Julian and Reidenbach, 2024; Walker and Thoms, 1993).

Water quality of S-79 discharges from the C-43 Canal into the CRE reflects inputs from Lake Okeechobee, the watershed surrounding the Canal, and biogeochemical processes within the Canal (Badylak et al., 2025; Julian and Osborne, 2018; Montefiore et al., 2024). Lake Okeechobee discharge is associated with high nutrient concentrations and frequent blooms of cyanobacteria (Faridmarandi et al., 2020; Havens et al., 2003; Krinsky et al., 2019), which can be dominated by toxic species, such as the hepatotoxin-producing species *Microcystis aeruginosa* (Phlips et al., 2025; Rosen et al., 2017). When major blooms are present, discharges from Lake Okeechobee can lead to transport of large quantities of HAB biomass into the CRE from the C-43 Canal (Fig. 1) (Burns, 2008; Kramer et al., 2018; Phlips et al., 2012, 2020, 2025; Schaefer et al., 2019; Tolley et al., 2010). Under high discharge rates from the S-79, freshwater cyanobacteria blooms introduced to the estuary can extend far into the estuary and even impact adjacent nearshore waters (Metcalf et al., 2021; Phlips et al., 2012, 2025; Rosen et al., 2017; Schaefer et al., 2020; Uejio et al., 2022).

Nutrients originating from Lake Okeechobee and the C-43 watershed can also fuel phytoplankton growth throughout the C-43 Canal, the CRE, and nearshore coastal waters (Armstrong, 2019; Badylak, 2024; Medina et al., 2022; Montefiore et al., 2024; Phlips et al., 2012, 2023; Tolley et al., 2010). As a result, every region of the Caloosahatchee ecosystem is capable of developing autochthonous HABs that can have ecosystem disruptive effects, such as hypoxia, toxin exposure food web alterations (Badylak et al., 2025; Mathews et al., 2015; Milbrandt et al., 2021; Montefiore et al., 2024; Phlips et al., 2023, 2025; Turley et al., 2022; Urakawa et al., 2024). Recent research further supports that nutrient-rich discharges from coastal watersheds along southwest Florida can intensify red tide events (Glibert et al., 2025; Medina et al., 2020, 2022; Phlips et al., 2023). For example, elevated rainfall and S-79 discharge rates that followed Hurricane Michael in 2018 were followed by an intense bloom of *Karenia brevis* (Hall et al., 2024; Phlips et al., 2023).

The aim of our study was to assess how S-79 discharges alter phytoplankton composition, biomass, and HAB potential across the estuary's shifting salinity ecocline. To address this, we identified the dominant phytoplankton groups associated with different salinity regimes within the CRE and adjacent nearshore waters, then determined the environmental conditions associated with blooms of the dominant groups, focusing on three factors: discharge rates from the S-79 water control structure, changing climatic conditions, and temporal shifts in nutrient concentrations and sources. One of the focuses was management of S-79 discharge rates as a potential tool for mitigating HABs.

METHODS

Site Description

The Caloosahatchee River Estuary (CRE) is located on the southwest coast of Florida (Fig. 2). The Caloosahatchee River (C-43 Canal) runs 67 km west from Lake Okeechobee at the S-77 water control structure to the Franklin Lock and Dam (S-79). The S-79 separates the freshwater C-43 Canal from the estuary. The estuary extends 40 km downstream to San Carlos Bay (Fig. 2). The Canal has been straightened, deepened, and three water control structures have been added (S-77, S78 and S-79). The last control structure, S-79, was completed in 1966, in part as a salinity barrier (Doering et al., 2006). The river has been artificially connected to Lake Okeechobee to regulate releases of water. The estuarine portion of the system has also been

modified, including a dredged navigation channel. Historically, oyster bars in the estuary were mined and removed for road construction (Doering et al., 2006). The estuary and San Carlos Bay provide vital habitat for many species of fish, manatees, and dolphins. San Carlos Bay is home to seagrass meadows (<https://chnep.wateratlas.usf.edu/>) and oyster reef restoration sites (<https://chnep.wateratlas.usf.edu/oyster-habitat-restoration/>).

Spatial and temporal patterns of salinity in the CRE depend on discharges from the S79 structure, outflows from small tidal creeks in the CRE and precipitation. When discharges from the S79 are high (i.e., $> 113 \text{ m}^3\text{s}^{-1}$ or 4000 cfs), freshwater/oligohaline conditions can extend far down the estuary. Conversely, at very low discharge tidal mixing can extend far up the estuary yielding mesohaline (i.e., salinities of 5-18 ppt) conditions.

Eight study site locations were selected to capture conditions in the estuary, San Carlos Bay, and the adjacent nearshore environment in the Gulf (Fig. 2). Site 1 (26.695°N, -81.814°W) was in the upper estuary within 2 miles of the S79, Site 2 (26.645°N, -81.879°W) in the mid-estuary, Site 3 (26.543°N, -81.940°W) near Cape Coral in the lower mid-estuary, Site 4 (26.523, -82.009) near the mouth of the estuary, Site 5 (26.472°N, -82.016°W) in mid-San Carlos Bay north of Sanibel Island, Site 6 (26.466°N, -82.065°W) in southwest San Carlos Bay, Site 7 (26.431°N, -81.963°W) in the Gulf offshore of Estero Island, and Site 8 (26.412°N, -82.020°W) south of Sanibel Island (Fig. 2).

Sampling Protocols

Water samples were collected monthly during three time periods: 2008-2009, 2018-2019, and 2021-2024. The 2018–2019 study period included gaps in coverage from November 2018 to April 2019. Water column samples and associated field data were collected at the eight sampling sites. Water samples were taken using a 3-m integrated pole sampler to help avoid misrepresentations due to uneven distribution of phytoplankton throughout the water column.

Field Measurements

For each sampling site water temperatures, dissolved oxygen, and salinity were recorded using a HACH (Loveland, Colorado) HJQ40D or YSI EXO2 sonde at approximately 0.5 m intervals to the bottom of the water column. Two-point calibrations were performed for salinity and oxygen measurements according to the manufacturers' guidelines.

Precipitation data was gathered from the National Oceanic and Atmospheric Administration (NOAA) National Centers for Environmental Information (NCEI) Page Field Station in Fort Myers, FL (Kantor et al., 2023). Daily rates of freshwater discharge from the S-79 Franklin Lock and Dam were obtained from the USGS R package for water data ‘*dataRetrieval*’ (DeCicco et al., 2025).

Nutrient Analyses

For the 2008-2010 sampling period, aliquots of whole unfiltered sample water were transported on ice and stored frozen, within National Environmental Laboratory Accreditation Program (NELAP)-specified time limits, until chemical analysis (NELAP Certification #E72883). Samples for TN and TP analyses were digested using the persulfate oxidation method (Strickland and Parsons, 1972; APHA, 2005) and measured calorimetrically on a Bran-Luebbe (Norderstedt, Germany) AA3 auto-analyzer and a Hitachi (Tokyo, Japan) U2810 dual-beam spectrophotometer, respectively. Chemical analyses for the 2018–2019 and 2021-2024 study periods were conducted at Benchmark EA (<http://www.benchmarkea.com>), using NELAP-certified methods (NELAP Certification #E85086). Aliquots of unfiltered water were fixed with sulfuric acid ($\text{pH} < 2$) and placed on ice ($4\text{ }^{\circ}\text{C}$), then transported to the laboratory. Samples were analyzed for NH_4^+ following EPA Method 350.1, for TP following persulfate digestion (EPA 365.3), and TN following a sulfuric acid digestion (EPA 351.2) prior to analysis on a Syssta Easychem Plus (Syssta, Italy).

Phytoplankton Analysis

Subsamples (100 mL) were preserved with 1% acidic Lugol’s solution and analyzed using the Utermöhl method (Karlson et al., 2010; Philips et al., 1999, Rott et al., 2007; Utermöhl, 1958). 5-mL or 10-mL aliquots were taken from these subsamples and settled on an even surface in a 19 mm cylindrical chamber for 24 hours or more, allowing cells to settle onto a glass cover slip, sealed to the chamber with vacuum grease. The plankton were inspected to ensure that they settled evenly across the cover slip before counting. The phytoplankton were identified and counted at both a 400X and 100X magnification using a Nikon TMS inverted microscope. The microscope field of view contains a grid for measuring area based on magnification. A minimum of 30 and a maximum of 100 grids were counted for each 400X count. At this magnification, the count was complete once 100 cells of a single taxon were reached and at least 30 grids were

observed (Phlips et al., 1999). If 100 individuals of a single taxon were not observed, or if the 100 individuals came from a non-taxonomic group (e.g. centric diatom), the count continued until 100 grids were completed. Only species smaller than 30 μm in a circular or square size and smaller than 10 μm x 75 μm for pennate diatoms were recorded at 400X magnification. A total bottom count of the settling chamber was completed for each 100X magnification count; all species larger than or equal to 30 μm in size for round species (centric diatoms and dinoflagellates) or longer than 75 μm for pennate diatoms were recorded at this magnification (Phlips et al., 1999).

For picocyanobacteria counts, subsamples of seawater were fixed with 2.5% glutaraldehyde in 0.1M sodium cacodylate buffer, then filtered onto 0.2 μm Nucleopore filters and mounted between a microscope slide and cover slip with immersion oil. Photoautotrophic picoprokaryotes were separated into spherical picoplankton (referred to as “picocyanos” in the species list) and *Synechococcus* spp. Picocyanobacteria were counted at 1000X magnification using a fluorescent microscope, for both phycocyanin- and phycoerythrin-containing taxa (Blanchot et al., 1992; Phlips et al., 1999).

Cell biovolumes were estimated by assigning combinations of geometric shapes to fit the characteristics of individual taxa (Smayda, 1978; Sun and Liu, 2003; Sicko-Goad, et al., 1984). Specific phytoplankton dimensions were measured for at least 30 randomly selected cells of each species. Species which vary in size, such as many diatom species, were placed into size categories. The number of cells of a species observed in a sample (cells/mL) was multiplied by the individual biovolume of that species, yielding the total biovolume of the respective species in the sample. Phytoplankton biomass as carbon values (μg carbon mL^{-1}), were calculated by using conversion factors by multiplying by the biovolume ($\mu\text{m}^3 \text{mL}^{-1}$), for different taxonomic groups. $0.065 \times$ biovolume of diatoms, $0.22 \times$ biovolume for cyanobacteria, and $0.16 \times$ biovolume for dinoflagellates or other taxa with adjustments to biovolumes for the effects of Lugol’s preservative (Ahlgren, 1983; Sicko-Goad et al., 1984; Strathmann, 1967; Verity et al., 1992).

As a means of describing the phytoplankton taxa that played major roles in the phytoplankton communities, subsets of the Top-125 highest biomass observations for individual taxonomic groups were created for five salinity regimes, i.e., freshwater (i.e., salinities < 1), oligohaline (i.e., salinities of 1-5), mesohaline (i.e., salinities >5 – 18), polyhaline (i.e., salinities >18 -30), and euhaline (i.e., salinities > 30 – 35) (Table 2). While not classified as

phytoplankton, ciliates are included in the Top-125 lists because they are often mixotrophic and are known to consume phytoplankton and retain their photosynthetic activity (Gustafson Jr et al., 2000; Stoecker et al., 2009; Stoecker et al., 1987).

Among the taxa observed during this study, 51 fall into the category of harmful algal bloom (HAB) species (Table 3), based on currently accepted guidelines (Lassus et al., 2016; Moestrup et al., 2009; Chorus and Welker, 2021). The taxa fall into four major categories of phytoplankton: diatoms (Fryxell and Hasle, 2003), dinoflagellates (Taylor et al., 2003), cyanobacteria (Cronberg et al., 2003), and haptophytes (Moestrup and Thomsen, 2003). Bases for categorization of harmful include toxin production, physical damage, and/or ability to reach biomass levels that cause ecosystem disruption (e.g., hypoxia, mucilage production, light limitation). No tests for the presence of the toxin were carried out during this study. For the purpose of discussion the term ‘bloom’ is used to describe biomass levels greater than $>350 \mu\text{g carbon L}^{-1}$, which relates to the top 20% of biomass levels observed over the study period.

Statistical Analyses

Phytoplankton were divided into six categories for site and seasonal comparisons of biomass, i.e. diatoms (Bacillariophyceae), dinoflagellates (Dinophyceae), other cyanobacteria (Cyanophyta), picocyanobacteria (Cyanophyta), ‘other’, and ciliates. The ‘other’ category includes species not described by the first four categories, and were mostly eukaryotics, such as chlorophytes, cryptophytes, haptophytes, raphidophytes and euglenoids. Statistical analyses were carried out using R (R Core Team, 2024).

Prior to community analyses, all size groups of the same species, genera, or non-taxonomic group (e.g. pennate diatom, nanoflagellates, etc.) were combined. Rare species can skew the analysis of a community by introducing many zero abundance sites to the analysis. Lower abundance species also have the issue of their counts having low precision (Karlson et al., 2010) and the abundance may not represent the true population distribution of rare species because of the low volumes 5-10 mL used (Gotelli and Colwell, 2001; Rodríguez-Ramos et al., 2014).

To examine the relationship between phytoplankton community composition and environmental variables, we performed a distance-based redundancy analysis (db-RDA) using the *vegan* package (Oksanen et al., 2024) in R (R Core Team, 2024). The species data were right-skewed, with a few species having high abundance. Density (cells mL^{-1}) is a commonly

used for characterizing species/group abundance, however it gives higher weight to smaller phytoplankton species as they tend to have higher cell densities. To control for differing size among the phytoplankton species, carbon biomass numbers were used as a proxy for ‘abundance’. Species abundance (carbon biomass) data were first transformed using the Hellinger transformation (*decostand* function in *vegan*), which converts raw abundances to the square root of relative abundances, downweighing the influence of rare taxa and making the data appropriate for linear methods (Legendre and Gallagher, 2001; Oksanen et al., 2024). A Hellinger distance matrix was then computed from the transformed data (*rda* function) and used as the basis for the db-RDA, which identifies linear combinations of environmental predictors. The significance of the overall model and individual environmental constraints was assessed using permutation tests (999 permutations) via the *anova.cca* function in *vegan* (Oksanen et al., 2024).

RESULTS

Precipitation and Discharge

Monthly-mean discharge rates exhibited seasonal variability over the three study periods (Fig. 3). In the two earlier sampling periods (2009–2010; 2018–2019) S-79 discharge rates into the CRE generally coincided with variability in rainfall levels associated with the local dry (i.e. Nov.-April) and wet (i.e., May-Oct.) seasonal patterns (Fig. 3). However, during the 2021–2024 period, discharge rates were kept at consistently elevated levels based on management priorities, with occasional periods of very high discharge, such as $170 \text{ m}^3\text{s}^{-1}$ (6000 cfs) that coincided with Hurricane Ian in 2022.

Salinity

During the first two sampling periods (2009/2010 and 2018/2019) salinities at Sites 1–3 in the CRE varied between wet and dry seasons, with lower salinities due to elevated precipitation and S-79 discharge rates (Fig. 4). In the 2021–2024 sampling period, consistently higher dry-season discharge resulted in lower salinity ranges at all three sites. Higher precipitation and S-79 discharge in 2024 resulted in further reductions in salinity at Sites 2 and 3. Hurricanes in 2022 (Ian in September) and 2024 (Debby in August, Helene in September and Milton in October) also contributed to lower salinities.

Salinities at Site 4 near the mouth of the estuary primarily varied within the polyhaline (18-30) range during the first two sampling periods and through the summer of 2023 (Fig. 4). Storms in 2018 (Tropical storm Gordon in September and Hurricane Michael in October) and 2022 (Hurricane Ian) were associated with depressed salinities driven by increased freshwater inputs. After the summer of 2023, higher precipitation levels and S-79 discharge rates in 2024 resulted in further reductions in salinity, including the effects of Hurricanes Debby, Helene and Milton.

Salinities at Sites 5 and 6 in San Carlos Bay generally fell within the upper polyhaline (i.e., 18-30) and euhaline range (i.e., > 30), except during the high rainfall and S-79 discharge periods associated with the hurricane events in 2022 and 2024 (Fig. 4). At the two Gulf sites adjacent to San Carlos Bay (Sites 7 and 8), salinities were consistently in the euhaline range.

Nutrient Concentrations

Ammonium - Ammonium concentrations exhibited spatial, seasonal, and interannual variability (Fig. 4). Ammonium concentrations were frequently higher in San Carlos Bay (Sites 5 and 6) and the adjacent nearshore Gulf (Sites 7 and 8) than in the estuary (Fig. 5). Upper estuary sites (Sites 1-3) ammonium concentrations were statistically lower ($p < .001$) for all months and years.

Overall, the wet seasons showed higher concentrations of ammonium than the dry seasons. One of the major features of the temporal pattern was the elevated ammonium concentrations in October/November 2022 and much of 2023. The latter period followed the massive disruptions associated with the direct impact of major Hurricane Ian on the CRE and watershed in late September 2022. The event resulted in large discharges of organically enriched water from the estuary into San Carlos Bay and the adjacent Gulf.

Total Nitrogen - TN was generally lowest at downstream sites (Sites 5–8) during the winter dry period, while upstream and mid-estuary sites (Sites 1–4) showed consistently higher concentrations for most months and years (Fig. 6). There were anomalies as seen during March and May of 2023, where high TN concentrations were observed in San Carlos Bay and the nearshore. The highest TN values occurred primarily in 2023. Periods of elevated TN often occurred without corresponding increases in ammonium (Fig. 5, Fig. 6).

Total Phosphorus - TP was consistently higher at upper and mid-estuary sites (Sites 1–3), particularly during the rainy season (May–October). Concentrations for all sites were heightened during May 2023 similar to TN (Fig. 7). Downstream sites (Sites 5–8) generally exhibited lower

TP concentrations, although anomalous peaks were present for site 4 - October 2019 and site 6 - May 2022. TP concentrations declined as the sites were further downstream into the nearshore for all dates (Fig. 7).

Chlorophyll *a* - Annual mean chlorophyll *a* concentrations were generally higher in the upper (Sites 1 and 2) than in the mid-estuary (Site 3) (Table 1). The range of annual mean chlorophyll *a* at the lower estuary (Site 4), San Carlos Bay (Sites 5 and 6) and nearshore (Sites 7 and 8) sites were mostly lower than in the upper and mid-estuary, with some exceptions, such as in 2018-19 when extended blooms of the red tide species *Karenia brevis* were observed. High individual chlorophyll *a* values (i.e. > 20 µg L⁻¹) were observed at many sites in association with blooms, such as 40 µg L⁻¹ for an *Akashiwo sanguinea* bloom at Site 3 in 2009 and 33 µg L⁻¹ for a *K. brevis* bloom at Site 7 in 2018.

Phytoplankton Composition and Biomass

Site 1 in the upper estuary was often dominated by dinoflagellates or diatoms during periods of low discharge (≤ 1000 cfs), which was primarily limited to the first two sampling periods (2009/10 and 2018/19) (Fig. 8). Multiple blooms (i.e., >350 µg carbon L⁻¹) of the HAB dinoflagellate *A. sanguinea* were observed during these two periods. During the higher-discharge sampling period (2021-2024), blooms were dominated by HAB cyanobacteria (e.g., *Microcystis aeruginosa*, *Raphidiopsis raciborskii*, *Dolichospermum circinale*, *Limnothrix redekei*, *Cuspidothrix tropicalis*). Site 2 in the upper estuary exhibited high variability in biomass with numerous bloom events. Dinoflagellate blooms involving *A. sanguinea* and HAB cyanobacteria were observed during the first and second sampling periods. In the third sampling period, the diatom *Skeletonema costatum* and HAB cyanobacteria generally dominated blooms. Site 3 in the mid-estuary had lower biomass overall than Sites 1 and 2, with greater influence of picocyanobacteria in the first two sampling periods and higher relative importance of diatoms and ‘other’ taxa in the third sampling period. In terms of blooms, there were two major blooms in the first two sampling periods, one dominated by the diatoms *Skeletonema costatum* and the other by the dinoflagellate *A. sanguinea*. During the third sampling period three major blooms were observed, dominated by picocyanobacteria, *S. costatum* and *Cuspidothrix tropicalis*.

Site 4 in the lower CRE near the mouth to San Carlos Bay had lower occurrence and intensity of blooms compared to the upper and mid estuary (Fig. 9). There were no blooms observed during the first two sampling periods and picoplanktonic cyanobacteria, diatoms and

‘other’ taxa were generally the major elements of total biomass. The same groups of phytoplankton shared dominance in the third sampling period, with some moderate blooms of diatoms and picocyanobacteria. Sites 5 and 6 in San Carlos Bay had bloom levels of *Karenia brevis* in 2018/19. A *K. brevis* bloom was again observed at Sites 5 and 6 in November of 2022, as well as a bloom of the HAB dinoflagellate *Peridinium quadridentatum* at Site 6 in July 2023. In 2024, moderate blooms of diatoms were observed at Site 6 involving *Coscinodiscus* spp., *S. costatum* and *Rhizosolenia setigera*. Notably, large increases in absolute biomass were usually driven by a particular phytoplankton group dominating during that period, indicating that biomass accumulation often occurred with a break in the species assemblage structure (Fig. 9).

At Sites 7 and 8 in the nearshore region outside of San Carlos Bay diatoms, picocyanobacteria and ‘other’ taxa were often major contributors to total phytoplankton biomass (Fig. 10). Blooms at both sites were dominated by the red tide species *K. brevis* in the Fall seasons of 2018, 2019 and 2022.

Dominant Phytoplankton Taxa

The dominant phytoplankton taxa in terms of biomass were identified using lists of the Top-125 observations of biomass for individual taxonomic groups under five salinity regimes: freshwater (< 0.5), oligohaline (0.5 – <5), mesohaline (5- <18), polyhaline (18 – 30), and euhaline (>30).

Cyanobacteria - The frequencies of occurrence of three broad groups of picoplanktonic ($\leq 2 \mu\text{m}$), *Synechococcus* spp., and nanoplanktonic ($>2 - 20 \mu\text{m}$) cyanobacteria taxa on the Top-125 were evenly distributed over all five salinity regimes (Table 2). Unicellular picocyanobacteria species had the highest frequency of occurrence on all five Top-125 lists of salinity regimes and reached bloom levels of biomass (i.e., $>350 \mu\text{g carbon L}^{-1}$) up to $937 \mu\text{g carbon L}^{-1}$ on the mesohaline Top-125 list. The wide distribution of these three broad taxonomic groups across salinity regimes is based on the presence of both freshwater and saline species.

The distribution of individual cyanobacteria genera and species on the freshwater and oligohaline Top-125 lists were largely limited to freshwater taxa. (Table 2). Seven freshwater species were on the freshwater Top-125 list, including four potential toxin-producing HAB species, *Microcystis aeruginosa*, *Raphidiopsis raciborskii*, *Limnothrix redekei* and *Pseudoanabaena*. Ten of the twelve individual cyanobacteria taxa on the oligohaline Top-125 list were freshwater species, reflecting the tolerance of these taxa to low levels of salinity.

Diatoms - Six freshwater diatom taxa were on the Top-125 lists under freshwater and/or oligohaline conditions in the CRE, most prominently *Aulacoseira* spp., with biomass levels up to 533 $\mu\text{g carbon L}^{-1}$ (Table 2).

Among the eleven marine diatom species observed in the Top-125 lists, two were frequently observed over oligohaline to euhaline conditions, i.e., *Skeletonema costatum*. and *Coscinodiscus* spp. *Skeletonema costatum* was notably represented on oligohaline and mesohaline Top-125 lists, with bloom levels of biomass (i.e., $>350 \mu\text{g carbon L}^{-1}$), with peaks up to 932 $\mu\text{g carbon L}^{-1}$ (Fig. 11; Table 2). The highest abundances of *S. costatum* were observed in the upper to mid-estuary during moderate to high levels of discharge from the S-79 water control structure (i.e., $>1000\text{-}3000 \text{ cfs}$) (Fig. 11; Table 2). Under the latter range of discharges, salinities in the upper and mid-estuary ranged from near freshwater to lower mesohaline salinities (Fig. 4).

Coscinodiscus spp. was most frequent on the Top-125 lists for mesohaline and polyhaline conditions, with peak biomass levels up to 626 $\mu\text{g carbon L}^{-1}$. Four marine diatom taxa were on the Top-125 lists under polyhaline and euhaline conditions, including *Rhizosolenia setigera*, *Cerataulina pelagica*, *Dactyliosolen fragilissimus* and *Thalassionema* sp.

Dinoflagellates - Six freshwater species of dinoflagellates were in the Top-125 list for freshwater conditions but did not appear in the lists of other salinity regimes (Table 2). Cells in the genus *Protoperidinium* were in the Top-125 lists for freshwater, oligohaline, polyhaline and euhaline, reflecting the presence of both freshwater and marine species.

Sixteen marine dinoflagellate taxa were on the Top-125 lists of one or more of the four saline regimes (Table 2). The HAB dinoflagellate *Akashiwo sanguinea* was represented on all four saline lists, including bloom levels under oligohaline, mesohaline and polyhaline conditions, at biomass levels up to 7420, 7164 and 4052 $\mu\text{g carbon L}^{-1}$, respectively. The most intense blooms occurred during periods of low S-79 discharge in the upper and mid-estuary (Sites 1-3) where salinities there ranged from oligohaline to mesohaline (Fig. 11).

Five other dinoflagellate species were prominent on the Top-125 list for mesohaline conditions, including three known toxin-producing species *Karlodinium veneficum*, *Prorocentrum minimum*, and *Polykrikos schwartzii*. Two HAB dinoflagellates were represented on the Top-125-list for polyhaline conditions, *Peridinium quadridentatum* and *Karenia brevis*, with biomass peaks up to 1927 and 4173 $\mu\text{g carbon L}^{-1}$, respectively (Table 2).

K. brevis was the dominant bloom-forming species in euhaline conditions during the study period, with biomass peaks up to 3637 $\mu\text{g carbon L}^{-1}$ (Table 2). Of the ten observations of major blooms *K. brevis* (i.e., >500 cells ml^{-1}) eight were associated with periods of moderate to high S-79 discharge rates (i.e., >1500 cfs) (Fig. 11). Only four of the 48 observations of *K. brevis* during the study period were associated with salinities below 28 (Fig. 11) — reflecting the species' preference for euhaline conditions (Steidinger, 2009; Vargo, 2009).

Other Taxa - Chlorophytes were on the Top-125 list for freshwater and oligohaline conditions at low frequency (Table 2). Euglenids were on the Top-125 lists for freshwater, oligohaline and mesohaline conditions, with peak biomass levels up to 802 $\mu\text{g carbon L}^{-1}$. Cryptophytes, undefined nanoeukaryotes and ciliates occurred on the Top-125 lists for all five salinity regimes.

Recognized Harmful Algal Bloom (HAB) Taxa

Diatoms - *Chaetoceros* and *Pseudo-nitzschia* species were included in the list of harmful taxa observed in this study (Table 3). These species were primarily observed in samples from polyhaline and euhaline salinities. The *Chaetoceros* species are known to have the potential to physically damage fish and invertebrate species due to the presence of rigid silica spines. *Pseudo-nitzschia* species of the delicatissima complex were observed 166 times, but none were observed at bloom levels of biomass. Numerous species have been associated with the production of the neurotoxin domoic acid (Lassus et al., 2016).

Dinoflagellates – 34 HAB dinoflagellate taxa were observed during the study period (Table 3), 16 of which have been shown to produce toxins in environments around the world (Table 3). The most frequently observed potential toxin-producing species in this study were *Prorocentrum texanum*, *Karlodinium veneficum*, *K. brevis* and *Gonyaulax polygramma*. Other potential toxic threats observed in this study include okadaic acid (aka, diuretic shellfish poison, DSP) production by *Prorocentrum* and *Dinophysis* species, karlotoxin (an ichthyotoxin) production by *K. veneficum*, and palytoxin production by *Ostreopsis* species (Lassus et al., 2016). *Peridinium quadridentatum* and *Akashiwo sanguinea* were prominent HAB dinoflagellates observed in our study but are not currently known to produce toxins (Table 3).

Most HAB dinoflagellates in our study occurred in polyhaline to euhaline environments (Table 3), though several species showed a euryhaline distribution including *A. sanguinea*,

Heterocapsa rotundata, *Karlodinium veneficum*, *Prorocentrum minimum*, *Prorocentrum rhathymum*, *Protoperidinium conicum*, and *Protoperidinium steinii*.

Cyanobacteria – Nine HAB cyanobacteria were observed during the study period (Table 3). All taxa were freshwater except *Trichodesmium erythraeum*, which is a cosmopolitan species that forms blooms in ocean ecosystems (Bergman et al., 2013). In this study, *T. erythraeum* was observed 13 times at moderate abundances and always at salinities greater than 30. A few reports suggest that *T. erythraeum* may produce toxins (Detoni et al., 2016).

Eight freshwater HAB cyanobacteria species observed in this study have been associated with the production of toxins (Chorus and Welker, 2021). Most of the species were observed at bloom levels of biomass (i.e. $>350 \mu\text{g carbon L}^{-1}$). All the species were largely found in freshwater and oligohaline conditions, with some remnant cells observed at low densities at higher salinities (Table 3).

Haptophytes – The haptophyte *Chrysochromulina* was observed in 25 samples at low concentrations. The observation is noteworthy since some species in this genus have been shown to produce ichthyotoxins that cause damage to fish gills leading to mass mortalities (Table 3) (Wang et al., 2024).

Environmental Correlations

Significant ($p < 0.05$) Spearman correlations for sites 1-3 showed that TN concentration correlated positively with precipitation but not discharge ($R = 0.31$), while TP correlated positively with discharge but not precipitation ($R = 0.27$). Only dinoflagellates showed a positive correlation to TP ($R = 0.28$). Temperature correlated positively with precipitation ($R = 0.46$), discharge ($R = 0.32$), and TP ($R = 0.27$). Strong positive covariance was observed between ammonium (NH_4) and TN ($r = 0.79$) (Fig. 12). For sites 4-6, chlorophyll a (CHL) was positively correlated with discharge ($r = 0.40$), along with dinoflagellates ($R = 0.42$) and diatoms ($R = 0.59$). Temperature was positively correlated with both precipitation and discharge along with picocyanobacteria ($R = 0.53$). For these sites, TP was also correlated with discharge and not precipitation, with TN showing correlation with precipitation (Fig. 13). For sites 7-8, in the nearshore, picocyanobacteria, other cyanobacteria, and diatoms are all correlated positively to temperature, discharge, and especially precipitation ($R = 0.53$) (Fig. 14). Dinoflagellates and other flagellates show a positive correlation with each other ($R = 0.23$) (Fig. 14).

Phytoplankton Composition – dbRDA

The distance-based redundancy analysis (dbRDA) showed associations between phytoplankton taxa and environmental gradients within the CRE and adjacent waters. The Canonical Analysis of Principal Coordinates (CAP) CAP1 axis (42.6% of constrained variation) primarily reflects discharge (Fig. 15). TN and TP vectors point toward *Skeletonema*, *Coscinodiscus*, and other diatoms, indicating that these taxa thrive under high-discharge, nutrient-dense conditions. The salinity and ammonium vectors are associated with mixotrophic marine dinoflagellate genera, such as *Karenia*, *Gyrodinium*, and *Prorocentrum*—along with some marine diatoms. CAP2 (23.4% of constrained variation) captures seasonal drivers with temperature and precipitation, aligning with picocyanobacteria and *Synechococcus*, respectively, suggesting that these taxa are favored by warmer conditions. These patterns suggest that rates of freshwater and nutrient inflows from the C-43 Canal and precipitation play important roles in shaping the structure of the phytoplankton community (Fig. 15).

DISCUSSION

Phytoplankton Taxa Across the Salinity Ecocline

In river-dominated estuaries, freshwater inflow is a major driver of salinity distribution, which in turn shapes phytoplankton composition and biomass (Snow et al., 2000; Bledsoe et al., 2004; Quinlan et al., 2007; Muylaert et al., 2009; Dorado et al., 2015; Cloern et al., 2017; Bilbao et al., 2023). In the CRE, regulated discharge rates from the C-43 Canal are the dominant factor shaping the salinity ecocline. (Sun et al., 2022). For example, at the low discharge rate of $17 \text{ m}^3 \text{ s}^{-1}$ (600 cfs) mesohaline conditions (salinity 5-18) can extend up into the upper reaches of the estuary near the S-79, while at the high discharge rate of $100 \text{ m}^3 \text{ s}^{-1}$ (3500 cfs) freshwater conditions can extend 28 km down the estuary, past the city of Ft. Myers (Sun et al., 2022). In the upper estuary, inflows from two tidal creeks (Popash Creek and Orange River) can also contribute to freshwater inflows to the estuary, particularly during high rainfall periods (Badylak et al., 2025, Philips et al., 2025). Shifting discharge rates are accompanied by changes in other factors that affect phytoplankton composition and biomass, such as water residence times and nutrient levels (Doering and Chamberlain, 1999; Mathews et al., 2015; Wan et al., 2018; Julian and Osborne, 2018; Sun et al., 2022; Montefiore et al., 2024). Below, we discuss how the salinity ecocline in the CRE and adjoining nearshore regions affect phytoplankton composition

and biomass using lists of the Top-125 individual biomass observations for taxonomic groups under four salinity regimes, i.e. freshwater (≤ 0.5), oligohaline (>0.5 to 5), mesohaline (>5 to 18), polyhaline (salinities >18 - 30), and euhaline (i.e., salinities >30 – 35).

Phytoplankton Taxa Under Freshwater Conditions - Under freshwater conditions in the CRE, cyanobacteria were the dominant group in terms of frequency on the Top-125 list, representing 54 of the 125 observations. The prominence of the group in part reflects inputs from the C-43 Canal, which is subject to cyanobacteria-rich inputs from Lake Okeechobee, particularly in the spring and summer (Doering and Chamberlain, 1999; Julian and Osborne, 2018; Phlips et al., 2023, 2025; Badylak et al., 2025). The influence of Lake Okeechobee on cyanobacteria composition in the canal is indicated by the presence of five HAB species on the freshwater Top-125 list (Table 2) that commonly form blooms in the lake, including *Microcystis aeruginosa*, *Raphidiopsis raciborski*, *Limnothrix redekei*, *Cuspidothrix tropicalis* and *Dolichospermum circinale* (Phlips et al., 1997; Havens et al., 1998; Kramer et al., 2018; Lefler et al., 2023; Mazzei et al., 2024). All five species have been linked to the production of hepatotoxins (e.g., microcystin, cylindrospermopsin) and/or neurotoxins (e.g., anatoxin, saxitoxin) (Chorus and Welker, 2021).

Unicellular picocyanobacteria (e.g. *Synechococcus* spp.) were also important elements of the freshwater Top-125 list, as well as in the other salinity regimes, highlighting their significance as a group across diverse coastal aquatic environments (Waterbury et al., 1979; Phlips et al., 1999; Gaulke et al., 2010; Scanlan, 2012; Paerl et al., 2020). Their small size and high surface area to volume ratios provide picocyanobacteria with high nutrient uptake and growth rate potentials (Suttle and Harrison, 1986; Pittera et al., 2014). Many picocyanobacteria also have high uptake rates for ammonium and organic nutrients, as opposed to preference of some other groups for nitrates, such as diatoms (Dorado et al., 2015; Glibert et al., 2023; Papacek et al., 2025; Zufia et al., 2021). Despite their ubiquity, picocyanobacteria did not frequently reach bloom-levels of biomass in the CRE, possibly due to grazing pressure by mixotrophic/heterotrophic species (dinoflagellates, nanoflagellates, euglenoids, ciliates) (Burkholder et al., 2008; Hammer and Pitchford, 2006; Hirose et al., 2007; Jeong et al., 2005; Stoecker et al., 2017; Taniguchi et al., 2014; Wang et al., 2013). All these potential grazer groups were prominently represented in the freshwater Top-125 list and their major presence across multiple salinity regimes highlights the importance of the microbial loop in the structure and

function of food webs in the CRE (Anderson et al., 2017; Arenovski et al., 1995; Fenchel, 2008). Many species in these groups have broad nutrient preferences and mixotrophic capabilities, traits that likely contribute to their success in the Caloosahatchee ecosystem, which receives watershed inflows enriched with organic nutrients from the surrounding agricultural land (Julian et al., 2018; Montefiore et al., 2024; Pisani et al., 2017).

Diatoms and dinoflagellates were less frequently represented in the freshwater Top-125 list for the CRE. Seven freshwater dinoflagellate taxa were on list, most prominently *Durinskia* and *Woloszynskia*, matching the prominence of these species in the C-43 Canal (Badylak et al., 2025). Three diatom taxa were on the Top-125 list, including *Aulacoseira spp.*, *Surirella spp.*, and *Skeletonema potamos*. *Aulacoseira* species also appeared in oligohaline conditions, consistent with evidence of their ability to form blooms in brackish water (Mohanty et. al., 2022; Wang et al., 2009, 2020).

Phytoplankton Taxa Under Oligohaline Conditions - Oligohaline conditions in the CRE reveal a transition in phytoplankton composition to salinity tolerant freshwater species and euryhaline marine taxa. Many of the freshwater cyanobacteria on the freshwater Top-125 list also appeared on the oligohaline Top-125 list, indicating their ability to tolerate oligohaline conditions. For example, *M. aeruginosa* (Harke et al., 2016; Ibelings et al., 2021; Preece et al., 2017;) is among the more salinity tolerant freshwater cyanobacteria taxa, with the ability to grow in oligohaline salinities, and survive at salinities up to 10, or even higher (Black et al., 2011; Melero-Jimenez et al., 2020; Phlips et al., 2025; Rosen et al., 2018; Tonk et al., 2007). A recent study of the movement of a major toxic *M. aeruginosa* bloom through the CRE showed that high concentrations (e.g., $>2 \times 10^9$ cells L⁻¹) of intact toxic cells were observed downstream in the mid-estuary, where salinities were up to 8 ppt (Phlips et al., 2025). In contrast to the salinity tolerance of many of the observed freshwater cyanobacteria, the six confirmed freshwater dinoflagellate species observed on the freshwater Top-125 list did not appear on the oligohaline Top-125 list.

An indicator of the transition status of the oligohaline zone is the presence of euryhaline marine dinoflagellates and diatoms on the oligohaline Top-125 list. *Skeletonema costatum* (Chen et al., 2007; Marić Pfannkuchen et al., 2018) was strongly represented in the oligohaline Top-125 list, sometimes at bloom levels. *S. costatum* is fast-growing with reported growth rates up to 3 d⁻¹ (Li et al., 2021). Fast growth is advantageous in the CRE, which is often characterized by high

nutrient concentrations, but low water residence times. *S. costatum* is one of the most adaptable marine species to low salinity (Balzano et al., 2011; Brand, 1984; Li et al., 2021), which helps to explain its wide distribution in the CRE across salinity regimes.

Another important element of the oligohaline Top-125 list was the euryhaline marine dinoflagellate *Akashiwo sanguinea*, that had the highest biomass observed over the study period, at 7430 $\mu\text{g carbon L}^{-1}$. *A. sanguinea* is associated with euryhaline and eurythermal tolerances (Badylak et al., 2014a; Matsubara et al., 2007; Shikata et al., 2008), ability to form resting cysts in the upper CRE (Badylak et al., 2017), and the ability to produce large quantities of extracellular mucilage (Badylak et al., 2014b), which can reduce zooplankton grazing and filter-feeding by macroinvertebrates (Badylak et al., 2014a; Kahru et al., 2004). High bloom biomass levels of *A. sanguinea* can be associated with hypoxia (Ok et al., 2023). Hypoxia was observed in May and June of 2009 in the upper CRE, with dissolved oxygen measurements of 0.1 and 0.25 $\text{mg O}_2 \text{ L}^{-1}$ in lower levels of the water column, coinciding with a major bloom of *A. sanguinea*. Hypoxia is one of the leading causes of aquatic animal mortality associated with HABs and can lead to disruptions of food web structure and function (Milbrandt et al., 2021; Montagna and Froeschke, 2009; Rabalais and Turner, 2019; Turner et al., 2015).

Phytoplankton Taxa Under Mesohaline Conditions - Mesohaline conditions were most common in the mid-estuary (Sites 2 and 3) but periodically extended into the upper estuary during low S-79 discharge and into the lower estuary near San Carlos Bay during high discharge. The mesohaline Top-125 list was characterized by the absence of most cyanobacteria taxa except for picocyanobacteria. By contrast, there was an increase in the number of dinoflagellate species on the Top-125 list, with bloom levels of biomass observed for *A. sanguinea*, and the toxic species *Polykrikos schwartzii* and *K. brevis*. In total, there were 16 known HAB species observed under mesohaline conditions over the study period. While the most intense blooms involved *A. sanguinea* and *P. schwartzii*, several other HAB species known for toxin production were observed numerous times, but not at bloom levels, such as *Karlodinium veneficum*, *Gonyaulax polygramma*, and *Prorocentrum minimum* (Hall et al., 2008; Heil et al., 2005; Lassus et al., 2016; Müller et al., 2019). These frequently observed species represent the presence of a potential inoculum for future HABs.

Diatoms also increased in frequency on the mesohaline Top-125 list relative to the oligohaline list in the CRE. The most prominent taxa were *S. costatum* and *Coscinodiscus* spp.,

both reaching bloom levels of biomass. The transition from *S. costatum* to *Coscinodiscus* spp. dominance at higher salinities has also been observed in the Yellow Sea (He et al., 2025). Although not toxic, both species have been known to form intense blooms associated with ecosystem disruptions, such as hypoxia (Laing et al., 2002; Chen et al., 2003; Nishikawa et al., 2010; Shen et al., 2012; Ogura et al., 2018). The euryhaline character and high growth rates of these taxa help to explain their success in the variable salinity ecoclines and shorter water residence times of the CRE. In terms of HAB species, *Pseudo-nitzschia* species in the delicatissima complex were observed multiple times under mesohaline conditions in the estuary. A number of the species in this complex are known for production of the toxin domoic acid, which is known for its serious neurotoxic effects such as memory loss for both aquatic animals and humans (Badylak et al., 2006; Trainer et al., 2012; Bates et al., 2018; Moore et al., 2020; Alarcon et al., 2023; Scheiber et al., 2023).

Phytoplankton Taxa Under Polyhaline and Euhaline Conditions - Polyhaline conditions predominate in the lowest reaches of the CRE (Site 4), while a mixture of polyhaline and euhaline conditions occur in San Carlos Bay (Sites 5 and 6), and the nearshore Gulf region is predominantly euhaline. As in the other salinity regimes, picocyanobacteria were the most frequent entries in both the polyhaline and euhaline Top-125 lists, showing their importance in the bay and nearshore regions. From a biomass perspective, dinoflagellates were the dominant phytoplankton group in the polyhaline Top-125 list, including *A. sanguinea*, *Peridinium quadridentatum* and the toxic red tide species *Karenia brevis*, which were all observed at bloom levels of biomass. Ecosystem-disruptive blooms of *P. quadridentatum* have been reported for several ecosystems in association with mass mortalities of marine fauna (Rodriguez-Gomez et al., 2019; 2021). Under euhaline conditions *K. brevis* was the singular dominant dinoflagellate on the euhaline Top-125 list. *K. brevis* has historically been the dominant species in toxic red tide events along the west coast of Florida (Steidinger, 2009; Vargo, 2009; Heil et al., 2014). *K. brevis* is known to prefer salinities greater than 20 ppt. (Steidinger, 2009; Vargo, 2009), which coincides with the observation that the species was primarily limited to upper polyhaline and euhaline conditions over the study period. In addition to the aforementioned taxa, several other HAB dinoflagellate species were frequently observed under polyhaline and euhaline conditions but did not make the Top-125 biomass lists, such as the known toxin-producing taxa *Karlodinium veneficum*, *Prorocentrum texanum*, *Dinophysis caudata*, and *Gonyaulax*

polygramma. The long list of HAB dinoflagellate species observed under mesohaline, polyhaline and/or euhaline conditions in the CRE and adjacent nearshore regions during our study highlight the breadth of potential HAB threats that span the salinity ecocline.

In terms of diatoms, *S. costatum* and *Coscinodiscus* spp. were both well represented on the polyhaline Top-125 list. In addition, under polyhaline and euhaline conditions, three cosmopolitan species of diatom were prominent on the list, including *Rhizosolenia setigera*, *Cerataulina pelagica*, and *Dactyliosolen fragilissimus*. All three are important components of many marine ecosystems around the world (Taylor et al., 1985; Yoshimatsu et al., 2020; Melnik et al., 2024; Yang et al., 2025), and intense blooms of these species have been implicated in ecosystem disruptions. For example, blooms of *C. pelagica* in New Zealand have been associated with mass mortalities of fish and benthic fauna because of “anoxia and clogging of gills with mucilage produced by the diatom” (Taylor et al., 1985). In another study, *C. pelagica* bloom was linked to low reproductive success of copepods in the Northern Adriatic Sea (Ianora et al., 2008). In terms of known toxic HAB diatom species (Lassus et al., 2016), *Pseudo-nitzschia* species were frequently observed in our study under polyhaline and euhaline conditions, but not at bloom levels of biomass. The high frequency of observations of *Pseudo-nitzschia* suggests a potential for bloom development in the CRE and nearshore regions.

HAB Potential in the CRE and Nearshore Region

Allochthonous HABs - Historically, the two most prominent HABs of allochthonous origin have been freshwater cyanobacteria HABs that are introduced to the estuary from Lake Okeechobee via the C-43 Canal and toxic red tides of the dinoflagellate *Karenia brevis*, emanating from the continental shelf off the west coast of Florida (Heil et al., 2014; Steidinger, 2009; Weisberg et al., 2019). Increased intensity of red tides over the past fifty years (Glibert et al., 2026) has elevated regional concerns about the serious adverse consequences of *K. brevis* in terms of marine animal and human health, regional economics, and overall ecosystem structure and function (Larkin and Adams, 2007; Bechard, 2020; Heil and Muni-Morgan, 2021; Ferreira, et al., 2023). Recent studies have shown that outflows from the CRE can provide nutrients that enhance the intensity of the red tides (Glibert et al., 2026; Medina et al., 2022; 2023; Heil et al., 2014; Philips et al., 2023). For example, major red tides near the outflow of the CRE in 2018 and 2022 followed the passage of hurricanes Michael and Ian (Alarcon et al., 2023; Chen and Li, 2025; Philips et al., 2023; Tillman et al., 2025). Both storms were associated with significant

increases in discharge into the estuary, delivering elevated concentrations of nutrients, including nitrogen, the nutrient typically most limiting to phytoplankton growth (Tillman et al., 2025). The passage of Hurricane Ian over the region involved washout of large amounts of organic matter from the CRE watershed into San Carlos Bay and adjacent the Gulf (Wang et. al., 2024). After the passage of the storm, ammonia, nitrate, nitrite and orthophosphate levels all increased significantly in the nearshore regions outside of the CRE (Tilman et al., 2025). Similar observations have been made in other coastal regions (e.g., Flynn, 2008; Paerl et al., 1998). These examples illustrate that the origin of red tides may be allochthonous, but their intensity, distribution and duration can be enhanced by discharges of water from coastal watersheds, highlighting the importance of managing discharges from flow-regulated ecosystems such as the CRE.

In terms of the CRE, most of the most intense cyanobacteria HABs over the past few decades have originated from Lake Okeechobee. The lake has long been subject to extensive cyanobacteria blooms (Phlips et al., 1995; Havens et al., 1998; Rosen et al., 2017; Schaefer et al., 2020; Dang et al., 2023). Discharges of HABs from the lake into the C-43 and C-44 Canals have coincided with large loads of toxic algal biomass into both the CRE (Fig. 1) and St. Lucie Estuary (Badylak et al., 2025; Lapointe et al., 2024; Metcalf et al., 2021; Phlips et al., 2012, 2025; Rosen et al., 2017; Schaefer et al., 2020). The highest toxin concentrations often involve *Microcystis aeruginosa* (Phlips et al., 2012, 2025; Rosen et al., 2017; Schaefer et al., 2020). Management of discharges from Lake Okeechobee during the presence of intense blooms has become a focus of efforts to help mitigate downstream negative impacts. Recent advances in satellite detection of HABs (Handler et al., 2023; Stumpf et al., 2022) and hydrologic modeling of surface water movement in Lake Okeechobee, the associated estuaries, and the west coast of Florida are providing new tools for forecasting the timing, distribution and movement of HABs (Dang et al., 2023; Hewageegana et al., 2023).

Even in the absence of blooms in Lake Okeechobee, the eutrophic character of the lake represents a source of cyanobacteria inoculum and high nutrient concentrations that can support bloom development in the adjoining canals (Faridmarandi et al., 2020; Phlips et al., 1993). The latter scenario was observed in a recent study, when low rates of discharge into the C-43 Canal provided the time needed for the development of a significant cyanobacteria biomass within the canal, which ultimately are discharged into the CRE (Badylak et al., 2025). Under moderate S-79

discharge rates (i.e. $71 \text{ m}^3 \text{ s}^{-1}$ or 2500 cfs), freshwater cyanobacteria blooms that initiate in the C-43 Canal can continue to expand in the upper half of the CRE, where freshwater or oligohaline conditions persist. In 2023, these conditions resulted in the transport of a major toxic *Microcystis aeruginosa* bloom through the upper half of the estuary (Phlips et al., 2025). Surface water chlorophyll *a* concentrations were as high as $888 \mu\text{g L}^{-1}$ and intra-cellular levels of the hepatotoxin microcystin were up to $624 \mu\text{g L}^{-1}$ in the mid-estuary. Although concentrations of intact *M. aeruginosa* cells dropped quickly upon reaching mesohaline salinities, extracellular toxin concentrations persisted, likely because degradation rates of freshwater toxins like microcystin can be slower in marine waters than in freshwater due to the more limited presence of toxin-degrading bacteria (Parker et al., 2016; Bormans et al., 2023).

From the perspective of aquatic animals and human health, limiting the presence of intact toxin producing cyanobacteria cells can be of particular importance because of the ability of cyanobacterial HABs to concentrate near the surface of the water column due to their ability to regulate buoyancy. Surface blooms can then be concentrated by wind-driven accumulations of biomass along shorelines (Ibelings et al., 2021). High surface concentrations of cells can be associated with exceptionally high toxin levels and can lead to localized hypoxic conditions (Paerl, 1988; Smucker et al., 2021). A recent study showed that surface concentrations of the microcystin in a bloom of *M. aeruginosa* in the CRE were up to 100-fold higher than concentrations in the water column (Phlips et al., 2025). Surface accumulations of toxic cyanobacteria can greatly elevate exposure levels for aquatic animals and humans swimming in affected waters or through breathing aerosolized toxins in the air (Loftin et al., 2016; Lim et al., 2023; Schürmann et al., 2024). Grazing of toxic cells by zooplankton or filter-feeding macroinvertebrates can lead to the bioaccumulation of toxins in the food web, including commercially important bivalves (Ibelings et al., 2007; Preece et al., 2017). It has been shown that exposure of some species of bivalve to intact toxic *M. aeruginosa* cells results in significantly longer depuration periods compared to exposure of the bivalves to extracellular toxin (Gibble et al., 2016).

Autochthonous HABs – Under saline conditions in the CRE euryhaline marine phytoplankton species can form autochthonous blooms (Hewageegana et al., 2023; Sun et al., 2022; Wan et al., 2013). Blooms of the euryhaline HAB dinoflagellate *A. sanguinea* in the estuary were primarily observed during periods of low S-79 discharge rates, during which saline conditions extended up

into the upper estuary. Low discharge rates also increased water residence times, providing the opportunity for comparatively slow-growing dinoflagellates like *A. sanguinea* (i.e., maximum growth rate of approximately 0.5 d⁻¹) (Matsubara et al., 2007) to reach bloom levels of biomass. The role of water residence time in defining HAB potential has been highlighted in numerous studies of coastal ecosystems (e.g., Monbet, 1992; Paerl et al., 2018; Philips et al., 2004, 2020; Qin and Shen, 2019; Ralston et al., 2015).

Another prominent marine phytoplankton species observed over a broad range of salinity regimes in the CRE was the diatom *Skeletonema costatum*. Like *A. sanguinea*, *S. costatum* is tolerant to a wide range of salinities (i.e., 2-45) (Brand, 1984; Li et al., 2021). Another key characteristic of *S. costatum* is its high maximum specific growth rate potential, up to 2-3 d⁻¹ (Li et al., 2021). Fast growth rates help to explain why *S. costatum* reached bloom levels of biomass even at moderately high S-79 discharge rates (i.e., 57-85 m³s⁻¹, or 2000-3000 cfs), when water residence times in the saline reaches of the CRE can be less than 10 days (Hewageegana et al., 2023).

From the perspective of limiting the potential for autochthonous HABs, it is important to identify practical management targets for controlling levels of phytoplankton biomass associated with harmful effects. Bloom development is the net result of biomass gain and loss processes. The central gain process is growth, which requires nutrients and light, and is modulated by temperature and salinity (Cloern, 1999; Glibert et al., 2016; Grosse et al., 2017; Grover, 1991; Paczkowska et al., 2020; Pinckney et al., 1999; Rhee, 1982). Biomass potential is then dependent on water residence time and the negative effects of loss processes, such as grazing, sedimentation, dilution with external inputs of water with lower biomass, and programmed cell death (Reynolds, 2006; Lucas et al., 2009). Historically, a major target for lowering HAB potential has been reduction of nutrient loads (Glibert et al., 2020; Moncada et al., 2021; Paerl et al., 2018; Roelke et al., 1999). Reducing the trophic state of a HAB-prone ecosystem is a desirable goal, but nutrient load reduction efforts can face challenges in regions with rapid human development and increases in cultural eutrophication (Cloern, 2001, Glibert et al., 2020; Pearl et al., 2018). The Caloosahatchee River Estuary-Lake Okeechobee-St .Lucie Estuary ecosystem is a case in point because of rapid and continuing human development in regional watersheds, including the accumulation of large legacy loads of nutrients in Lake Okeechobee (Krimsky et al., 2019).

Another tool for mitigating the intensity of HABs in the CRE could be the management of water residence times, salinity ecoclines and nutrient loads through the regulation of discharges from the existing water control structures (i.e., S77, S78 and S-79) (Julian et al., 2025; Tarabih et al., 2025). In the Netherlands, introduction of saline waters to water masses with cyanobacteria HABs has been shown to disrupt bloom development (Verspagen et al., 2006). In other studies, regulation of discharge levels from structures into estuaries have been shown to help control HABs by increasing flushing rates and limiting water residence times (Sin et al., 2013; 2015; Odebrecht et al., 2015; Wang et al., 2017; Harris et al., 2024). In the CRE, the presence of the water control structures in the C-43 Canal could be used to mitigate the frequency, intensity and duration of HABs by modifying salinity ecoclines, limiting water residence times, and altering the sources of water inputs associated with discharges (Julian et al., 2025; Philips et al., 2025; Tarabih et al., 2025). From a nutrient load perspective, changes in the volume of discharges from the S-79 alters the nutrient loads to the estuary, but nutrient concentrations in the discharges are also important to consider and can vary temporally. For example. during a typical dry season, the relative contributions of water from Lake Okeechobee to the S-79 discharge increases, while contributions from the watershed surrounding the C-43 decline (Montefiore et al., 2024). While not dramatically affecting phosphorous levels, nitrogen concentrations can be elevated in the dry season because of the elevated inputs from Lake Okeechobee (Montefiore et al., 2024). This distinction can be important since the growth of marine phytoplankton in the estuary and nearshore regions can be more subject to nitrogen than phosphorus limitation. Understanding the shifting sources of water in the S-79 discharge can help manage the inputs leading to phytoplankton growth downstream.

CONCLUSION

The results of this study show that the composition and biomass of phytoplankton in the CRE and nearby coastal regions are significantly affected by the rate and timing of discharges from the S-79 water control structure. The effects are related to changes in hydrologic conditions (e.g., water residence times), the character of the salinity ecocline, and quality of the water discharged from the C-43 Canal (e.g. nutrient levels, phytoplankton composition). Mitigation of HABs in and downstream of the CRE requires co-management of hydrology, nutrient loads, and upstream allochthonous sources of HABs. High discharge rates result in freshwater and oligohaline zones that extend down the estuary, expanding the potential exposure of the CRE to

freshwater HABs. Conversely, low S-79 discharge rates expand the region of mesohaline conditions up the estuary and increase water residence times, opening opportunities for autochthonous blooms of euryhaline marine species, such as the HAB dinoflagellate *Akashiwo sanguinea*. High discharge rates during the study period also increased nutrient loading rates to nearshore regions outside the estuary, elevating the potential for intense red tide events, such as the *Karenia brevis* blooms that coincided with high discharge periods associated with Hurricane Michael in 2018 and Hurricane Ian in 2022.

From nutrient perspectives, the origins and composition of water discharged from the S-79 varied temporally, with higher nitrogen concentrations occurring when the influence of inputs from Lake Okeechobee to the C-43 Canal increased relative to inputs from the watershed surrounding the C-43 Canal. This distinction can be important since the growth of marine phytoplankton in the estuary and nearshore regions can be more subject to nitrogen than phosphorus limitation. Managing the sources of water entering the C-43 Canal can thus help define the amount of nitrogen entering the estuary, which can affect the intensity of nearshore phytoplankton blooms in the estuary and nearby coastal regions.

Globally, there have been increases in the number of estuaries subject to the incorporation of water control structures that regulate freshwater discharges. While the presence of these structures adds another layer of complexity for defining spatial and temporal variability in phytoplankton composition and biomass along the freshwater to marine continuum, they also provide a potential tool for mitigating the intensities and impacts of HABs.

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Authors Contributions

BDS participated in research plan development, field sample collection, sample analysis, data acquisition, analysis and interpretation, manuscript drafting and editing. EJP participated in research plan development, funding acquisition, project management, data interpretation, manuscript drafting and editing. ECM participated in research plan development, data acquisition, led field collection teams, data interpretation, and manuscript editing. SG participated in research plan development, data analysis and interpretation, manuscript editing. SL field sample collection, sample analyses, data acquisition, data interpretation, and manuscript editing. LL field sample collection, sample analyses, data acquisition. ESM participated in

research plan development, field sample collection, data interpretation, and manuscript editing. MEA participated in research plan development, funding acquisition, project management, and manuscript editing. DK participated in research plan development, funding acquisition, project management, and manuscript editing.

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Data Availability

The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Competing Interests

The authors have no relevant financial or non-financial interests to disclose.

The authors have no competing interests to declare that are relevant to the content of this article.

All authors certify that they have no affiliations with or involvement in any organization or entity with any financial interest or non-financial interest in the subject matter or materials discussed in this manuscript.

The authors have no financial or proprietary interest in any material discussed in this article.

Compliance with Ethical Standards

The authors do not have any potential conflicts of interest.

The research did not involve human participants and/or animals.

FIGURES

Fig. 1. S-79 water control structure in the C-43 Canal at the upper boundary of the Caloosahatchee Estuary. Bloom of the toxic cyanobacterium *Microcystis aeruginosa* is shown accumulating at the structure (Milbrandt, Sanibel Captiva Conservation Foundation).



Fig. 2. Caloosahatchee River Estuary including all 8 sites analyzed during the 3 periods of analysis. The 2008-2010 study period covered the estuarine sites (1-4), while all other sites are included in the 2018-2019 and 2021-2023 study periods. Sites 1-2 are considered the upper estuary, 3-4 the lower estuary, site 5 is the entrance to Tarpon Bay, site 6 the intersection of the Gulf of Mexico and the Caloosahatchee Estuary, and site 7-8 are in the Gulf of Mexico.

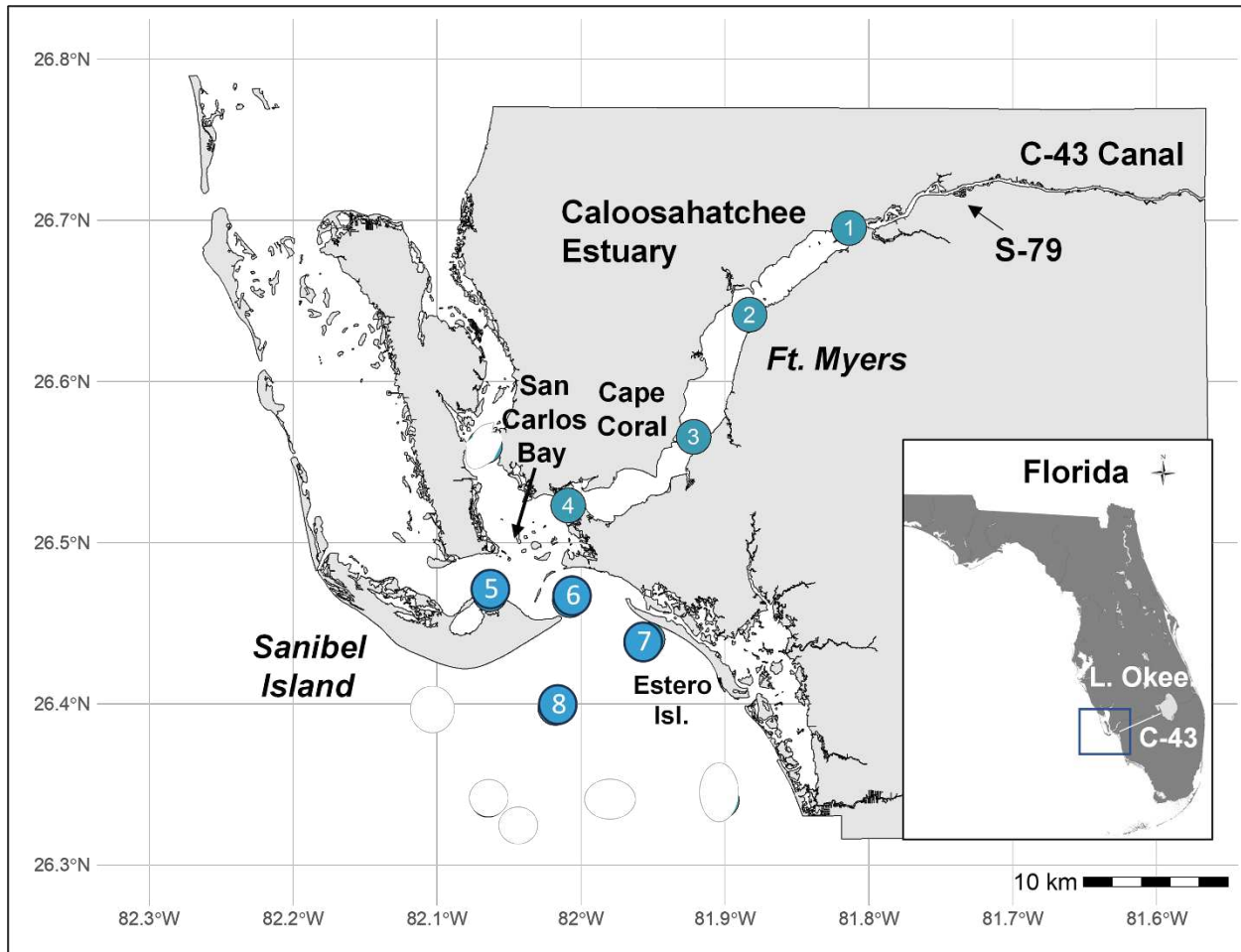
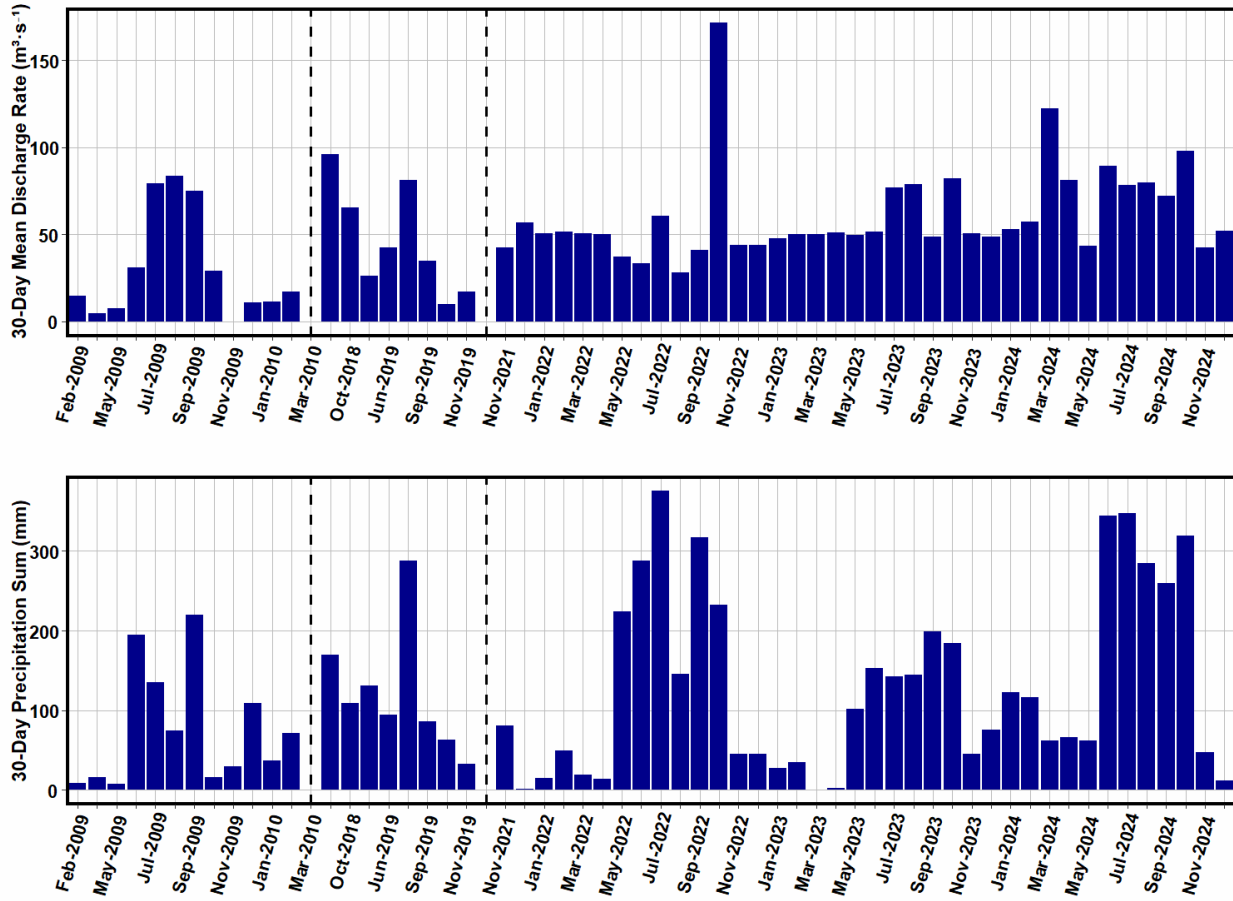
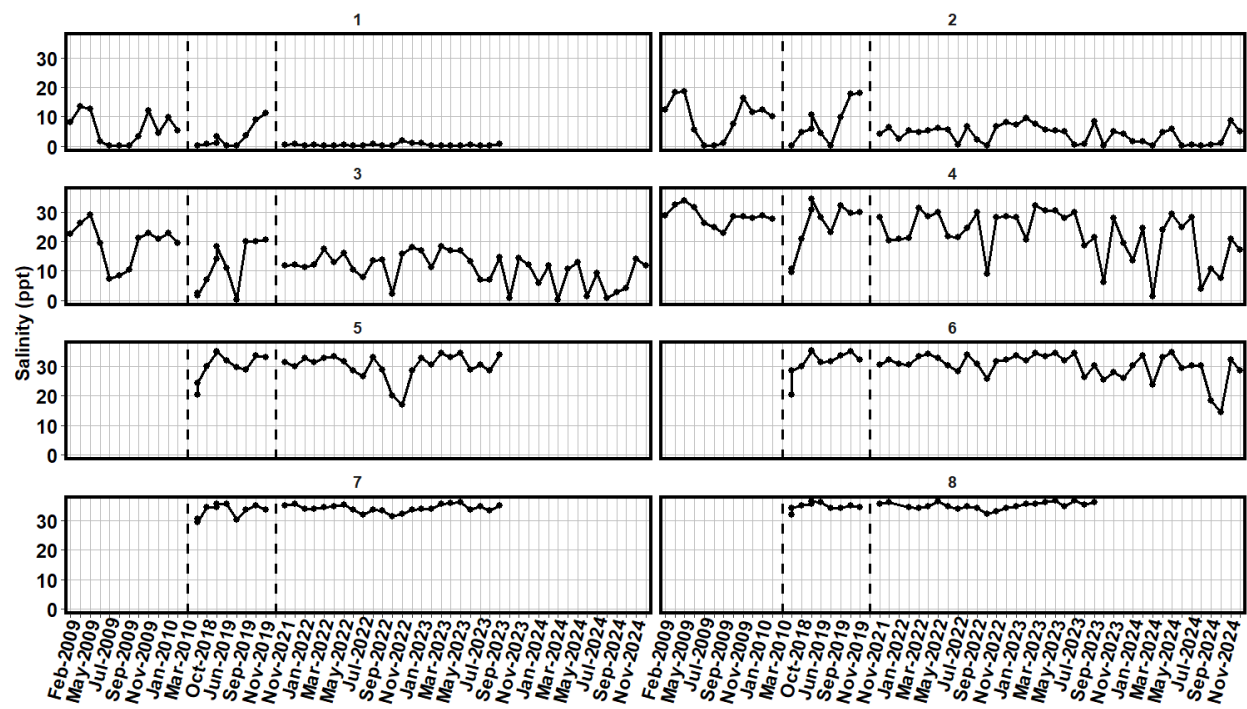


Fig. 3. Mean discharge rate from the S-79 control structure (m^3s^{-1}) and sum of precipitation in Lee County (mm) over a 30-day period ending in the collection day. The vertical dashed lines represent a break where sampling was not occurring.



848 **Fig. 4.** Salinity (ppt) of each of the 8 sites shown in Fig. 1 during the 3 study periods: Feb 2009 -
 849 Feb 2010, Aug 2018 – Oct 2019, and Sep 2021 – Dec 2024.
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Fig. 5. Ammonium concentrations (mg/L) from each grab sample across Sites 1–8 from 2009 to 2024, faceted by calendar month. Each cell represents the measured chlorophyll concentration of a grab sample. Missing data are shown as blank cells.

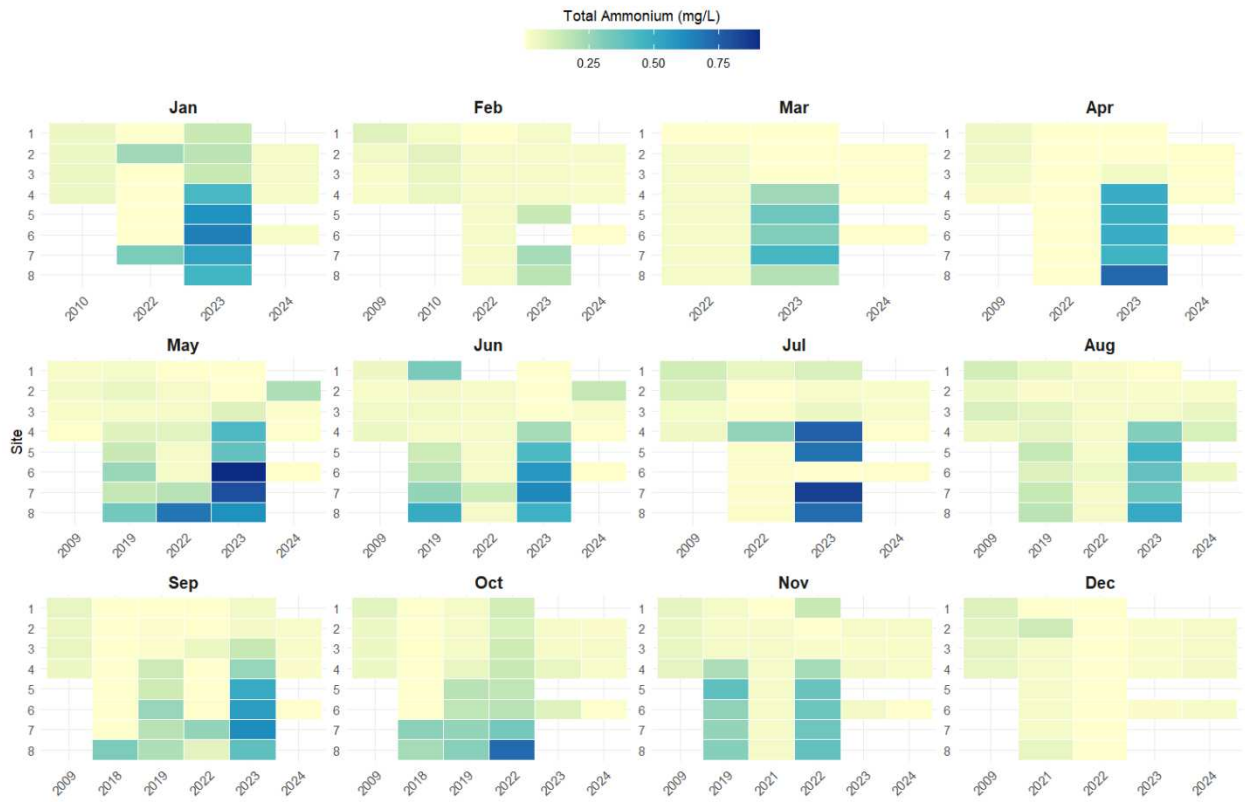


Fig. 6. Total Nitrogen (mg/L) from each grab sample across Sites 1–8 from 2009 to 2024, faceted by calendar month. Each cell represents the measured chlorophyll concentration of a grab sample. Missing data are shown as blank cells.

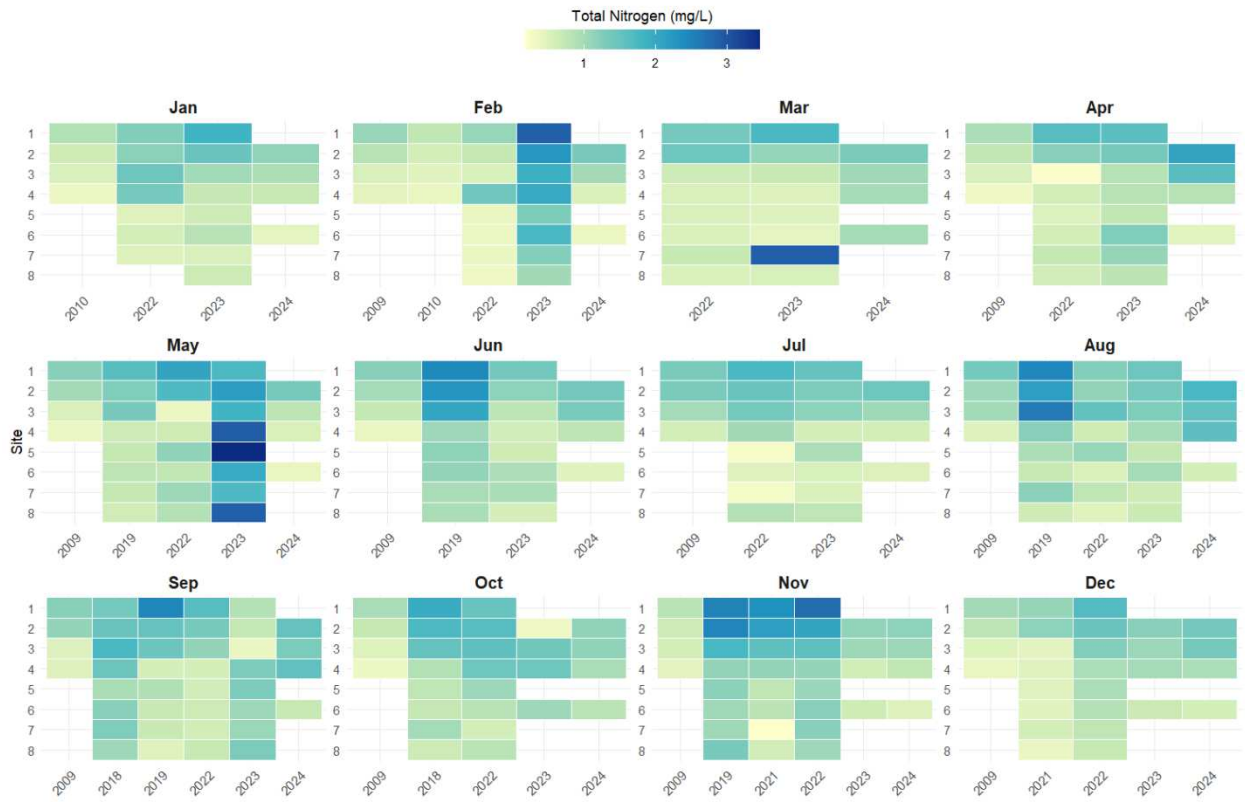


Fig. 7. Total Phosphorus (mg/L) from each grab sample across Sites 1–8 from 2009 to 2024, faceted by calendar month. Each cell represents the measured chlorophyll concentration of a grab sample. Missing data are shown as blank cells.

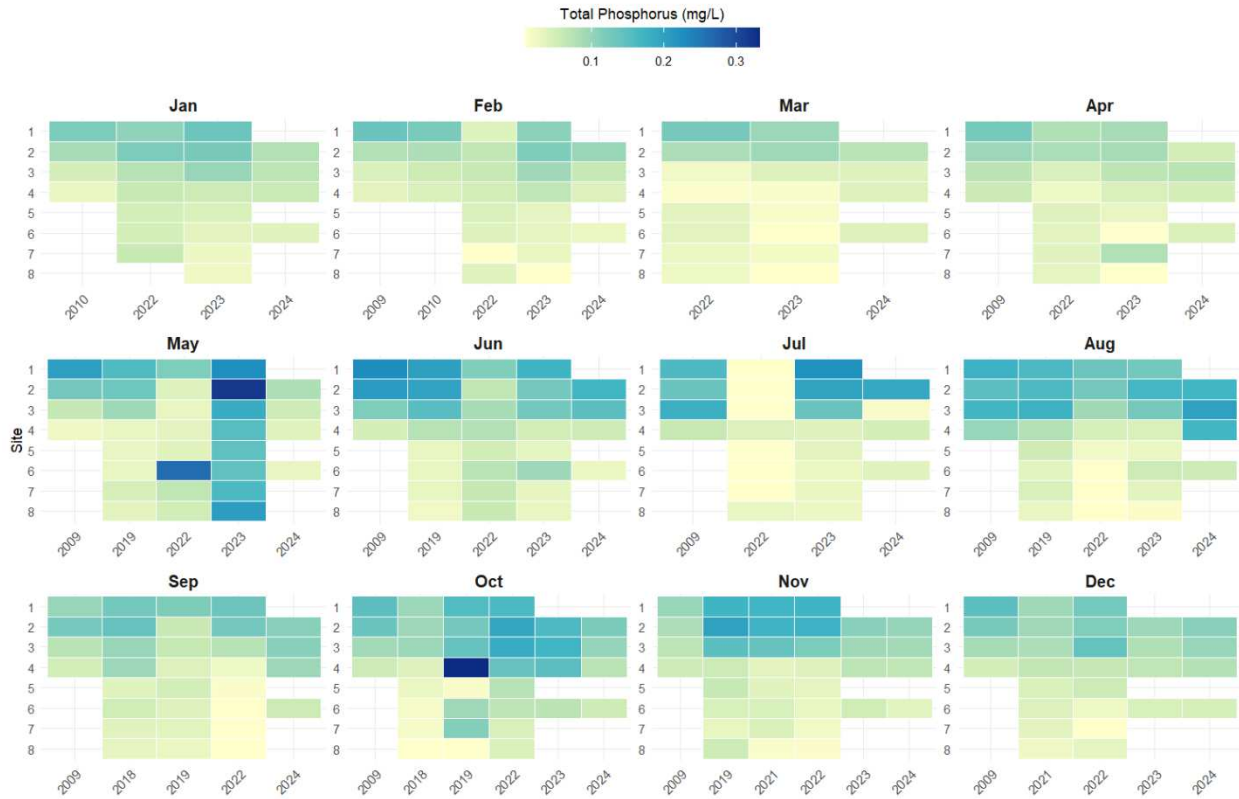


Fig. 8. Temporal trends in phytoplankton biomass at Sites 1, 2, and 3 from 2009 to 2024. Left panels: Stacked bar plots showing total summed biomass per site ($\mu\text{g C L}^{-1}$) partitioned by major phytoplankton groups: Dinoflagellate (red), Diatom (yellow), Other Cyanobacteria (blue), Picocyanobacteria (green), and Other (purple). Right panels: Corresponding relative biomass (%) of each phytoplankton group over time. Vertical dashed lines indicate splits between sampling periods.

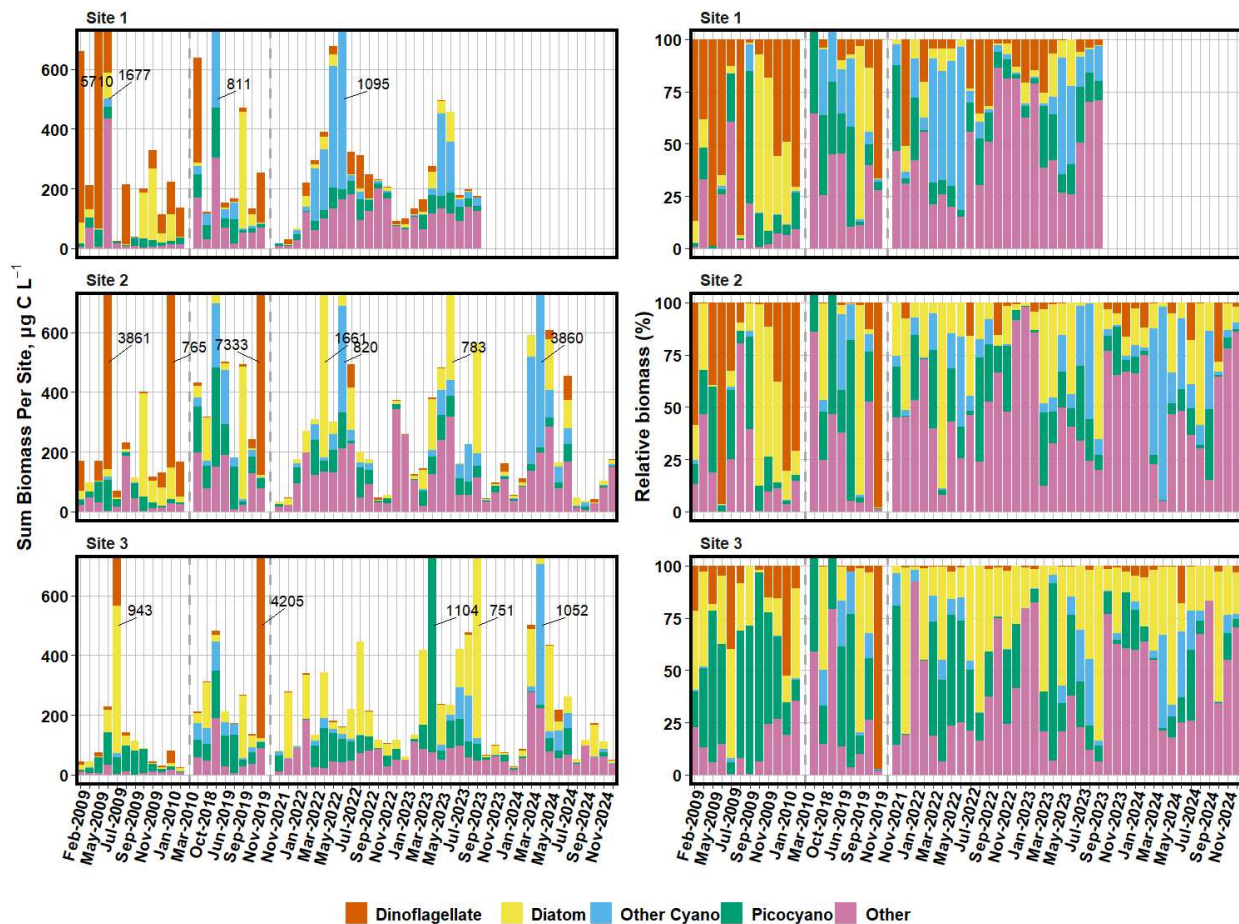


Fig. 9. Time series of phytoplankton biomass at Sites 4, 5, and 6 from 2009 to 2024. Left panels: Stacked bar plots showing total summed biomass per site ($\mu\text{g C L}^{-1}$) partitioned by major phytoplankton groups: Dinoflagellate (red), Diatom (yellow), Other Cyanobacteria (blue), Picocyanobacteria (green), and Other (purple). Right panels: Corresponding relative biomass (%) of each phytoplankton group over time. Vertical dashed lines indicate splits between sampling periods.

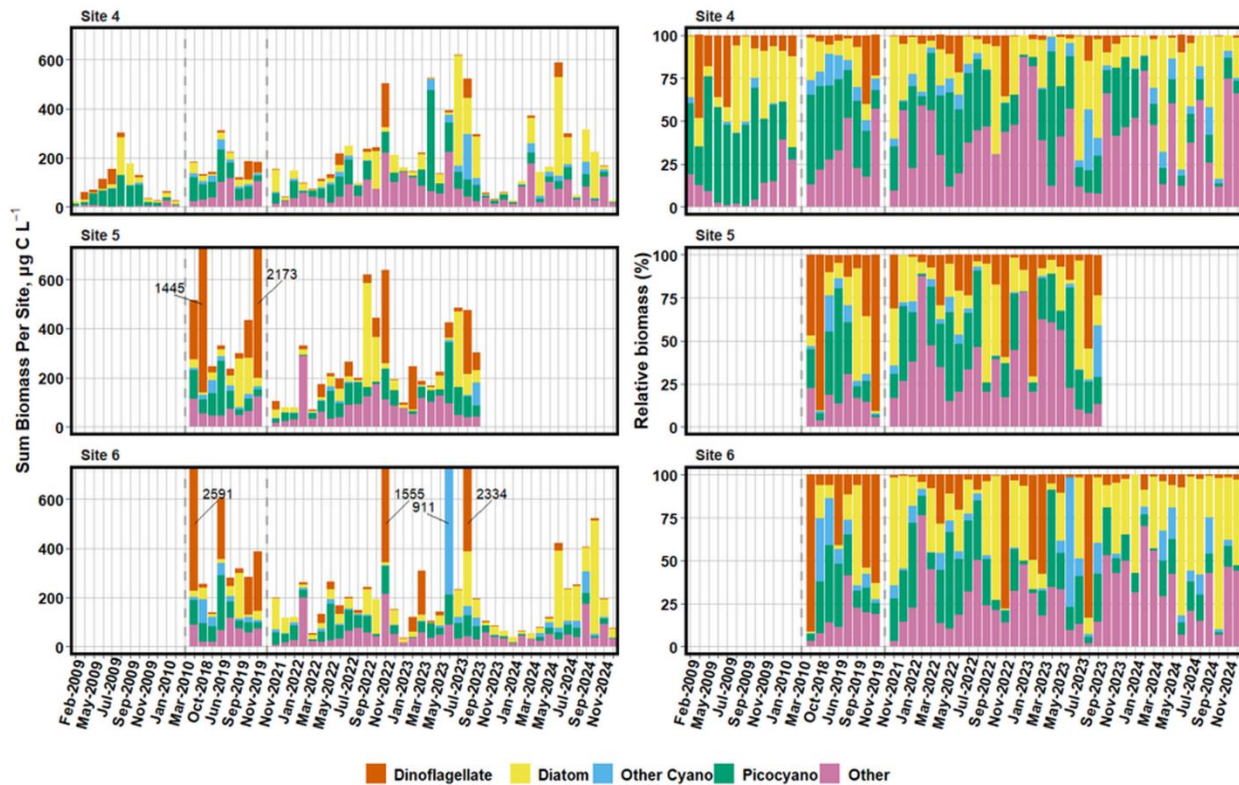


Fig. 10. Time series of phytoplankton biomass at Sites 7 and 8 from 2018 to 2024. Left panels: Stacked bar plots showing total summed biomass per site ($\mu\text{g C L}^{-1}$) partitioned by major phytoplankton groups: Dinoflagellate (red), Diatom (yellow), Other Cyanobacteria (blue), Picocyanobacteria (green), and Other (purple). Right panels: Corresponding relative biomass (%) of each phytoplankton group over time. Vertical dashed lines indicate splits between sampling periods.

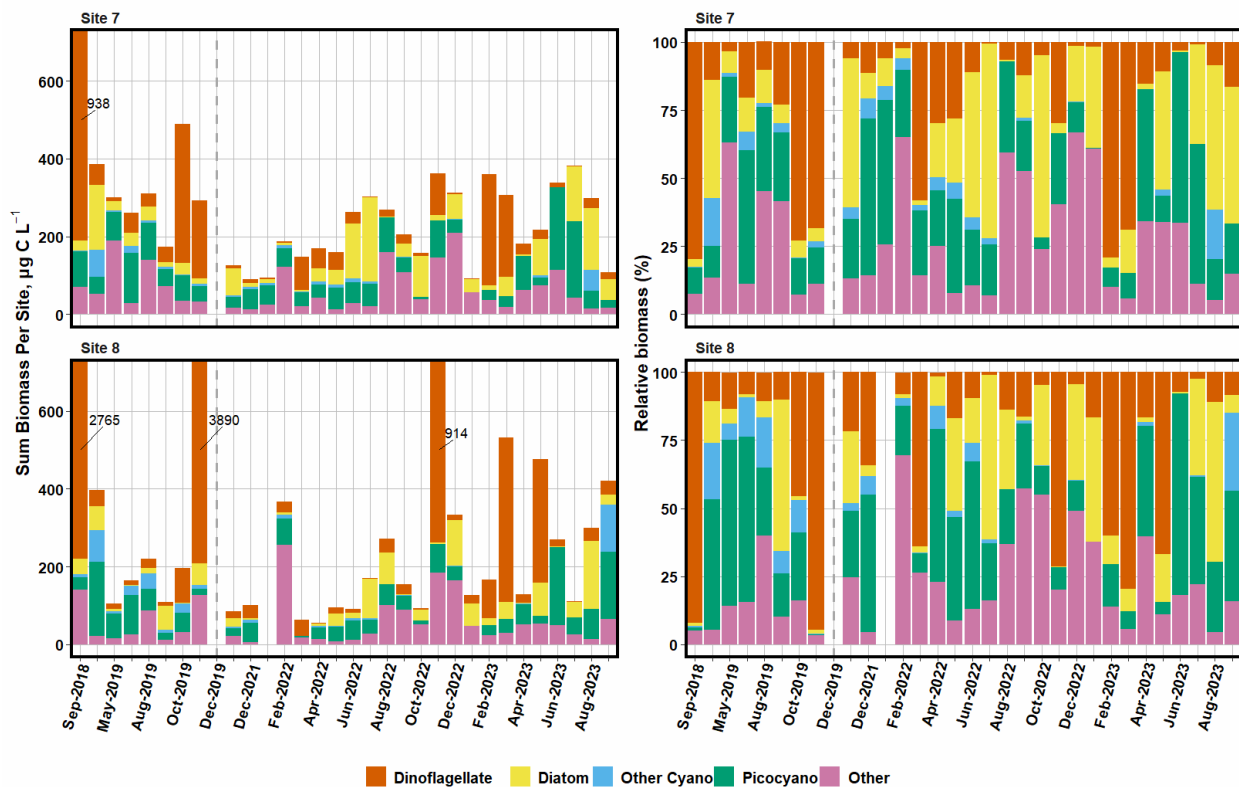


Fig. 11. Cell abundance (cells mL⁻¹) of three harmful algal bloom species: *Akashiwo sanguinea* (top row), *Skeletonema costatum* (middle row), and *Karenia brevis* (bottom row) plotted against S-79 discharge (left column) and salinity (right column). Each point represents a single sample, colored by site group: Sites 1–3 in the upper estuary (red), Sites 4–6 in the lower estuary and San Carlos Bay (blue), and Sites 7–8 in the adjacent nearshore Gulf (open circles).

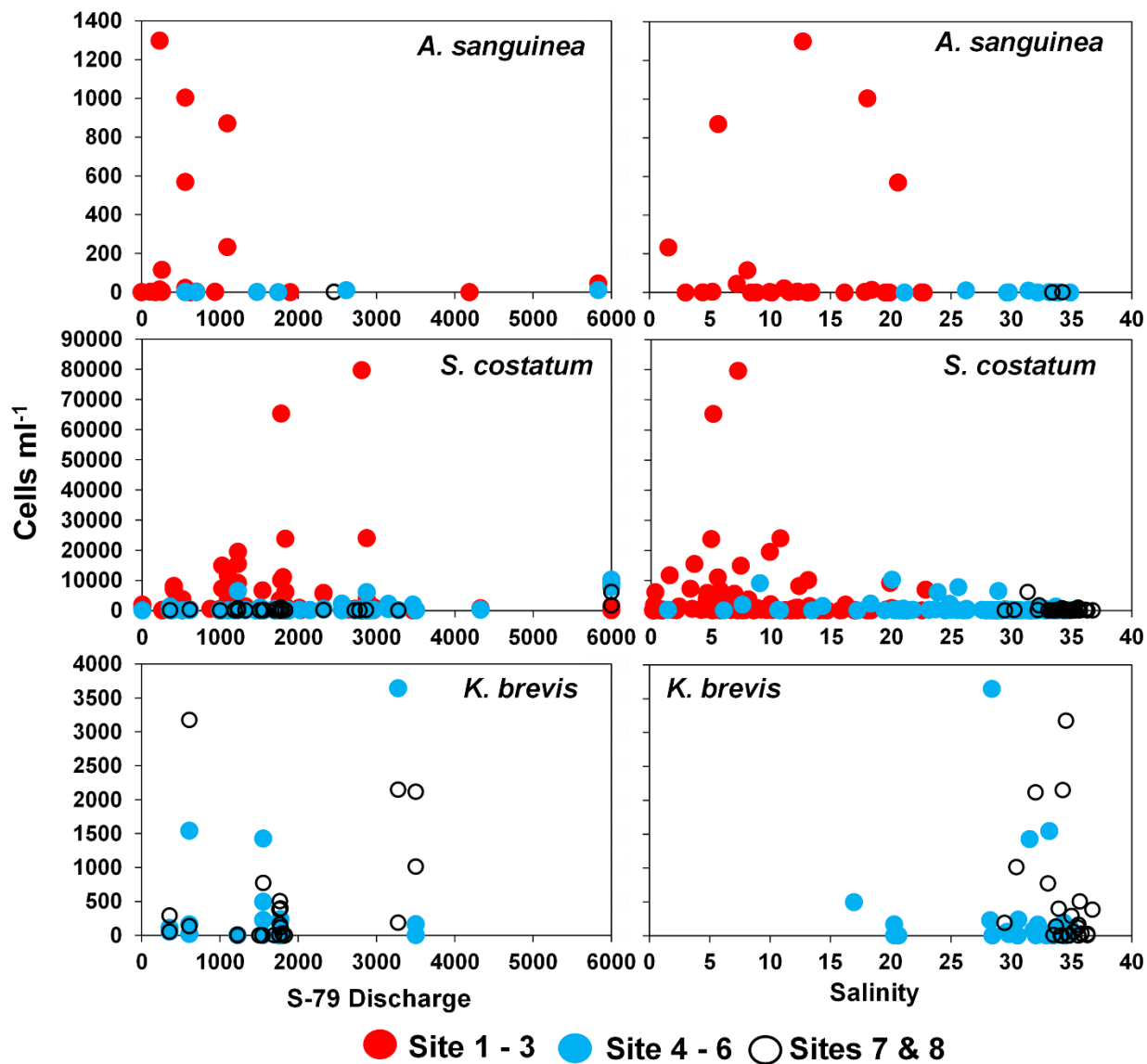


Fig. 12. Spearman correlation matrices of environmental and phytoplankton variables at estuarine sites 1–3 (upper estuary) Only statistically significant correlations ($p < 0.05$) are shown. Cell colors indicate the strength and direction of correlation. DISCH represents the mean daily discharge 15 days prior to the sampling date and PRCP represents the precipitation sum for 15 days leading up to the sampling date.

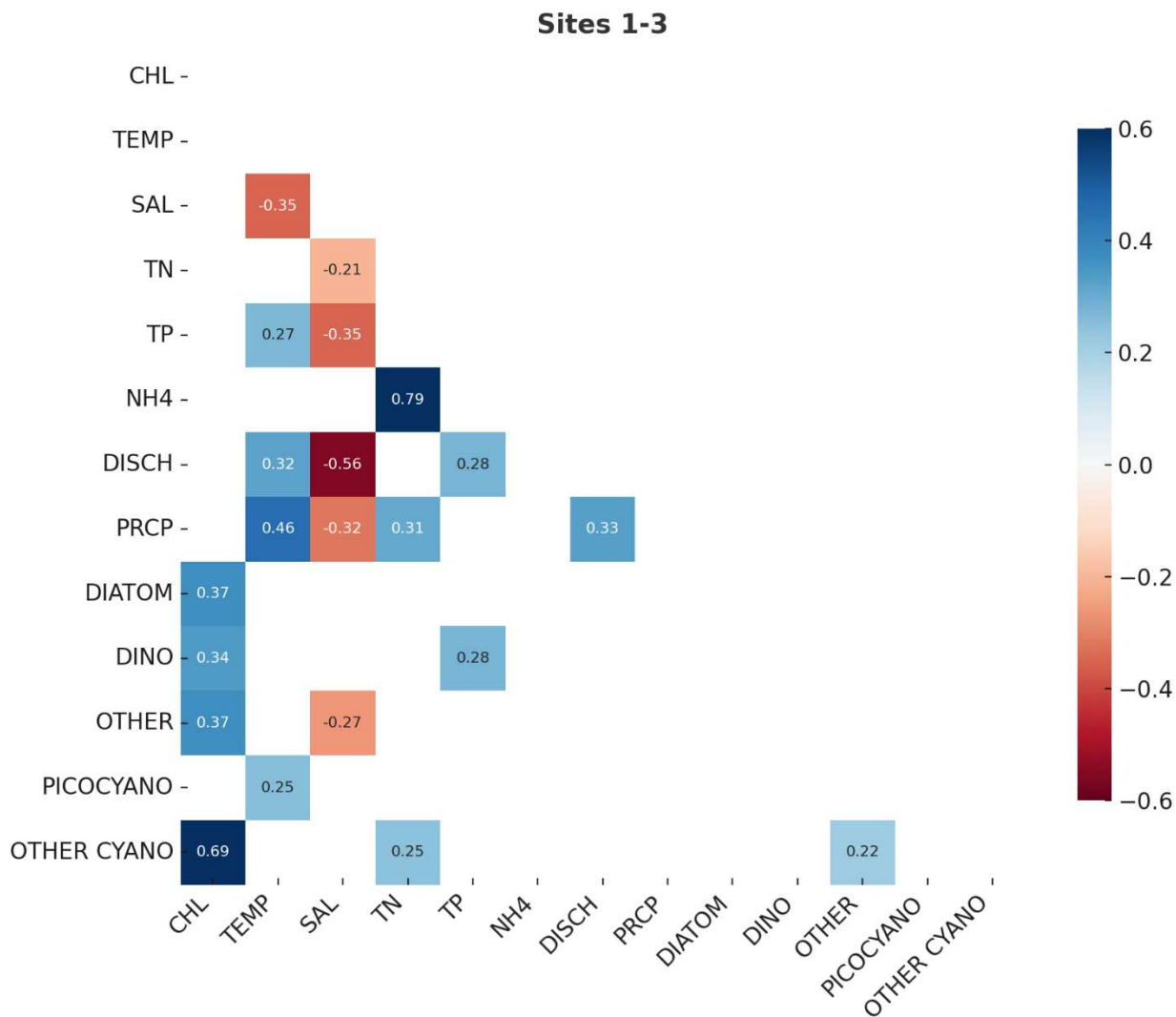


Fig. 13. Spearman correlation matrices of environmental and phytoplankton variables at estuarine sites 4–6 (mid-estuary). Only statistically significant correlations ($p < 0.05$) are shown. Cell colors indicate the strength and direction of correlation. DISCH represents the mean daily discharge 15 days prior to the sampling date and PRCP represents the precipitation sum for 15 days leading up to the sampling date.

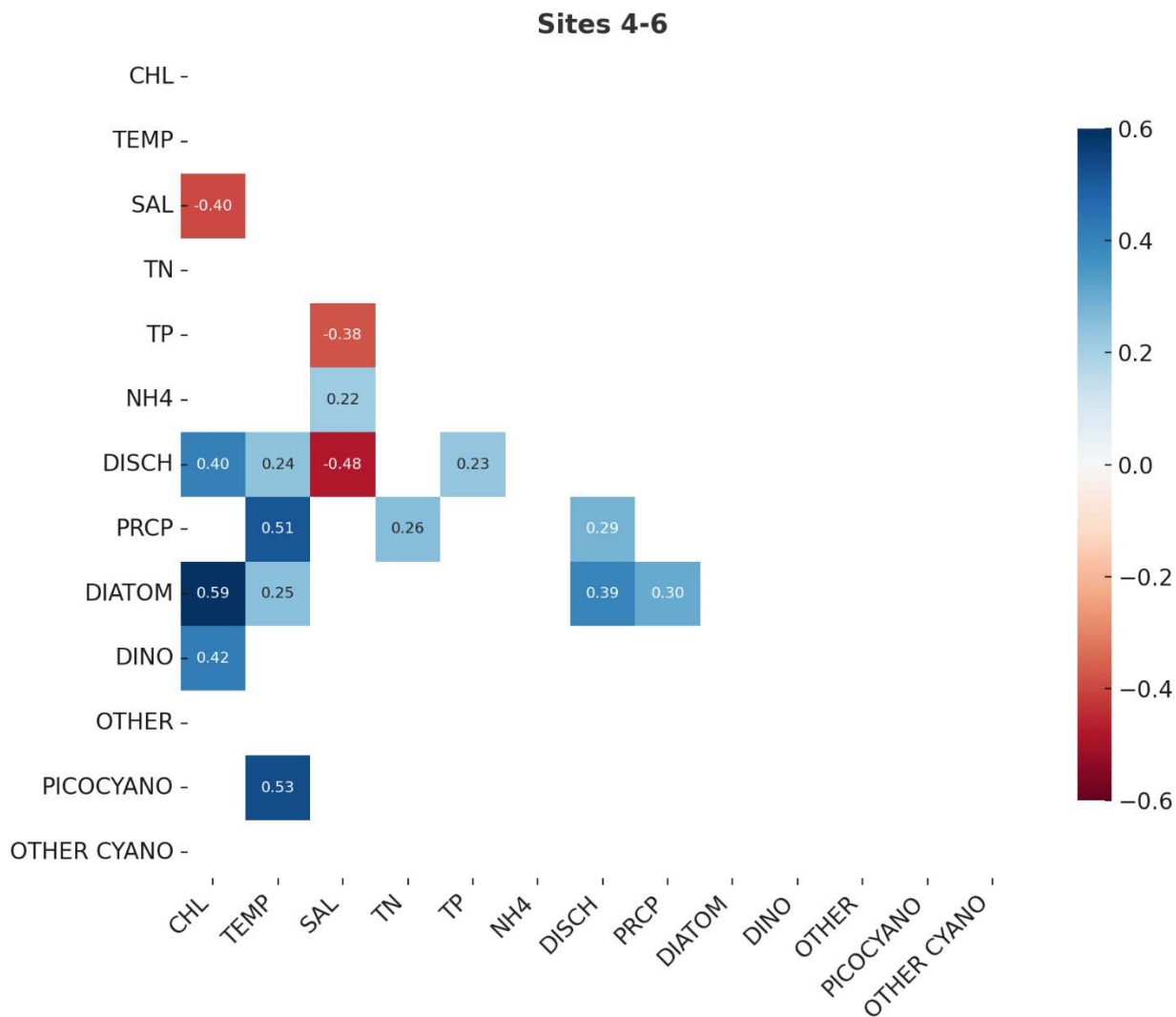


Fig. 14. Spearman correlation matrices of environmental and phytoplankton variables at estuarine sites 7–8 (nearshore). Only statistically significant correlations ($p < 0.05$) are shown. Cell colors indicate the strength and direction of correlation. DISCH represents the mean daily discharge 15 days prior to the sampling date and PRCP represents the precipitation sum for 15 days leading up to the sampling date.

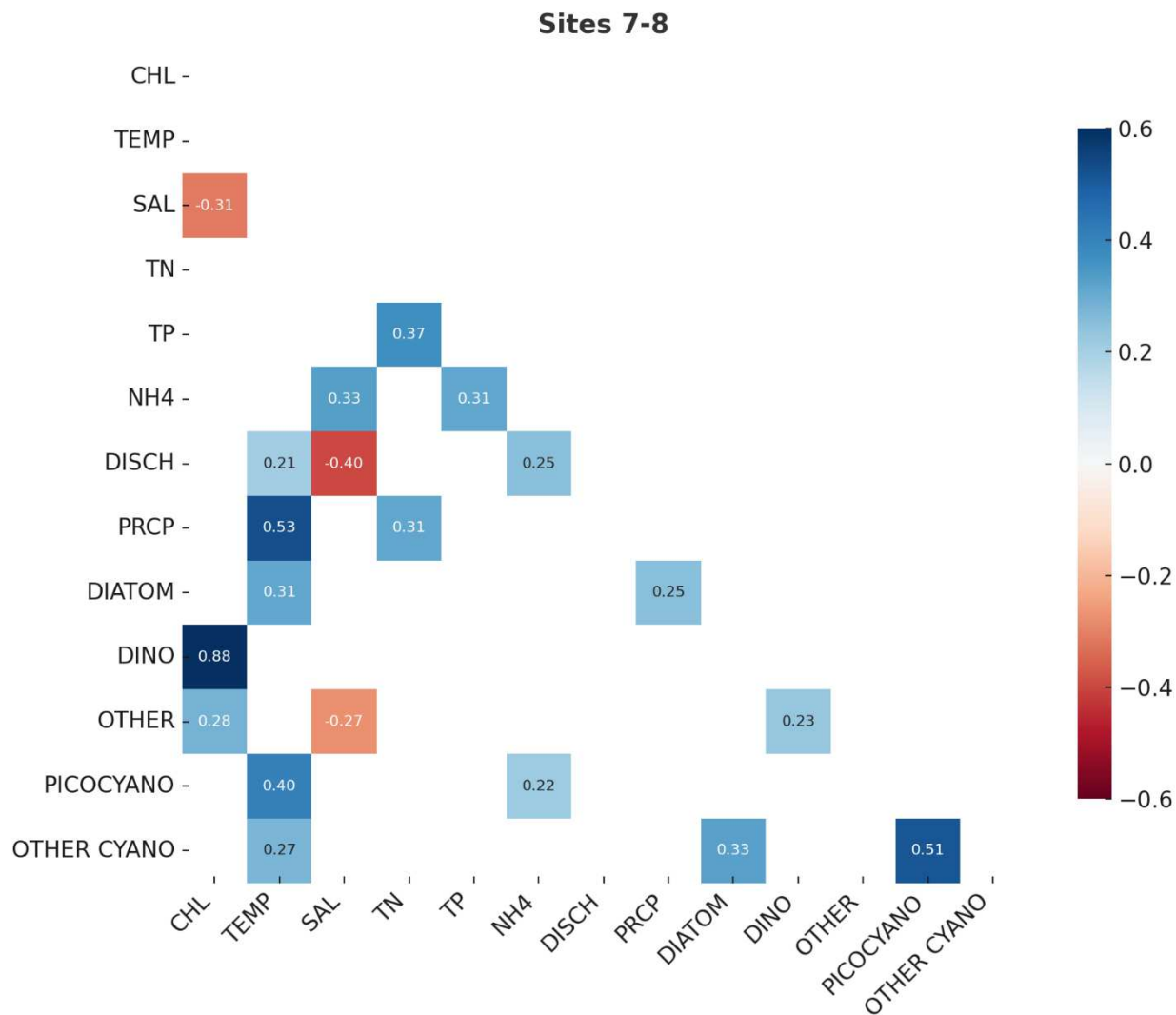
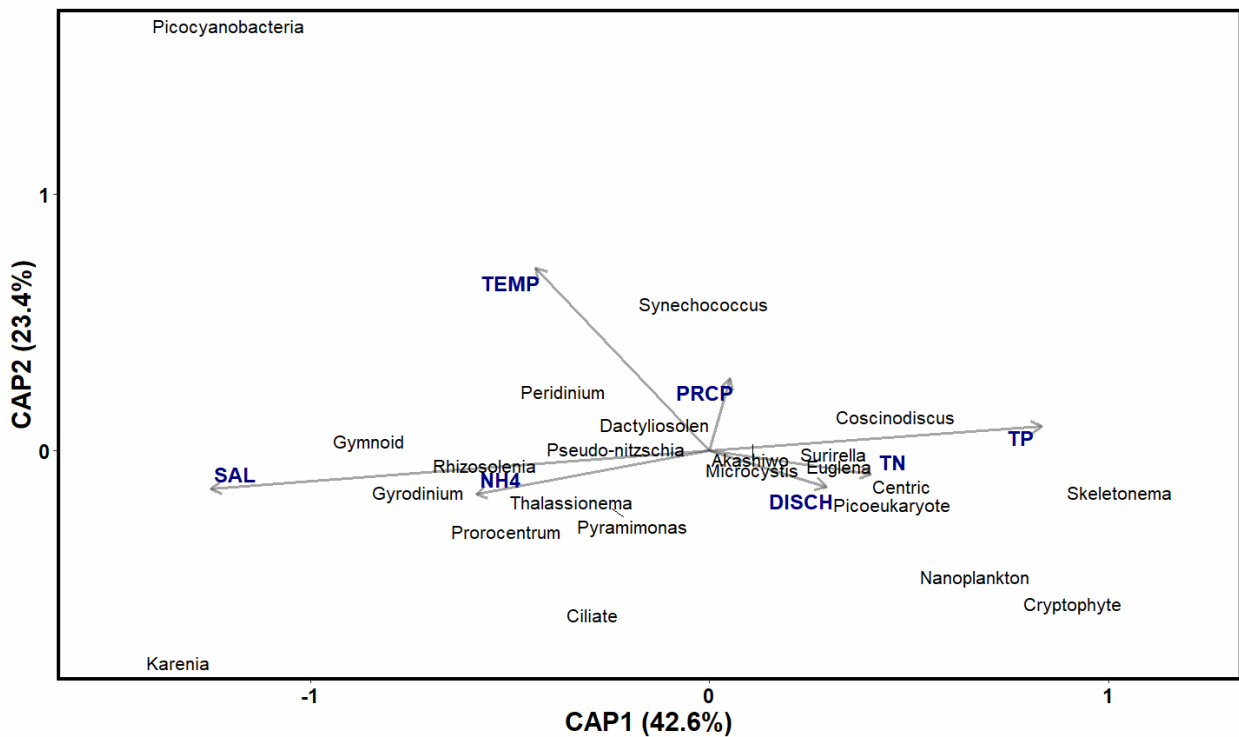


Fig. 15. RDA biplot illustrating the relationships between phytoplankton genera and environmental variables across sampling sites. Genera are displayed as text labels positioned according to their correlations with the first two canonical axes (CAP1 and CAP2), which explain 42.6% and 23.4% of the constrained variation, respectively. Arrows represent environmental variables (TP, TN, TEMP, SAL, NH₄, DISCH) with their directions and lengths indicating the strength and gradient of influence on community composition. Gray points denote individual sampling sites.



928 **Table 1.** Annual mean chlorophyll *a* concentrations at the eight sampling sites for the five years
 929 of sampling. Range of values observed for each year at the eight sites is shown in parentheses.

Site	2009-2010	2018-2019	2022	2023	2024
1	12.6 (2.3-33.8)	7.8 (2.5-17.5)	9.3 (1.4-24.5)	8.4 (3.3-17.9)	--
2	9.3 (3.8-33.2)	7.7 (1.8-22.2)	10.4 (1.3-39.0)	9.2 (3.2-28.4)	16.9 (2.6-100)
3	5.9 (1.6-40.0)	6.4 (1.8-21.4)	8.1 (2.4-50.4)	7.5 (1.9-28.7)	12.9 (1.8-57.1)
4	3.2 (1.1-9.6)	4.8 (0.9-12.7)	4.0 (0.9-7.7)	4.1 (1.7-11.3)	11.5 (1.4-31.0)
5	--	6.2 (1.7-10.0)	5.7 (1.8-15.2)	4.9 (0.5-9.6)	--
6	--	8.2 (0.7-33.1)	4.4 (1.1-11.1)	5.7 (1.8-25.3)	10.8 (1.4-45.6)
7	--	4.8 (1.0-13.3)	3.4 (1.6-6.4)	5.1 (2.1-9.3)	--
8	--	7.1 (0.4-21.3)	2.9 (0.8-7.4)	4.0 (1.3-7.9)	--

930

Table 2. Top-125 biomass observations of individual taxonomic groups in five salinity regimes over the study period. Number of observations per taxon in each regime are shown, along with the range of biomass concentrations as $\mu\text{g carbon L}^{-1}$ in parentheses. Taxa shown in red text are known HAB species (Moestrup et al., 2009; Lassus et al., 2016; Chorus and Welker, 2021).

	Frequency in Top-125 and (Biomass Range)				
CYANOBACTERIA	Freshwater	Oligohaline	Mesohaline	Polyhaline	Euhaline
Picocyanobacteria spp.	27 (28-140)	20 (32-235)	32 (47-937)	43 (54-411)	46 (50-221)
<i>Synechococcus</i> spp.	4 (30-38)	6 (30-144)	6 (46-59)	3 (71-95)	7 (52-69)
Nanocyanobacteria spp.	3 (28-171)	2 (40-71)	2 (103-151)	1 (182)	4 (53-686)
<i>Microcystis aeruginosa</i>	6 (69-120)	1 (30)			
<i>Raphidiopsis raciborskii</i>	5 (29-319)	2 (78-403)			
<i>Limnothrix redekei</i>	4 (35-279)	5 (66-333)			
<i>Cuspidothrix tropicalis</i>	1 (50)	4 (57-914)			
<i>Pseudanabaena</i> spp.	4 (31-66)	2 (32-565)			
<i>Aphanacapsa</i> sp.	1 (28)	1 (50)			
<i>Planktolyngbya limnetica</i>	1 (179)				
<i>Dolichospermum circinale</i>		4 (34-789)			
<i>Coelomorpha tropicalis</i>		2 (29-76)			
<i>Oscillatoria</i> sp.		1 (56)			
<i>Chroococcus</i> sp.		1 (50)			
<i>Planktothrix</i> sp.		1 (51)			
DIATOMS	Freshwater	Oligohaline	Mesohaline	Polyhaline	Euhaline
<i>Aulacosiera granulata</i>	5 (34-49)	2 (29-55)			
<i>Aulacoseira</i> sp.		3 (30-533)			
<i>Aulacoseira ambigua</i>		1 (34)			
<i>Surirella</i> sp.	2 (84-91)				
<i>Skeletonema potamos</i>	1 (87)				
<i>Urosolenia</i> sp.	1 (74)				
<i>Skeletonema costatum</i>		13 (58-932)	12 (79-875)	5 (86-208)	1 (87)
<i>Coscinodiscus</i> spp.		3 (39-72)	21 (45-626)	16 (53-247)	8 (53-127)
<i>Coscinodiscus granii</i>			1 (101)	1 (277)	
<i>Odontella sinensis</i>		1 (45)	2 (75-129)		
<i>Cyclotella</i> spp.		2 (28-42)	2 (55-79)		1 (78)
<i>Chaetoceros lorenzianus</i>			2 (51-58)		
<i>Chaetoceros</i> sp.			1 (369)		
<i>Rhizosolenia setigera</i>				3 (101-418)	1 (166)
<i>Cerataulina pelagica</i>				2 (183-241)	3 (48-111)
<i>Dactyliosolen fragilissimus</i>				2 (113-199)	2 (58-89)
<i>Thalassionema</i> sp.					2 (79-157)

937 Table 2. continued
938

	Frequency in Top-125 and (Biomass Range)				
DINOFLAGELLATES	Freshwater	Oligohaline	Mesohaline	Polyhaline	Euhaline
<i>Durinskia baltica</i>	4 (27-66)				
<i>Peridinium</i>	4 (43-346)				
<i>Woloszynskia</i>	2 (60-314)				
<i>Woloszynskia reticulata</i>	1 (87)				
<i>Gymnodinium fuscum</i>	2 (34-39)				
Undentified thecate sp.	2 (33-34)				
<i>Protopteridinium</i> spp.		2 (27-84)		1 (67)	1 (62)
<i>Akashiwo sanguinea</i>		3 (30-7420)	5 (153-7164)	3 (92-4052)	1 (123)
<i>Scrippsiella</i> spp.		3 (29-119)	4 (59-159)		
<i>Karlodinium veneficum</i>		1 (54)	1 (58)		
<i>Polykrikos schwartzii</i>			2 (124-1208)		
<i>Pyrophacus</i> sp.			1 (254)		
<i>Prorocentrum minumum</i>			1 (100)		
<i>Peridinium quadridentatum</i>		1 (96)		6 (64-1927)	1 (78)
<i>Gyrodinium instriatum</i>			1 (44)		
<i>Karenia brevis</i>			1 (348)	7 (71-4173)	19 (55-3637)
<i>Tripos hircus</i>				1 (183)	
Gymnoid sp.				1 (88)	
<i>Gyrodinium spirale</i>				1 (82)	
<i>Gonyaulax</i> sp.				1 (73)	
<i>Gyrodinium pingue</i>				1 (51)	
<i>Protopteridinium excentricum</i>					1 (73)
<i>Prorocentrum belizeanum</i>					1 (49)
OTHER GROUPS	Freshwater	Oligohaline	Mesohaline	Polyhaline	Euhaline
Chlorophytes	2 (54-87)	2 (29-33)			
Euglenoids	3 (29-206)	3 (49-802)	1 (98)		
Cryptophytes	6 (32-46)	7 (35-118)	6 (47-62)	2 (52-68)	1 (186)
Other Nanoeukaryotes	25 (28-140)	17 (28-171)	2 (78-85)	1 (64)	3 (49-132)
Ciliates	9 (30-192)	9 (43-150)	19 (45-260)	24 (50-201)	22 (48-224)

939

940 **Table 3.** List of HAB taxa observed during the study period, including number of observation in
941 each of the five salinity regimes and highest cells ml⁻¹ and biomass (µg carbon L⁻¹) (Moestrup et
942 al., 2009; Lassus et al., 2016; Chorus and Welker, 2021).

		# of	Peak	Peak	Temp.					
			Density	Biomass	Range	Salinity	Frequency in Salinity Ranges			
Group	Species	Obs.	cells mL ⁻¹	µg C L ⁻¹	°C	Range	≤ 5	6-18	>18-30	>30
Diatoms	<i>Chaetoceros curvisetus</i>	3	4.8	0.5	21-25	28-36			1	2
	<i>Chaetoceros peruvians</i>	1	0.3	0.1	22	35				1
	<i>Chaetoceros tenuissimus</i>	43	1365.0	14.3	18-33	21-35			18	25
	<i>Pseudo-nitzschia calliantha</i> *	19	133.0	1.8	27-32	25-36			5	14
	<i>Pseudo-nitzschia</i> spp.*	102	686.6	9.4	18-31	0.2-36	3	8	31	60
	<i>Pseudo-nitzschia turgidula</i> *	45	647.7	4.3	19-33	25-36		2	17	26
Dinoflagellates	<i>Akashiwo sanguinea</i>	38	1297.6	7420.0	16-32	4-34	4	14	12	8
	<i>Alexandrium</i> sp.*	1	13.5	12.0	29	31				1
	<i>Amphidinium</i> spp.	13	27.3	8.2	21-33	5-36		2	1	10
	<i>Dinophysis caudata</i> *	15	0.2	1.2	21-31	18-36		3	3	9
	<i>Durinskia baltica</i>	10	60.4	44.1	22-32	0.2-0.8	10	1		
	<i>Gonyaulax polygramma</i> *	28	3.8	27.7	19-32	5-36		8	3	17
	<i>Gonyaulax</i> spp.	19	30.3	72.9	15-33	10-36		3	6	10
	<i>Heterocapsa pygmaea</i> *	1	15.1	3.9	30	30			1	
	<i>Heterocapsa niei</i> *	7	90.0	39.7	29-33	29036			2	5
	<i>Heterocapsa rotundata</i>	24	767.3	34.1	15-30	4-36	4	9	6	5
	<i>Heterocapsa</i> spp.	17	539.0	34.3	21-32	13-35			5	12
	<i>Heterocapsa triquetra</i>	3	54.4	16.0	27-29	29-36			1	2
	<i>Karenia brevis</i> *	48	3642	4172.8	21-32	20-36			11	37
	<i>Karenia longicanalis</i>	3	0.4	1.1	21-33	20-33			1	2
	<i>Karenia mikimoto</i> *	7	26.0	10.7	21-29	17-33			1	6
	<i>Karlodinium veneficum</i> *	81	385.7	54.1	15-32	3-36	2	11	28	40
	<i>Margalefidinium polykrikoides</i>	12	4.5	22.2	15-33	5-35	2	2	4	4
	<i>Ostreopsis</i> sp.*	1	1.0	1.7	25	35				1
	<i>Oxyphysis oxytoxoides</i>	12	4.0	9.6	21-32	24-36			4	8
	<i>Oxytoxum</i> spp.*	7	68.0	19.7	22-29	31-36			1	6
	<i>Oxytoxum lohmannii</i> *	1	30.2	5.5	33	33				1
	<i>Peridinium quadridentatum</i>	43	1814	1927.0	18-33	6-35		6	22	15
	<i>Polykrikos schwartzii</i> *	11	68.0	1208.1	15-31	8-35		5	2	4
	<i>Prorocentrum balticum</i>	3	25.9	7.3	15-29	12-28			2	1
	<i>Prorocentrum gracile</i>	17	0.3	0.9	21-33	30-36			1	16
	<i>Prorocentrum micans</i>	18	0.8	3.5	14-30	20-31			6	12
	<i>Prorocentrum minimum</i> *	18	392.0	100.1	17-33	0.2-35	4	7	1	6
	<i>Prorocentrum rathymum</i> *	11	1.5	5.3	25-33	28-36			5	6
	<i>Prorocentrum texanum</i> *	92	13.0	43.7	18-33	7-36	1	3	13	75
	<i>Protoperidinium bipes</i>	13	30.2	20.7	23-33	27-36			5	8
	<i>Protoperidinium conicum</i>	21	18.2	346.0	22-33	7-36		9	5	7
	<i>Protoperidinium excentricum</i>	5	9.1	73.2	22-32	7-32		3	1	
	<i>Protoperidinium steinii</i>	19	27.3	20.7	19-32	6-36		5	5	9
	<i>Takayama tasmanica</i> *	5	60.4	22.8	21-31	13-36		1		4
Cyanobacteria	<i>Cuspidothrix tropicalis</i> *	16	169703	914.7	23-30	0.2-11	14	1	1	
	<i>Dolichospermum circinale</i> *	11	70626	789.3	24-33	0.2-6	9	2		
	<i>Dolichospermum</i> spp.*	14	65489	413.5	22-33	0.2-24	5	3	6	
	<i>Limnothrix redekei</i> *	21	68040	333.8	19-32	0.2-7	20	1		
	<i>Microcystis aeruginosa</i> *	23	308106	120.5	19-32	0.2-6	20	3		
	<i>Oscillatoria</i> spp.	33	105.8	55.8	24-33	0.2-34	18	4	7	4
	<i>Planktothrix</i> sp.*	1	60.5	51.3	24	24			1	
	<i>Raphidiopsis raciborskii</i> *	10	78008	403.3	24-31	0.2-6	8	2		
	<i>Trichodesmium erythraeum</i> *	13	2.5	16.2	21-33	31-36				13
Other	<i>Chrysochromulina</i> sp.*	25	141.4	4.6	14-31	0.2-36	9	3	11	2

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