INFLUENCE OF COLORADO RIVER DISCHARGE VARIABILITY ON PHYTOPLANKTON COMMUNITIES IN MATAGORDA BAY, TEXAS

A Thesis

by

MOLLY ROSE MCBRIDE

BS, LaSalle University, 2018

Submitted in Partial Fulfillment of the Requirements for the Degree of

MASTER OF SCIENCE

in

MARINE BIOLOGY

Texas A&M University-Corpus Christi Corpus Christi, Texas

August 2022

© Molly Rose McBride

All Rights Reserved

August 2022

INFLUENCE OF COLORADO RIVER DISCHARGE VARIABILITY ON PHYTOPLANKTON COMMUNITIES IN MATAGORDA BAY, TEXAS

A Thesis

by

MOLLY ROSE MCBRIDE

This thesis meets the standards for scope and quality of Texas A&M University-Corpus Christi and is hereby approved.

Michael Wetz, PhD Chair

Jeffrey Turner, PhD Committee Member Rance Hardison, PhD Committee Member

August 2022

ABSTRACT

Phytoplankton are important primary producers in estuaries and are also indicators of environmental changes, such as freshwater inflow or nutrient loadings. Some phytoplankton are also harmful algal bloom (HAB) species, negatively impacting estuaries with toxin production or by generating hypoxia during bloom termination. Blooms of the HAB *Dinophysis sp.* have negatively affected the Matagorda Bay (Texas) ecosystem on multiple occasions since 2008. Estuaries of the Texas coast, such as Matagorda Bay, are vulnerable to long-term decreases in freshwater inflow due to increasing human freshwater needs as well as climate change. It is critical to understand how phytoplankton communities, including HABs, respond to freshwater inflow variability to estuaries in order to project how future inflow changes may affect estuaries. Over a 24-month period, a suite of environmental parameters along with phytoplankton community composition and biovolume was measured to determine the influence of freshwater inflow from the Colorado River on these parameters in Matagorda Bay. Spatiotemporal distribution of nutrients, chlorophyll and phytoplankton were influenced by riverine inflow. In particular, all of these factors decreased moving away from the river mouth, indicating a strong influence of the river on their distributions. *Dinophysis sp.* was observed in January, February and April 2020 during a period of cool temperatures and higher salinities, and its biovolume was positively correlated with nitrate+nitrite and the ratio of silicate to dissolved inorganic nitrogen. Other non-HAB phytoplankton taxa had distinct responses to environmental variability. Future work should consider HAB taxa on an individual basis, as well as consider more frequent sampling and toxin analysis. The unique environment, as well as phytoplankton communities and responses of Matagorda Bay underscore the necessity of investigating changes over time on an individual estuary basis, and for potential blooms, on a species-specific basis.

DEDICATION

This thesis is dedicated to my parents, Charlie and Sandi McBride. You always believed in me and my abilities. Thank you for your unconditional love and know that it is returned, always.

ACKNOWLEDGEMENTS

I would like to thank Dr. Michael Wetz for advising and teaching me. I would also like to thank Dr. Jeffrey Turner for being on my committee and guiding me through the thesis process. I also greatly appreciate Dr. Rance Hardison's mentorship for my NERTO and thesis. Thank you to my fellow lab members, Jordana Cutajar, Elani Morgan, Lily Walker, Tiffany Chin, Sarah Tominack, Ken Hayes, Dominic Burch, Laura Beecraft, and Sankar Sasidharan. Immense gratitude to my friends, Lexie Neffinger, Alyssa Outhwaite, Mo Sugla, Devin Comba, Jen Gilmore, and Neina Chapa. I would not have survived, let alone had some of the best times of my life, without all of you. Last, I would like to thank Jim Church for being a constant support and uplifter for many years.

TABLE OF CONTENTS

ABSTRACTiv
DEDICATIONv
ACKNOWLEDGEMENTS vi
TABLE OF CONTENTS vii
LIST OF FIGURES ix
LIST OF TABLES xi
1. INTRODUCTION 1
2. METHODS
Site Description
Sampling
Biogeochemical Analyses
Statistical Analyses
3. RESULTS
Environmental factors
Chlorophyll and biovolume
Phytoplankton community composition 10
Harmful algae
4. DISCUSSION
Nutrient patterns
Chlorophyll patterns

Biovolume patterns	14
Phytoplankton community composition	16
Dinophysis	18
Future implications	20
Conclusion	21
REFERENCES	23
FIGURES	37

LIST OF FIGURES

Page	
Figure 1. Map of sample sites in Matagorda Bay. Pink boxes represent segments created to	
represent site area for normalizing of biovolume	
Figure 2. Average weekly discharge from Colorado River up to sampling dates	
Figure 3. Mean salinity from November 2019-October 2021 (shade is 95% confidence interval).	
Figure 4. Salinity gradient from river mouth	
Figure 5. Mean temperature from November 2019-October 2021 (shade is 95% confidence	
interval)	
Figure 6. Mean Secchi depth from November 2019-October 2021 (shade is 95% confidence	
interval)	
Figure 7. Secchi depth gradient from river mouth	
Figure 8. Mean N+N from November 2019-October 2021 (shade is 95% confidence interval) 44	
Figure 9. N+N gradient moving away from river mouth	
Figure 10. Mean N+N versus mean temperature for all dates	
Figure 11. Mean ammonium from November 2019-October 2021 (shade is 95% confidence	
interval)	
Figure 12. Ammonium gradient moving away from river mouth	
Figure 13. Mean orthophosphate from November 2019-October 2021 (shade is 95% confidence	
interval)	
Figure 14. Orthophosphate gradient across sites moving away from river mouth	
Figure 15. Mean orthophosphate versus discharge for all dates	

Figure 16. Mean DIN:DIP ratio from November 2019-October 2021 (shade is 95% confidence
interval)
Figure 17. Mean silicate from November 2019-October 2021 (shade is 95% confidence interval).
Figure 18. Silicate gradient across sites moving away from river mouth
Figure 19. Mean silicate versus discharge for all dates
Figure 20. Mean silicate versus mean temperature for all sites and dates
Figure 21. PCA by season
Figure 22. PCA by site
Figure 23. Mean chlorophyll (a) concentration from November 2019-October 2021 (shade is
95% confidence interval)
Figure 24. Chlorophyll gradient moving away from river mouth
Figure 25. Total biovolume over time
Figure 26. Site A1 functional group biovolume over time
Figure 27. A2 functional group biovolume over time
Figure 28. A4 functional group biovolume over time
Figure 29. A6 functional group biovolume over time
Figure 30. A9 functional group biovolume over time
Figure 31. MAD functional group biovolume over time

LIST OF TABLES

Table 1. Kruskall-Wallis test for environmental factors and each site (adjusted p-values for
multiple comparisons with Dunn Test). Shared letters/colors signify no significant difference
between two sites
Table 2. Kendall's tau correlation results between chlorophyll and environmental variables, as
well as biovolume for all sites. Highlighted variables indicate significant correlations (α =0.05).
Table 3. Kendall's tau correlation results between phytoplankton total and functional group
biovolume and environmental variables. Highlighted variables indicate significant correlations
(α=0.05)
Table 4. Kendall's tau correlation results between HAB biomass/Dinophysis and environmental
variables. Highlighted variables indicate significant correlations (α =0.05)

1. INTRODUCTION

Freshwater inflow is a major driver of environmental conditions in estuaries (Gillanders and Kingsford 2002; Burford et al. 2011). Changes in freshwater inflow are due to rainfall and runoff, both in the short-term (storms, seasonal changes) and long-term. In Texas, variability in the El Niño/La Niña cycle largely controls rainfall patterns (Kim et al., 2014), with El Niño characterized by increased rainfall and La Niña by dry conditions (Kim et al., 2014). Freshwater inflow is also influenced by diversions of water away from rivers into reservoirs for human use (Flemer and Champ 2006). Lastly, climate changes such as warming may cause greater evaporation rates or extended drought periods, decreasing river flow (Konapala et al., 2020).

Inflow variability can affect important estuary attributes. For example, decreased inflow can increase salinity in estuaries, resulting in reduced mixing and introduction of diseases and parasites from saltier water (Longley 1994; Gillanders and Kingsford 2002). Riverine-derived nutrients may decrease while contaminants may concentrate (Longley 1994; Gillanders and Kingsford 2002). Fewer nutrients can result in decreased primary and secondary production as well as loss of fish harvests and nursery habitats (Longley 1994; Boynton and Kemp 2000; Barbosa et al. 2010; Burford et al. 2011; Barroso et al. 2018). In contrast, high inflow can expand the brackish zone and dilute contaminants (Longley 1994). The dilution of estuarine water helps create hospitable nursery habitats for various organisms including juvenile fish, shrimp and oysters (Longley 1994). Increased river inflow can also bring a fresh supply of nutrients (Burford et al. 2011; Bruesewitz et al. 2013). With sufficient nutrients and light, primary production can increase (Flemer and Champ 2006). Increased inflow can create stratification, leading to hypoxia in bottom waters of the estuary (Longley 1994; Gillanders and Kingsford 2002). Sediment input and therefore turbidity may increase, which may decrease light to, or bury, bottom dwelling

organisms (Longley 1994; Gillanders and Kingsford 2002). River inflow intensity is also a physical characteristic that can affect flushing time of the estuary. High inflow rates can push phytoplankton populations out of the estuary, while low inflow rates may increase residence time and allow biomass to increase (Ketchum 1954). Production and biomass in turn affect fish recruitment and fish yields (Boynton and Kemp 2000).

Phytoplankton are important for energy transfer: almost half of global primary production is attributed to phytoplankton (Field et al., 1998). A decrease in phytoplankton biomass may have a negative effect in estuaries by depriving crucial production from the system, while an increase could have the opposite effect, stimulating greater production (Cloern et al. 2014). Some genera of phytoplankton, however, are undesirable toxin producers or physically obstructive due to spines, making an increase harmful to the estuary (Smayda 1997a). In addition, an excess of any one genus can generate hypoxia in the system when a bloom decomposes (Smayda 1997a, Steidinger and del Castillo 2018). Harmful algal blooms (HABs) are increasing around the world and have also been recorded in the study area, Matagorda Bay (Hallegraeff 1993; Harred and Campbell 2014). For example, *Dinophysis sp.* blooms were the cause of shellfish harvesting closure seven times since 2008 in Matagorda Bay (Campbell et al., 2010, Harred and Campbell 2014).

Past drought conditions have stopped river flow completely to Matagorda Bay (Montagna et al. 2002). Freshwater decreased significantly between 1940-1950 due to drought (Longley 1994). A dry period in the 1960s also decreased inflow rates (Longley 1994). In 1993, river flow to Matagorda Bay was reduced by diversion from the Colorado River (Kim et al. 2009). With increasing urbanization and population growth in its watershed, freshwater demand will also

increase, which will likely further decrease freshwater inflow (Texas Water Development Board 2017).

Each estuary, like Matagorda Bay, has its own unique watershed, hydrological features, and level of vulnerability to land-use change and climate change. It is imperative we understand how specific estuaries may respond to changes in freshwater inflow in terms of their ecology and ecosystem health, especially considering climate change and future water diversion projections. In this study, I sampled Matagorda Bay for 24 months to assess phytoplankton biomass and community structure in varying environmental conditions, including changing freshwater input. I evaluated three hypotheses: 1) Chlorophyll *a* and phytoplankton biovolume will correlate with freshwater inflow, 2) chlorophyll maximum will be at the site closest to the Colorado River, and 3) the phytoplankton community will be dominated by functional groups that prefer brackish, nutrient-rich conditions.

2. METHODS

Site Description

The Matagorda Bay system is located on the central Texas coast and has the second largest surface area of Texas estuaries (Figure 1). The system is lagoonal, mostly isolated from the Gulf of Mexico, and comprised of a main bay (Matagorda Bay) and several subsystems including Lavaca Bay and East Matagorda Bay (Ward and Armstrong 1980). The mean depth of Matagorda Bay is 2.8 meters, and the residence time is about 2.5 months (Ward and Armstrong 1980; Armstrong 1982; Palmer et al., 2011). Depending on the declination of the moon, the tidal range can be semi-diurnal at about 0.2 meters (minimum declination) or diurnal at about 0.8 meters (at maximum declination) (Ward and Armstrong 1980). Circulation in the bay is also influenced by wind-driven wave action, mainly from south to southeastern winds of the Gulf of Mexico that keep the bay well-mixed (Ward and Armstrong 1980). For this study, sampling locations were in the main bay, which receives freshwater input from the Colorado River. Six sites (A1, MAD, A2, A4, A6, A9) were chosen along a river inflow gradient (Figure 1).

Sampling

From November 2019 to October 2021, monthly sampling was conducted in Matagorda Bay, excluding March 2020 due to COVID precautions. At each site, water was collected at 10 cm below the surface in brown HDPE bottles and stored on ice for nutrient and chlorophyll *a* (chlorophyll) analysis. Additional samples were kept at room temperature for phytoplankton enumeration. Light attenuation was measured with a Secchi disk. Salinity, pH, dissolved oxygen (DO;mgL⁻¹), and temperature (°C) were recorded at 10 cm below surface with a YSI multiparameter sonde. Colorado River inflow data were obtained from USGS at gauge 08162501. Freshwater inflow was recorded based on a seven-day average leading up to and

including the sampling date, based on Roelke et al. (2017), for the best reflection of the relationship between freshwater input and phytoplankton growth.

Biogeochemical Analyses

Chilled water samples were filtered through 25 mm GF/F filters for nutrient analysis and stored in a -20 °C freezer. Samples were thawed to room temperature and then analyzed on a Seal QuAAtro autoanalyzer. Standard curves with five different concentrations were run daily at the beginning of each run. Fresh standards were made prior to each run by diluting a primary standard with low nutrient surface seawater. Deionized water (DIW) was used as a blank, and DIW blanks were run at the beginning and end of each run, as well as after every 8-10 samples to correct for baseline shifts. Method detection limits were 0.02 μ M for nitrate plus nitrite (N+N) and ammonium (NH₄⁺), and < 0.01 μ M for orthophosphate (PO₄³⁻) and silicate (SiO₄). Dissolved inorganic nitrogen (DIN) was calculated as the sum of NH₄⁺ and N+N.

Phytoplankton Analyses

Chlorophyll (Chl) *a* was obtained by filtering 25 mL of chilled sample water through Whatman 25 mm GF/F filters that were stored in a -20°C freezer until extracted. To extract Chl *a*, filters were placed in tubes with 10 mL of 90% HPLC grade acetone for 16-24 hours. Then for analysis, a Turner Trilogy fluorometer was used to read Chl *a* levels using a non-acidified method (Welschmeyer 1994; EPA method 445.0).

To determine microplankton abundance, 60 mL of sample from the bottle stored at ambient temperature was preserved with 1 mL acid Lugol's solution. Between 1-10 mL of sample was settled in an Utermohl chamber for 1 hour per mL before counting on an Olympus 1X-71 inverted microscope at 20x magnification. To calculate biovolume, formulas from Hillebrand et al. (1999) and Sun and Liu (2003) were used based on the geometric shape of the

genus, using average cell measurements from counts. Sun and Liu (2003) formulas were used if there was a conflict between the two paper's formulas. If no third dimension of a cell was visible, this dimension was estimated based on relationships observed from cells for which all dimensions could be obtained.

Sample water (4 mL) was fixed with 80 μ L glutaraldehyde for flow cytometric analysis and stored at -20 °C until analysis. Samples were thawed in the dark at room temperature then filtered through 20 μ m Nytex mesh. Picoplankton were enumerated with an Accuri C6 Plus flow cytometer. The detection limit for picoplankton was 1040 cells mL⁻¹ and values below the detection limit were treated as zeros.

Statistical Analyses

Due to non-parametric data, Kendall's tau correlations were used to determine correlations between phytoplankton total biovolume as well as functional group biovolume and environmental variables at each site. Kendall's tau was also used to determine correlations between chlorophyll and environmental variables, as well as *Dinophysis* and environmental variables. The Kruskall-Wallis test with a post-hoc Dunn test was used to determine differences between non-normal environmental variables. All previous analyses and figures were generated in R 4.1.2 or Microsoft Excel. Principal components analysis and figure generation was performed in PRIMER-E Ltd. ANOVA was only used for data that met assumptions (normal).

3. RESULTS

Environmental factors

The mean Colorado River discharge was 276 m³s⁻¹. The lowest discharge was 33 m³s⁻¹ (August 2020) and the highest discharge was 2940 m³s⁻¹ (May 2021; Figure 2). Mean salinity ranged from 5.7 in May 2021, during the peak flow of 2940 m³s⁻¹, to 29.2 in August 2020 (Figure 3). There was an increasing salinity gradient for sites with distance from the river mouth (Figure 4). Median salinities at the three sites closest to the river mouth (A1, MAD and A2) were significantly lower than the three sites farther away (A4, A6 and A9; p<0.001, Table 1). There was distinct seasonality in surface temperature, with highest average temperatures observed in August 2020 and July 2021 (30.3 °C and 29.7 °C respectively; Figure 5) and lowest temperatures in November of 2019 and December 2020 (15.9 °C and 14.8 °C respectively; Figure 5). Mean Secchi depth was less than 1 m for all sites over the duration of the study (Figure 6). Secchi depth at the sites closest to the river mouth were consistently shallower than A4, A6 and A9 (p<0.01, Table 1). There was no significantly shallower Secchi depth with different amounts of discharge (p=0.153).

Mean N+N concentration was <20 μ M for the duration of the study and reached two maximums in the winter season (January 2020, 14.48 μ M and December 2020, 16.67 μ M; Figure 8). A1, MAD and A2 had significantly higher median N+N concentrations than A4, A6 and A9 (p<0.01; Table 1). N+N had a significant negative linear relationship with increasing distance from the river (p<0.01; Figure 9) and temperature (p=0.05; Figure 10). Mean ammonium concentration was <9 μ M for the duration of the study and reached two maximums, 5.17 μ M in January 2021 and 6.93 μ M in April 2021 (Figure 11). Ammonium had a significant negative

linear relationship with increasing distance from the river (p=0.01; Figure 12). There was no significant difference in median ammonium between sites (Table 1).

The mean orthophosphate concentration for all six sites across sampling dates was 1.68 μ M, and the maximum orthophosphate concentration (3.39 μ M) occurred on the same sampling date as the maximum discharge (May 2021; Figure 13). Orthophosphate had a significant negative linear relationship with increasing distance from the river mouth (p<0.01; Figure 14). Median orthophosphate was significantly higher at A1 compared to all other sites, and A9 had a significantly lower median orthophosphate than A1, MAD and A2 (Table 1). Orthophosphate had a significant positive linear relationship with discharge (p=0.01; Figure 15). The system is consistently nitrogen-limited, based on nutrient ratios (DIN:PO4<16; Figure 16).

Silicate concentration ranged from 6.21 μ M to 133.87 μ M and the mean silicate concentration across sites was 56.03 μ M (Figure 17). Mean silicate concentration was relatively low at the beginning of the study (November 2019) through April 2020, increased through November 2020, and decreased until March 2021. After March 2021, silicate concentration increased and peaked in May 2021. Silicate had a significant negative linear relationship with increasing distance from the river mouth (p<0.01; Figure 18). Silicate had a significant positive linear relationship with both discharge (p<0.01) and temperature (p=0.01; Figure 19; Figure 20). Potential silicate limitation (Si:DIN<1) only occurred on two dates, January (0.72) and February (0.69) of 2020 (data not shown).

Principal components analysis yielded a PC1 characterized by salinity, with most nutrients inversely related to salinity, and a PC2 characterized by temperature and chlorophyll inversely related to DO (Figure 21). PC1 explained 34.1% of variation, and PC2 23.0% variation, cumulatively, 57.1% total explanation of variation. Winter and spring separated from

the other two seasons on PC1 and were characterized by higher nutrient concentrations and lower salinity (Figure 21). PC2 shows that summer and fall had higher temperatures and lower DO generally (Figure 21). The only spatial difference seen in the PCA by site is a separation of A1, which had higher nutrient concentrations and lower salinity (Figure 22).

Chlorophyll and biovolume

The mean chlorophyll concentration across all sites was 16.0 μ g/L, with a minimum of 5.7 μ g/L and maximum of 38.4 μ g/L (Figure 23). The chlorophyll maximum occurred at the site closest to the river mouth in December 2019. Chlorophyll concentration had a significant negative linear relationship with distance from river mouth (p<0.01; Figure 24). A9, the site farthest from the river mouth, had a significantly lower median chlorophyll than all other sites except A6 (p<0.001; Table 1). Chlorophyll was strongly (τ >±0.3) negatively correlated with salinity (p<0.01) and Secchi depth (m) (p<0.01; Table 2), and weakly positively correlated (τ <0.3) with orthophosphate (p=0.02), silicate (p=0.05), temperature (p=0.02) and total biovolume (p<0.01, Table 2).

While chlorophyll concentrations were significantly lower at one site (A9), total biovolume did not significantly differ between any sites (p=0.6; Table 1). There were also no significant differences in the biovolume of diatoms (p=0.74), euglenoids (p=0.12), or cryptophytes (p=0.51) between sites (Table 1). Dinoflagellates were significantly lower at A4 compared to A1 (p=0.02, Table 1). Chlorophyll and total biovolume were also not significantly correlated (p=0.14; Table 2). For example, while there was a chlorophyll maximum (125.6 μ g/L) at site A1 in December 2019, this did not correspond with a biovolume maximum (not shown).

In November 2020, the opposite pattern occurred, with a biovolume maximum (5.4 x $10^6 \ \mu m^3/mL$) but no corresponding chlorophyll maximum (data not shown).

Diatom biovolume had a positive correlation (τ =0.13, p=0.05) with salinity and a negative correlation with ammonium (τ =-0.28, p<0.01; Table 3). Cryptophyte biovolume had a negative correlation with salinity (τ =-0.30, p<0.001) and temperature (τ =-0.43, p<0.001), as well as a positive correlation with discharge (τ =0.25, p<0.001; Table 3). Dinoflagellate biovolume was positively correlated with temperature (τ =0.15, p=0.03) and salinity (τ =0.20, p<0.01) and negatively correlated with N+N (τ =-0.18; p<0.01) and ammonium (τ =-0.20, p<0.01). Picocyanobacteria were negatively correlated with ammonium (τ =-0.22, p<0.01) and N+N (τ =-0.21, p<0.01) and positively correlated with salinity (τ =0.14, p=0.04) and temperature (τ =0.27, p<0.01; Table 3). Picoeukaryotes were negatively correlated with N+N (τ =-0.14, p=0.04) and positively correlated with temperature (τ =0.33, p<0.01; Table 3). Total biovolume was negatively correlated with ammonium (p<0.01) and positively correlated with temperature (τ =0.33, p<0.01; Table 3).

Phytoplankton community composition

The study area is a diatom-dominated system, with diatoms comprising of 55% of total biovolume for the entire sampling period, followed by picoeukayotes (25%), euglenoids (12%), dinoflagellates (6%), and picocyanobacteria (2%). Chlorophytes and cryptophytes contributed negligible biovolume compared to other functional groups. Diatom biovolume increased beginning in the fall of 2020 at sites A1 and A2 (Figure 32; Figure 33). Diatom biomass at A4, A6 and A9 was more constant over time (Figure 34; Figure 35; Figure 36). The minimum mean total biovolume of all sites occurred at MAD (7.96 x $10^6 \mu m^3/mL$; Figure 37). Euglenoid biovolumes generally peaked during December 2019 and March 2021 when present at a site.

Mean total microplankton biovolume for each site ranged between approximately 8-10 x 10^6 μ m³/mL. Picocyanobacteria biovolume was very low compared to other functional groups and after September 2020 decreased to below the detection limit until May 2021. Picoeukaryotes generally increased from the beginning of the study to a maximum of 2.65 x 10^7 microns³/mL in April 2020 at site A2 (Figure 27). Picoeukaryote biovolume then decreased between April 2020 and June 2020, and then increased for a second maximum of 1.48 x 10^7 microns³/mL in September 2020 again at site A2. Like picocyanobacteria, picoeukaryote biovolume decreased to almost zero after this September 2020 peak. Picoeukaryote biovolume significantly decreased moving away from the river mouth (p<0.01; data not shown).

Harmful algae

Several genera present in samples were potential harmful algal bloom formers (HABs). Dinoflagellate potential HABs included *Heterocapsa, Prorocentrum, Akashiwo, Gonyaulax, Cochlodinium, Karenia, Oxyphysis oxytoxoides* and *Dinophysis* (FMRI 2002; Steidinger and del Castillo 2018). *Dinophysis* was present during three sampling dates of this study: January 2020, February 2020 and April 2020. *Dinophysis* concentration was strongly positively correlated only with N+N (τ =0.42, p=0.04) and strongly negatively correlated Si:DIN (τ =-0.48, p=0.03; Table 4).

4. DISCUSSION

Phytoplankton are important components of the estuarine food web because of their role as primary producers (Field et al., 1998). Altered freshwater inflow has influenced phytoplankton communities in estuaries across the world (Cloern et al., 1983; Barroso et al., 2018). Freshwater inflow is projected to be further altered in the future, whether due to anthropogenic uses (e.g., agriculture and consumption), or climate change (e.g., changes in frequency or intensity of rainfall, storms and warming). Resource managers must work to understand how environmental changes, including shifts in freshwater inflow, may alter phytoplankton communities because of effects on water quality, estuarine ecology and economically important species at higher trophic levels. To elucidate the influence that freshwater inflow has on environmental conditions and phytoplankton in Matagorda Bay, I quantified relevant parameters in relation to inflow over a 24 month period. Freshwater inflow influenced the spatiotemporal patterns of nutrients, chlorophyll and biovolume. We observed the greatest mean nutrient concentrations, chlorophyll and biovolume at a site closest to the river mouth. During the study, diatoms were consistently the dominant functional group in terms of biovolume. A harmful dinoflagellate, *Dinophysis sp.*, was observed for several months, although not at bloom levels. This study exemplifies the need for more frequent and long-term monitoring to investigate conditions associated with blooms and *Dinophysis* presence.

Nutrient patterns

Freshwater inflow, distance from the river mouth, and seasonality affected the concentration and distribution of nutrients within Matagorda Bay. All nutrients measured (N+N, ammonium, orthophosphate and silicate) were highest near the river mouth and decreased in sites farther away from the mouth, a spatial pattern that indicates the river is an important source of

nutrients to the estuary. High riverine inflow is known to increase total phosphorous in Matagorda Bay (Longley et al., 1994), which is consistent with the maximum orthophosphate concentration that co-occurred with maximum riverine discharge in May 2021 in our study. Matagorda Bay historically has low dissolved inorganic nitrogen (DIN), and only the area closest to the river mouth sees a marked increase in nitrogen from river discharge (Longley et al., 1994). DIN limitation was observed for the duration of this study, and the highest DIN concentration was also found near the mouth of the river. Silicate had a significant positive relationship with discharge, indicating the Colorado River was an important source, and studies have shown rivers (either dissolved silicate or derived from dissolution of river particulate matter) are a significant source of silicate to coasts worldwide (Frings 2017). Temperature changes associated with seasonality can also affect nutrient availability in the water column. Increasing temperature has been correlated to increasing silicate solubility, which may explain the significant positive linear relationship between silicate concentration and temperature observed in this study (Varkouhi and Wells 2020). Another nutrient that can be influenced by environmental variation is ammonium, which was negatively correlated with total biovolume, diatom biovolume, dinoflagellate and picocyanobacteria biovolume in this study. This negative correlation could be due to the phytoplankton preference for ammonium as a nitrogen source, so as phytoplankton biomass increased, ammonium was depleted (Olofsson et al., 2019). Recommended future studies include tracking nutrient changes over time and how these changes correlate to biovolume changes, and identifying the source of nutrients, riverine or otherwise. This is because understanding the relationship between nutrient availability and the phytoplankton response is key to establishing the sensitivity of phytoplankton communities in Matagorda Bay to nutrient changes that may result from climate change and other human impacts.

Chlorophyll patterns

Similar to nutrients entering the estuary from the river, chlorophyll concentrations were influenced by spatiotemporal factors such as proximity to the river mouth and inflow amount. High chlorophyll has been observed in other estuaries near river mouths, and often has a negative relationship to salinity, a trend we also observed in this study (Cloern et al., 1983; Masotti et al., 2018). Higher chlorophyll concentration may be due to the higher concentration of nutrients near the river mouth, as observed in Masotti et al. (2018). We observed the highest mean chlorophyll concentration at site A1 (21.3 µg/L), and the maximum single recording of chlorophyll was also at site A1 (125.6 μ g/L). Long-term trends show a similar mean chlorophyll concentration in other estuaries in the region, such as Galveston Bay ($18.4 \pm 3.1 \,\mu g/L$; Bugica et al., 2020). Chlorophyll was negatively correlated with Secchi depth in this study, indicating that algal biomass was an important contributor to light attenuation in this system. This could have implications for bottom-dwelling organisms by shading them, perhaps decreasing benthic primary production (Dunton 1994). Because riverine inflow appears related to chlorophyll concentration in Matagorda Bay, potential future decreases could have an impact on the food web by decreasing water column primary production but perhaps increasing light availability to benthic producers (Dunton 1994).

Biovolume patterns

Although chlorophyll was higher at sites near the river mouth, there was no significant difference in total biovolume between sites. Total biovolume homogeny across the estuary may be due to zooplankton grazers acting as a top-down control on phytoplankton (Cloern and Dufford 2005; Buyukates and Roelke 2005). While there was a weak (τ <0.3) correlation between total biovolume and chlorophyll, there were several instances of a mismatch between maximums

of one and not the other. The general lack of relationship between chlorophyll maximums and biovolume maximums is not surprising, as other authors have found this as well (Felip and Catalan 2000; Lancelot and Muylaert 2011; Alvarez-Fernandez and Riegman 2014). For example, there was a chlorophyll maximum in December 2019 without a corresponding biovolume maximum, possibly due to increased chlorophyll per cell. Conversely, a November 2020 biovolume maximum did not correspond to a chlorophyll maximum. Variability in the amount of chlorophyll per cell can be due to a variety of factors including species composition, light and nutrient availability (Falkowski 1980; Langdon 1987; Geider et al., 1997). Boyer et al. (2009) observed variability of 0.1 to 9.6% chlorophyll *a* content in fresh algal mass, exemplifying that chlorophyll can vary widely within cells. This study underscores the necessity of multiple measures of phytoplankton biomass to characterize the communities more accurately in estuaries.

Across the 24 months, the highest average total biovolume occurred in November 2020 at site A1, which corresponded with a Nitzschioid diatom bloom. This bloom occurred after a period of decreased discharge, which may have increased residence time and allowed the bloom to develop in the presence of ample nutrient supply (Ketchum 1954). Conversely, a bloom of the diatom genus *Leptocylindrus* corresponded with maximum inflow in May 2021 and was located at site A6. Another study observed a *Leptocylindrus* bloom following an extreme inflow increase to a low-inflow temperate estuary (Bate and Adams 2000). The high inflow at the time of the bloom may have pushed phytoplankton farther into the estuary, and fueled production through increased nutrient availability, as shown by simultaneous increases in N+N, orthophosphate and silicate in May 2021 (Burford et al., 2011; Bruesewitz et al., 2013). Other studies have shown the location of the chlorophyll maximum moves downstream after periods of elevated inflow

(Pennock 1985; Paerl et. al., 2014). The high inflow was sufficient to affect the distribution of the bloom, but not enough to flush cells out of the estuary. In short, the blooms in this study exemplify that different taxa proliferate under different conditions, which may require resource managers to examine the factors that influence each taxon that generates high biovolume in Matagorda Bay individually.

Phytoplankton community composition

Matagorda Bay's high wind action and prevalence of river-derived nutrients allowed diatoms to dominate over other phytoplankton functional groups in this system (Longley 1994; Smayda 1997). Previous research in Matagorda Bay also observed dominance of diatoms over other functional groups (Longley et al., 1994; Roelke et al., 2013). Carrick et al. (1993) observed a two-fold increase in diatom biomass during increased wind speed in a shallow Florida lake, potentially due to resuspension of benthic diatoms and decreased light limitation (Carrick et al., 1993). A diatom bloom was also observed in the oligotrophic, subtropical Gulf of Eilat when wind speeds increased from 3 ms⁻¹ to 10 ms⁻¹ (Iluz et al., 2009). In several studies, biovolume in the estuary was dominated by diatoms when the wind speeds were between >3 and 9 ms⁻¹ (Arfi and Bouvy 1995; de Jonge and van Beusekom 1995; Fejes et al., 2005). The mean monthly wind speed for this study in Matagorda Bay was 7.4 ms⁻¹, so these constant elevated wind speeds in Matagorda Bay may explain why diatoms dominated biovolume for the entire study. This may be because diatom physiology is better adapted than other phytoplankton for utilizing nutrients during turbulent conditions (Margalef 1978). Diatom biovolume also had a positive correlation with salinity, indicating that this functional group was successful not only near the river mouth, but throughout the estuary. Upwelling favorable winds in the northwestern Gulf of Mexico promote diatom success over other functional groups, and these diatoms may be advected into

the more saline parts of the estuary, such as site A9 (Anglès et al., 2019). A ship channel between another Texas subtropical estuary (Aransas Bay) and the Gulf of Mexico sampled had a community comprised mostly of diatoms, so the Gulf of Mexico is a possible source of diatoms to Texas estuaries (Reyna et al. 2017). Also, blooms observed in another wind-driven estuary on the Texas coast (Galveston Bay) were diatom-dominated (Roelke et al. 2013). The ratio of Si:DIN remaining above 1 for the majority of the study period could have also contributed to diatom success over dinoflagellates or other functional groups (Longley et al., 1994).

Picoeukaryote biovolume was positively correlation with temperature (p<0.01). The higher temperatures in the summer corresponded with significantly greater picoeukaryotes than during other seasons (p<0.01). Stawiarski et al. (2016) found that picoplankton generally increase with increasing temperatures until they reach the optimal temperature for their species. Temperature was beginning to increase in March 2020, and this correlates with a picoeukaryote cells/mL maximum in April 2020. Temperature reached a maximum for summer 2020 in August, and picoeukaryotes again peaked in September 2020. It appears there is a month lag time between temperature increases and picoeukaryote increases in Matagorda Bay. Picoeukaryotes had a negative correlation with N+N (p=0.04), which may be due to depletion of this nutrient as picoeukaryotes may have capitalized on this maximum as they started to increase in February 2020 and reached a maximum in April 2020. In April 2020, N+N decreased to almost zero, indicating it was almost completely assimilated in picoplankton cells.

Picocyanobacteria also a positive correlation with temperature (p<0.01). Cyanobacteria cell count was positively correlated with temperature in other studies (Paerl 2014; Smucker et al., 2021). While picocyanobacteria biovolume was weakly correlated with salinity (tau<0.30),

studies have found that some cyanobacteria species grow in salinities of 0-20 (Moisdander et al., 2002), but one study found highest growth of subtropical cyanobacteria at salinities between 16 and 25 (Rai and Rajashekhar 2016), which is similar to the range of the salinities in which most cells occurred in our study (15-30). Picocyanobacteria had a negative correlation with both nitrogen forms measured (ammonium and N+N). Another study found a negative correlation between picocyanobacteria and nitrate, but a positive correlation between picocyanobacterial and ammonium (Aldunate et al., 2020). A different correlation could have resulted from less sampling dates (four) compared to the present study, which collected every month for a period of two years. More frequent sampling may have allowed a more exact dynamic between ammonium and picocyanobacteria. Because ammonium is the preferred nitrogen source, this nutrient could have been depleted as picocyanobacterial increased (Olofsson et al., 2019). As ammonium increased between June 2020 to September 2020, picocyanobacteria cells also increased to a maximum in September 2020. Ammonium decreased after this maximum until November 2020. In the winter of 2021, ammonium reached two peaks, without corresponding growth of picocyanobacteria, probably due to the colder temperatures inhibiting picocyanobacteria growth (Paerl 2014).

Dinophysis

Dinophysis was present in January, February and April 2020, corresponding with the window of temperature (~11-19°C) in which past blooms have occurred in the Gulf of Mexico (Harred and Campbell 2014). It appears nutrient input was less connected to discharge when *Dinophysis* was present, as the taxon had sufficient nutrient resources despite lower discharge, or there was a month-long lag between elevated nutrients and *Dinophysis* presence. Ammonium, N+N, and orthophosphate all increased in concentration from December 2019 to January 2020

with elevated discharge, so Dinophysis presence may have been a delayed response to these increases. Past studies have linked harmful algal blooms to increased nutrient input, and our results show *Dinophysis* biomass was positively correlated with N+N (Rebich et al., 2011). Other studies did not find a correlation between nutrients and *Dinophysis*. However, silicate limitation in January and February 2020, as indicated by Si:N<1, may explain this *Dinophysis* success over diatoms, considering dinoflagellates are not silicate limited (Flynn and Martin-Jézéquel 2000). Our study and others (Swanson et al., 2010) did not find a correlation between Dinophysis and salinity, where other studies observed a negative correlation (Godhe and Rehnstam-Holm 2002). *Dinophysis* has bloomed in the Gulf of Mexico in salinity ranging from 28 to 33, while in our study salinity was lower (20-23) during Dinophysis presence. This disparity may be why Dinophysis never reached bloom levels. Lastly, prey availability could have contributed to *Dinophysis* presence, as previous studies have linked this taxon to the ciliate prey Mesodinium (Díaz et al., 2013; Harred and Campbell 2014). Mesodinium was present yearround in Matagorda Bay, which may have supplemented the growth of Dinophysis. Dinophysis was not observed again after January 2020-April 2020 in this study. Because the ratio of Si:DIN increased ten-fold between February 2020 and April 2020, silicate limitation may have ceased and thus diatoms outcompeted *Dinophysis*, causing the decline of the dinoflagellate. The ratio of Si:DIN never fell below 1 again, and this may be why we did not observe *Dinophysis* after April 2020. These results indicate that Dinophysis may only succeed and potentially bloom when silicate is limiting in Matagorda Bay, because all other year-round conditions are more favorable for diatoms, including high wind action. If nitrogen concentrations increase in the future, this could be cause for concern for Dinophysis blooms.

Future implications

Texas' population is rapidly growing and is projected to increase by more than 70 percent from 2020-2070 (Texas Water Development Board 2017). With this growth, water demand is projected to increase by 17 percent, introducing possible effects on aquatic ecosystems (Texas Water Development Board 2017). In addition, projected climate changes could affect the amount of freshwater inflow reaching Matagorda Bay. Texas already experiences cycling between heavy precipitation periods and extreme drought periods, and both parts of this cycle are predicted to intensify with the changing climate (Montroy 1997). For one, temperatures are projected to increase, with evaporation rates exceeding precipitation rates (Seager et al., 2007; Banner et al., 2010). While quantitative projections of droughts in Texas through modeling are not available, factors indicate an increase in drought severity (Nielsen-Gammon et al., 2021). During these times, evaporation will likely further decrease freshwater inflow (Konapala et al., 2020). These decreases in freshwater inflow could result in a decrease in phytoplankton biovolume due to unfavorable changes in salinity or decreases in nutrient inputs (Wetz et al., 2011, Phlips et al., 2012). Decreased freshwater inflow may conversely increase phytoplankton biovolume closest to the river mouth, possibly due to increased residence time, as we saw a diatom bloom and *Dinophysis* presence during periods of decreased discharge in this study (Flemer and Champ 2006). Increased residence time is especially concerning for harmful dinoflagellates as extended residence times allow this slow-growing functional group time to reproduce (Murrell et al., 2002). These opposing responses from different taxa to the same environmental changes again highlights the necessity of researching bloom causes on a taxa-by-taxa basis.

While drought events and evaporation may increase in severity based on current indicators, average precipitation, as well as extreme rainfall events, are also expected to increase

(Nielson-Gammon et al., 2021). Increased precipitation in the wet portion of the Texas climate cycle could cause greater riverine inflow, potentially bringing more nutrients and increasing biovolume in the estuary. If inflow increases above a critical point, however, any gains in biovolume may be flushed out of the estuary (Peierls et al., 2012). To determine different environmental change effects on the phytoplankton in Matagorda Bay, all of these climate factors, as well as freshwater inflow and nutrients, should be measured. A long-term study would be needed to parse out the natural climate oscillations effects versus anthropogenic effects.

To better elucidate mechanistic linkages between freshwater inflow and the ecosystem, future studies could consider more frequent sampling and nutrient source identification. While more frequent sampling was not possible in this study, future studies may consider daily sampling upon detection of a potential HAB species, such as *Dinophysis*, because phytoplankton biovolume and communities can change on this shorter time scale (Cloern et al., 2014). More frequent sampling could give a clearer understanding of influential environmental factors on blooms. For example, blooms and the species *Dinophysis* was present under different freshwater inflows and nutrient concentrations. *Dinophysis* specifically was present during a period of decreased inflow, despite increasing nutrients. This indicates recycled nutrients may play a larger role than riverine nutrients. Identifying the source of nutrients would be helpful in determining how important riverine nutrients are to bloom/HAB species in Matagorda Bay.

Conclusion

This study shows the importance of freshwater inflow to the biochemical and physical changes in Matagorda Bay, Texas. Freshwater inflow influences nutrient location and availability, which in turn had an impact on where biovolume was greatest: closest to the river mouth. Chlorophyll was also highest at our sites closest to the river mouth. Chlorophyll was

affected by freshwater inflow, potentially due to higher nutrients at the river mouth. Increased freshwater inflow can also push biovolume further into the estuary from the mouth, while decreased freshwater inflow can allow for biovolume accumulation. The biovolume of the Matagorda Bay community is dominated by diatoms, likely due to high wind action associated with this system and nutrient ratios favorable against silicate limitation. Decreased freshwater inflow is projected with climate change and anthropogenic influence, which could lead to effects such as (1) biovolume concentrating near the river mouth and changing in magnitude in Matagorda Bay and (2) inducing conditions, such as silicate-limitation, associated with success of HAB-forming genera, such as *Dinophysis*, over less harmful diatom genera. Biovolume could increase during low inflow conditions due to reduced flushing times, but also decrease due to less nutrient input. These effects could alter the structure and functioning of estuarine food webs and negatively impact ecological health and economic/recreational usage of Matagorda Bay. Because every estuary has unique physicochemical conditions, resource managers should investigate estuaries on an individual basis to inform decisions and plan for the potential impacts of phytoplankton community and biovolume changes. This study was a critical starting point for determining the influence of various environmental changes, including freshwater inflow, on phytoplankton and the health of Matagorda Bay and will help resource managers understand baseline conditions as they plan for changes associated with climate change and anthropogenic water diversion.

REFERENCES

- Alvarez-Fernandez, S. and R. Riegman. 2014. Chlorophyll in North Sea coastal and offshore waters does not reflect long term trends of phytoplankton biomass. J. Sea Res. 91: 35-44. doi: 10.1016/j.seares.2014.04.005
- Aldunate, M., C. Henríquez-Castillo, Q. Ji,, J. Lueders-Dumont, M. R. Mulholland, B. B. Ward,
 P. von Dassow, and O. Ulloa. 2020. Nitrogen assimilation in picocyanobacterial
 inhabiting the oxygen-deficient waters of the eastern tropical North and South Pacific.
 Limn. and Oceanogr. 65: 437-453. doi: 10.1002/lno.11315
- Anglès, S., A. Jordi, D. W. Henrichs, and L. Campbell. 2019. Influence of coastal upwelling and river discharge on the phytoplankton community composition in the northwestern Gulf of Mexico. Prog. Oceanogr. 173: 26-36. doi: 10.1016/j.pocean.2019.02.001
- Arfi, R., M. Bouvy. 1995. Size, composition and distribution of particles related to wind induced resuspension in a shallow tropical lagoon, J. Plankt. Res. 17: 557-574, <u>https://doi.org/10.1093/plankt/17.3.557</u>
- Armstrong, N. E. 1982. Responses of Texas estuaries to freshwater inflows. In: V. S. Kennedy [ed.], Estuarine comparisons. Academic Press.
- Banner, J. L., C. S. Jackson, Z. Yang, K. Hayhoe, C. Woodhouse, L. Gulden, K. Jacobs, G.
 North, R. Leung, W. Washington, X. Jiang, and R. Casteel. 2010. Climate Change
 Impacts on Texas Water: A White Paper Assessment of the Past, Present and Future and
 Recommendations for Action. Texas Water Journal 1: 1-19. doi: 10.21423/twj.v1i1.1043
- Barbosa, A. B., R. B. Domingues, H. M. Galvão. 2010. Environmental Forcing of Phytoplankton in a Mediterranean Estuary (Guadiana Estuary, South-western Iberia): A Decadal Study

of Anthropogenic and Climatic Influences. Estuar. Coasts. 33:324-341. doi: 10.1007/s12237-009-9200-x

- Barroso, H. dS., T. C. L. Tavares, M. dO. Soares, T. M. Garcia, B. Rozendo, A. S. C. Vieira, P.
 B. Viana, T. M. Pontes, T. J. T. Ferreira, J. P. Filho, C. A. F. Schettini, S. T. Santaella.
 2018. Intra-annual variability of phytoplankton biomass and nutrients in a tropical estuary during a severe drought. Estuar. Coast. Shelf Sci. 213: 283-293. doi: 10.1016/j.ecss.2018.08.023
- Bate, G., and J. Adams. 2000. The effects of a single freshwater release into Kromme Estuary. Water S. A. 26: 329-332.
- Boyer, J.N., Kelble, C.R., Ortner, P.B., Rudnick, D.T., 2009. Phytoplankton bloom status:
 Chlorophyll a biomass as an indicator of water quality condition in the southern estuaries of Florida, USA. Ecol. Indic. 9S, S56–S67. doi: 10.1016/j.ecolind.2008.11.013
- Boynton, W. R., and W. M. Kemp. 2000. Influence of river flow and nutrient loads on selected ecosystem processes—A synthesis of Chesapeake Bay data. In: Hobbie, J.E. (Ed.),
 Estuarine Science—A Synthetic Approach to Research and Practice. Island Press,
 Washington, DC, 269–298. Print.
- Bruesewitz, D. A., W. S. Gardner, R. F. Mooney, L. Pollard, and E.J. Buskey. 2013. Estuarine ecosystem function response to flood and drought in a shallow, semiarid estuary: Nitrogen cycling and ecosystem metabolism. Limn. and Oceanogr. 58: 2293–2309.
 Stable URL: https://www.jstor.org/stable/26955828
- Bugica, K., B. Sterba-Boatwrite, M. S. Wetz. Water quality trends in Texas estuaries. 2020. Mar. Pollut. Bull. 152: 1-8. doi: 10.1016/j.marpolbul.2020.110903

- Burford M. A., A. T. Revill, D. W. Palmer, L. Clementson, B. J. Robson, and I. T. Webster.
 2011. River regulation alters drivers of primary productivity along a tropical river-estuary system. Mar. Freshw. Res. 62: 141-151. doi: 10.1071/MF10224
- Buyukates, Y. and D. Roelke. 2005. Influence of pulsed inflows and nutrient loading on zooplankton and phytoplankton community structure and biomass in microcosm experiments using estuarine assemblages. Hydrobiologica 548: 233-249. doi: 10.1007/s10750-005-5195-x.
- Campbell, L., R. J. Olsen, A. Abraham, D. W. Henrichs, C. J. Hyatt, and E. J. Buskey. 2010. First harmful *Dinophysis* (dinophyceae, dinophysiales) bloom in the U.S. is revealed by automated imaging flow cytometry. J. Phycol. 46: 66-75. doi: 10.1111/j.1529-8817.2009.00791.x
- Carrick, H. J., F. J. Aldridge, and C. L. Schelske. 1993. Wind influences phytoplankton biomass and composition in a shallow, productive lake. Limn. And Oceanogr. 38: 1179-1192. doi: 10.4319/lo.1993.38.6.1179
- Cloern, J. E., A. E. Alpine, B. E. Cole, R. L. J. Wong, J. F. Arthur, and M. D. Ball. 1983. River discharge controls phytoplankton dynamics in the Northern San Francisco Bay Estuary. Estuar. Coast. Shelf Sci. 16: 415–429. doi: 10.1016/0272-7714(83)90103-8
- Cloern, J. E., and R. Dufford. 2005. Phytoplankton community ecology: Principles applied in San Francisco Bay. Mar. Ecol. Prog. Ser. 285: 11–25. doi: 10.3354/meps285011
- Cloern. J. E., S. Q. Foster, and A. E. Kleckner. 2014. Phytoplankton primary production in the world's estuarine-coastal ecosystems. BG. 11: 2477-2501. doi: 10.5194/bg-11-2477-2014
- Cloern, J. E. 2017. Why large cells dominate estuarine phytoplankton. Limnol. Oceanogr. 62: S272-S291. doi:10.1002/lno.10749
- Díaz, P. A., B. Reguera, M. Ruiz-Villarreal, Y. Pazos, L. Velo-Suárez, H. Berger, and M. Sourisseau 2013. Climate variability and oceanographic settings associated with interannual variability in the initiation of Dinophysis acuminata blooms. Mar. Drugs. 11: 2964–2981.
- Dunton, K. 1994. Seasonal growth of the subtropical seagrass *Halodule wrightii* in relation to continuous measurements of underwater irradience. Mar. Bio. 120: 479-489. doi: 10.1007/BF00680223
- Falkowski, P. G. 1980. Light-Shade Adaptation in Marine Phytoplankton. Plant Physio. 66: 592-595. https://doi.org/10.1007/978-1-4684-3890-1_6
- Fejes, E., D. Roelke, G. Gable, J. Hellman, K. McInnes, and D. Zuberer. 2005. Microalgal productivity, community composition, and pelagic food web dynamics in a subtropical, turbid salt marsh isolated from freshwater inflow. Estuaries. 28: 96–107. doi: 10.1007/BF02732757
- Felip, M. and J. Catalan. 2000. The relationship between phytoplankton biovolume and chlorophyll in a deep oligotrophic lake: decoupling in their spatial and temporal maxima.J. Plankt. Res. 22: 91-106. doi: 10.1093/plankt/22.1.91
- Field C. B., M. J. Behrenfeld , J. T. Randerson, P. Falkowski. Primary production of the biosphere: integrating terrestrial and oceanic components. 1998. Science 281:237-40. doi: 10.1126/science.281.5374.237
- Flemer, D. A., and M. A. Champ. 2006. What is the future fate of estuaries given nutrient overenrichment, freshwater diversion and low flows? Mar. Pollut. Bull. 52: 247-258. doi: 10.1016/j.marpolbul.2005.11.027

- Flynn, K. J. and V. Martin-Jézéquel. 2000. Modelling Si–N-limited growth of diatoms. J. Plankt. Res. 22: 447-472. doi: 10.1093/plankt/22.3.447
- FMRI. 2002. Florida Marine Research Institute, HAB Species sub- category of the harmful algal blooms and red tides. Available at www.floridamarine.org/redtide.
- Fournier, R. O. and R W. Potter II.1982. Revised and expanded silica (quartz) geothermometer. Bull., Geotherm. Resour. Counc. 11: 3-12.
- Frings, P., 2017. Revisiting the dissolution of biogenic Si in marine sediments: a key term in the ocean Si budget. Acta Geochim. 36: 429-432. doi: 10.1007/s11631-017-0183-1
- Fujita, C. C. and C. Odebrecht. 2007. Short term variability of chlorophyll *a* and phytoplankton composition in a shallow area of the Patos Lagoon estuary (Southern Brazil). Atlântica. 29: 93-106.
- Iluz, D., G. Dishon, E. Capuzzo, E. Meeder, R. Astoreca, V. Montecino, P. Znachor, D. Ediger, and J. Marra. 2009. Short-term variability in primary productivity during a wind-driven diatom bloom in the Gulf of Eilat (Aqaba). Aquat. Microb. Ecol. 56: 205-215.
- Gameiro, C., J. Zwolinski, and V. Brotas. 2011. Light control on phytoplankton production in a shallow and turbid estuarine system. Hydrobiologia. 669: 249-263. doi: 10.1007/s10750-011-0695-3
- Geider, R. J., H. L. MacIntyre, and T. M. Kana. 1997. Dynamic model of phytoplankton growth and acclimation: responses of the balanced growth rate and the chlorophyll a: carbon ratio to light, nutrient-limitation and temperature. Mar. Ecol. Prog. Ser. 148: 187-200. doi: 10.3354/meps148187
- Georgakakos, A., P. Fleming, M. Dettinger, C. Peters-Lidard, T. C. Richmond, K. Reckhow, K. White, and D. Yates. 2014. Water Resources. Climate Change Impacts in the United

States: The Third National Climate Assessment, J. M. Melillo, T. C. Richmond, and G. W. Yohe, Eds. USGCRP. 69-112. doi:10.7930/ J0G44N6T

- Gillanders, B. M., and M. Kingsford. 2002. Impact of Changes in Flow of Freshwater on Estuarine and Open Coastal Habitats and the Associated Organisms. Oceanogr. and Mar. Bio. 40: 233-309. doi: 10.1201/9780203180594.ch5
- Glibert, P. M., F. P. Wilkerson, R. C. Dugdale, J. A. Raven, C. L. Dupont. P. R. Leavitt, A. E. Parker, J. M. Burkholder, T. M. Kana. 2015. Pluses and minuses of ammonium and nitrate uptake and assimilation by phytoplankton and implications for productivity and community composition, with emphasis on nitrogen-enriched conditions. Limn. And Oceanog. 61: 165-197. doi: 10.1002/lno.10203
- Godhe, A., and A. Rehnstam-Holm. 2002. Oceanographic settings explain fluctuations in
 Dinophysis spp. and concentrations of diarrhetic shellfish toxin in the plankton
 community within a mussel farm area on the Swedish west coast. Mar. Ecol. Progr. Ser.
 240: 71-83. 10.3354/meps240071.
- Gomes, H. R., J. I. Goes, and T. Saino. 2000. Influence of physical processes and freshwater discharge on the seasonality of phytoplankton regime in the Bay of Bengal. Cont. Shelf Res. 20: 313-330. doi: 10.1016/S0278-4343(99)00072-2
- Hallegraeff, G. 1993. A Review of Harmful Algal Blooms and Their Apparent Global Increase. Phycologia 32: 79-99. doi:10.2216/i0031-8884-32-2-79.1
- Harred, L. B., and L. Campbell. 2014. Predicting harmful algal blooms: a case study with Dinophysis ovum in the Gulf of Mexico. J. Plankt. Res. 36: 1434-1445. doi:10.1093/plankt/fbu070

- Hillebrand, H., C.-D. Durselen, D. Kirschtel, U. Pollingher, and T. Zohary. 1999. Biovolume calculation for pelagic and benthic macroalgae. J. Phycol. 35: 403–424. doi: 10.1046/j.1529-8817.1999.3520403.x
- Hutchings, L. G.C. Pitcher, and T.A. Probyn. G.W. Bailey, C.P. Summerhayes, K.C. Emeis,
 M.V. Angel, R.L. Smith, B. Zeitschel (Eds.). 1995. The chemical and biological consequences of coastal upwelling. In: Upwelling in the Oceans; Modern Processes and Ancient Records. John Wiley and Sons, New York. 65-81.
- de Jonge, V. N., and J. E. E. van Beusekom. 1995. Wind- and tide-induced resuspension of sediment and microphytobenthos from tidal flats in the Ems estuary. Limnol. Oceanogr. 40: 766-778. doi: 10.4319/lo.1995.40.4.0776
- Keller, A.A., C.A. Oviatt, H.A. Walker, and J.D. Hawk. 1999. Predicted impacts of elevated temperature on the magnitude of the winter-spring phytoplankton bloom in temperate coastal waters: A mesocosm study. Limn. and Oceanogr. 44: 344–356. doi: 10.4319/lo.1999.44.2.0344
- Ketchum, B. H. 1954. Relation Between Circulation and Planktonic Populations in Estuaries. Ecology 35: 191-200. Stable URL: http://www.jstor.org/stable/1931117
- Kim, H., and P. A. Montagna. 2009. Implications of Colorado river (Texas, USA) freshwater inflow to benthic ecosystem dynamics: A modeling study. Estuar. Coast. Shelf Sci. 83: 491-504. doi:10.1016/j.ecss.2009.04.033
- Kim, H., S. Son, P. Montagna, B. Spiering, and J. Nam. 2014. Linkage between Freshwater Inflow and Primary Productivity in Texas Estuaries: Downscaling Effects of Climate Variability. J. Coast. Res. 68: 65-73. doi: 10.2112/SI68-009.1

- Konapala, G., A. K. Mishra, Y. Wada and M. E. Mann. 2020. Climate change will affect global water availability through compounding changes in seasonal precipitation and evaporation. Nat. Commun. 11: 1-10. doi: 10.1038/s41467-020-16757-w
- Lancelot, C., and K. Muylaert. 2011. Trends in Estuarine Phytoplankton Ecology. Estuar. Coast. Shelf Sci. 7: 5-15. doi: 10.1016/B978-0-12-374711-2.00703-8
- Langdon, C. 1987. On the causes of interspecific differences in the growth-irradiance relationship for phytoplankton. Part I. A comparative study of the growth-irradiance relationship of three marine phytoplankton species: *Skeletonema costatum, Olisthodiscus luteus* and *Gonyaulax tamarensis*. J. Plankt. Res. 9: 459-482. doi: 10.1093/plankt/9.3.459
- Lomas, M. W., and P. M. Glibert. 1999. Interactions between NH₄⁺ and NO₃⁻ uptake and assimilation: comparison of diatoms and dinoflagellates at several growth temperatures. Mar. Bio. 133: 541-551. doi: 10.1007/s002270050494
- Longley, W. L. 1994. Freshwater Inflows to Texas Bays and Estuaries: Ecological Relationships and Methods for Determination of Needs. Texas Water Development Board and Texas Parks and Wildlife Department.
- Maguire, T. J., and R. W. Fulweiler. 2017. Fate and effect of dissolved silicon within wastewater treatment effluent. Environ. Sci. Technol. 51: 7403-7411. doi: 10.1021/acs.est.7b01276
- Marañón, E., P. Cermeño, M. Latasa, and R. D. Tadonléké. 2012. Temperature, resources, and phytoplankton size structure in the ocean. Limnol. Oceanogr. 57: 1266-1278. doi: 10.4319/lo.2012.57.5.1266
- Margalef, R. 1978. Life-forms of phytoplankton as survival alternatives in an unstable environment. Oceanologica Acta. 1: 493-509.

- Masotti, I., P. Aparicio-Rizzo, M. A. Yevenes, R. Garreaud, L. Belmar, L. Farías. 2018. The Influence of River Discharge on Nutrient Export and Phytoplankton Biomass Off the Central Chile Coast (33°–37°S): Seasonal Cycle and Interannual Variability. Front. Mar. Sci. 5: 1-12. doi: 10.3389/fmars.2018.00423
- Matos, J.B., Sodré, D.K.L., Da Costa, K.G., Pereira, L.C.C., Da Costa, R.M., 2011. Spatial and temporal variation in the composition and biomass of phytoplankton in an Amazonian estuary. J. Coast. Res. 1525–1529, http://www.jstor.org/stable/26482430.
- McManus, G. B. and L. A. Katz. 2009. Molecular and morphological methods for identifying plankton: what makes a successful marriage? J. Plankt. Res. 31: 1119-1129. doi: 10.1093/plankt/fbp061
- Moisander, P. H., E. McClinton 3rd, H. W. Paerl. 2002. Salinity effects on growth,
 photosynthetic parameters, and nitrogenase activity in estuarine planktonic cyanobacteria.
 Microb. Ecol. 43: 432-442. doi: 10.1007/s00248-001-1044-2
- Montroy, D. L. 1997. Linear Relation of Central and Eastern North American Precipitation to Tropical Pacific Sea Surface Temperature Anomalies. J. Clim. 10: 541-558. doi: 10.1175/1520-0442(1997)010<0541:LROCAE>2.0.CO;2
- Moon, C., and W. M. Dunstan. 1990. Hydrodynamic trapping in the formation of the chlorophyll *a* peak in turbid, very low salinity waters of estuaries. J. Plankt. Res. 12: 323-336. doi: 10.1093/plankt/12.2.323
- Montagna, P. A., M. Alber, P. Doering, and M. S. Connor. 2002. Freshwater inflow: Science, policy, management. Estuaries 25: 1243–1245. doi: 10.1007/BF02692221

- Murrell, M. C., R. S. Stanley, E. M. Lores, G. T. DiDonato, and D. A. Flemer. 2002. Linkage between microzooplankton grazing and phytoplankton growth in a Gulf of Mexico estuary. Estuaries 25: 19–29. doi:10.1007/BF02696046
- Natarjan, K. V. 1970. Toxicity of Ammonia to Marine Diatoms. J. Water Pollution Control Federation. 42: R184-R190. Stable URL: https://www.jstor.org/stable/25036590
- Nielsen-Gammon, J., J. Escobedo, C. Ott, J. Dedrick, and A. Van Fleet. 2021. Assessment of Historic and Future Trends of Extreme Weather in Texas, 1900-2036. Texas A&M University, Office of the Texas State Climatologist.
- Odebrecht, C., P. C. Abreu, and J. Carstensen. 2015. Retention time generates short-term phytoplankton blooms in a shallow microtidal subtropical estuary. Estuar. Coast.Shelf Sci. 162: 35-44. doi: 10.1016/j.ecss.2015.03.004
- Olofsson, M., E. K. Robertson, L. Edler, L. Arneborg, M. J. Whitehouse, H. Ploug. 2019. Nitrate and ammonium fluxes to diatoms and dinoflagellates at a single cell level in mixed field communities in the sea. Sci. Rep. 9: 1-12. doi: 10.1038/s41598-018-38059-4
- Paerl, H. 1985. Enhancement of marine primary production by nitrogen-enriched acid rain. Nature. 315, 747–749. doi:10.1038/315747a0
- Paerl, H. W., N. S. Hall, B. L. Peierls and K. L. Rossignol. 2014. Evolving Paradigms and Challenges in Estuarine and Coastal Eutrophication Dynamics in a Culturally and Climatically Stressed World. Estuar. Coasts. 37: 243-258. doi: 10.1007/s12237-014-9773-x
- Palmer, T. A., P. A. Montagna, J. Beseres Pollack, R. D. Kalke, H. R. DeYoe. 2011. The role of freshwater inflow in lagoons, rivers, and bays. Hydrobiologia. 667: 49-67. doi: 10.1007/s10750-011-0637-0

- Pednekar, S. M., S. S. Bates, V. Kerkar, and S. G. Prabhu Matondkar. 2018. Environmental Factors Affecting the Distribution of *Pseudo-nitzschia* in Two Monsoonal Estuaries of Western India and Effects of Salinity on Growth and Domoic Acid Production by *P. pungens*. Estuar. Coasts 41: 1448-1462. doi: 10.1007/s12237-018-0366-y
- Peierls, B. L., N. S. Hall, and H. W. Paerl. 2012. Non-monotonic responses of phytoplankton biomass accumulation to hydrologic variability: A comparison of two coastal plain North Carolina estuaries. Estuar. Coasts. 35: 1376–1392. doi:10.1007/s12237-012-9547-2
- Pennock, J. R. 1985. Chlorophyll Distributions in the Delaware Estuary: Regulation by Lightlimitation. Estuar. Coast. Shelf Sci. 21: 711-725. doi: 10.1016/0272-7714(85)90068-X
- Phlips, E. J., S. Badylak, J. Hart, D. Haunert, J. Lockwood, K. O'Donnell, D. Sun, P. Viveros and M. Yilmaz. Climatic Influences on Autochthonous and Allochthonous Phytoplankton Blooms in a Subtropical Estuary, St. Lucie Estuary, Florida, USA. Estuar. Coasts. 35: 335-352. doi: 10.1007/s12237-011-9442-2
- Rai, S. V., and M. Rajashekhar. 2016. Effect of pH, salinity and temperature on the growth of six species of cyanobacteria isolated from Arabian sea coast of Karnataka. International Journal of Biosciences and Technology. 9: 1-6.
- Rebich, R. A., N. A. Houston, S. V. Mize, D. K. Pearson, P. B. Ging, and C. E. Hornig. 2011. Sources and delivery of nutrients to the Northwestern Gulf of Mexico from streams in the South-Central United States. Am. J. Water Resour. Assoc. 47: 1061–1086. doi:10.1111/j.1752-1688.2011.00583.x
- Redfield, A.C. 1934 On the Proportions of Organic Derivatives in Sea Water and Their Relation to the Composition of Plankton. James Johnstone Memorial Volume, University Press of Liverpool, 176-192.

- Reyna, N. E., A. K. Hardison, Z. Liu. 2017. Influence of Major Storm Events on the Quantity and Composition of Particulate Organic Matter and the Phytoplankton Community in a Subtropical Estuary, Texas. Front. Mar. Sci. 4: 1-14. doi: 10.3389/fmars.2017.00043
- Roelke, D. L., H. Li, N. J. Hayden, C. J. Miller, S. E. Davids, A. Quigg and Y. Buyukates. 2013.
 Co-occurring and opposing freshwater inflow effects on phytoplankton biomass,
 productivity and community composition of Galveston Bay, USA. Mar. Ecol. Prog. Ser.
 477: 61-76. doi: 10.3354/meps10182
- Roelke, D. L., H. Li, C. J. Miller-DeBoer, G. M. Gable, and S E. Davis. 2017. Regional shifts in phytoplankton succession and primary productivity in the San Antonio Bay System (USA) in response to diminished freshwater inflows. Mar. Freshw. Res. 68: 131-145. doi: 10.1071/MF15223
- Seager R., M. Ting, I. Held, Y. Kushnir, J. Lu, G. Vecchi, H-P. Huang, N. Harnik, A. Leetsmaa, N-C. Lau, et al. 2007. Model projections of an imminent transition to a more arid climate in southwestern North America. Sci. 316:1181-1184.
- Schroeder, W. W., S. P. Dinnel, W. J. Wiseman Jr. 1990. Salinity stratification in a riverdominated estuary. Estuaries. 13: 145-154. doi: 10.2307/1351583
- Shannon, C. E. 1948. A Mathematical Theory of Communication. The Bell System Technical 27: 379-423, 623-656. doi: 10.1002/j.1538-7305.1948.tb01338.x
- Sierra, J. P., A. Sánchez-Arcilla, J. G. Del Río, J. Flos, E. Movellán, C. Mösso, R. Martínez, M. Rodilla, S. Falco, and I. Romero. 2002. Spatial distribution of nutrients in the Ebro estuary and plume. Cont. Shelf Res. 22: 361-378. doi: 10.1016/S0278-4343(01)00061-9

Simpson, E.H. (1949) Measurement of diversity. Nature, 163: 668. doi:10.1038/163688a0.

- Sin, Y., R. L. Wetzel, and I. C. Anderson. 1999. Spatial and temporal characteristics of nutrient and phytoplankton dynamics in the York River Estuary, Virginia: Analyses of long-term data. Estuaries 22: 260–275. doi: 10.2307/1352982
- Smayda, T. J. 1997, a. What is a Bloom? A Commentary. Limn. And Oceanogr. 42: 1132-1136. Stable url: https://www.jstor.org/stable/2839006
- Smayda, T. J. 1997, b. Harmful algal blooms: their ecophysiology and general relevance to phytoplankton blooms in the sea. Limn. and Oceanogr. 42: 1137-1153. doi: 10.4319/lo.1997.42.5_part_2.1137
- Smith, E. L. 1938. Limiting factors in photosynthesis: light and carbon dioxide. J. Gen. Physiol.22: 21-35. doi: 10.1085/jgp.22.1.21
- Smucker, N. J., J. J. Beaulieu, C. T. Nietch, and J. L. Young. 2021. Increasingly severe cyanobacterial blooms and deep water hypoxia coincide with warming water temperatures in reservoirs. Glob Chang Biol. 11 :2507-2519. doi: 10.1111/gcb.15618
- Stawiarski, B., E. T. Buitenhuis, and C. Le Quéré. 2016. The Physiological Response of Picophytoplankton to Temperature and Its Model Representation. Front. Mar. Sci. 3. doi: 10.3389/fmars.2016.00164
- Steidinger, K. and M. del Castillo. 2018. Guide to the Identification of Marine Harmful Microalgae in the Gulf of Mexico. Florida Institute of Oceanography and Florida Fish and Wildlife Conservation Commission.
- Sun, J., and D. Liu. 2003. Geometric models for calculating cell biovolume and surface area for phytoplankton. J. Plankt. Res. 25: 1331–1346. doi:10.1093/plankt/fbg096

- Swanson, K. M., L. J. Flewelling, M. Byrd, A. Nunez, T. A. Villareal. 2010. The 2008 Texas *Dinophysis ovum* bloom: Distribution and toxicity. Harmful algae 9: 190-199. doi:10.1016/j.hal.2009.10.001
- Texas Water Development Board. 2017. Chapter 5: Future population and water demand. Water for Texas.
- Varkouhi, S. and J. Wells. 2020. The relation between temperature and silica benthic exchange rates and implications for near-seabed formation of diagenetic opal. Results in Geophysical Sciences. 1: 1-14. doi: 10.1016/j.ringps.2020.100002
- Ward., G and Armstrong, N.E. 1980. Matagorda Bay, Texas: its hydrography, ecology, and fishery resources. No. FWS/OBS-81/52. Washington, D.C.: Fish and Wildlife Service, U.S. Department of the Interior.
- Welschmeyer, N. A. 1994. Fluorometric analysis of chlorophyll a in the presence of chlorophyll b and pheopigments. Limn. and Oceanogr. 39: 1985-1992. doi:10.4319/lo.1994.39.8.1985
- Wetz, M. S., E. A. Hutchinson, R. S. Lunetta, H. W. Paerl, and J. C. Taylor. 2011. Severe droughts reduce estuarine primary productivity with cascading effects on higher trophic levels. Limnol. Oceanogr. 56: 627-638. doi:10.4319/lo.2011.56.2.0627

FIGURES



Figure 1. Map of sample sites in Matagorda Bay.



Figure 2. Average weekly discharge from Colorado River up to sampling dates.



Figure 3. Mean salinity from November 2019-October 2021 (shade is 95% confidence interval).



Figure 4. Salinity gradient from river mouth.



Figure 5. Mean temperature from November 2019-October 2021 (shade is 95% confidence interval).



Figure 6. Mean Secchi depth from November 2019-October 2021 (shade is 95% confidence interval).



Figure 7. Secchi depth gradient from river mouth.



Figure 8. Mean N+N from November 2019-October 2021 (shade is 95% confidence interval).



Figure 9. N+N gradient moving away from river mouth.



Figure 10. Mean N+N versus mean temperature for all dates.



Figure 11. Mean ammonium from November 2019-October 2021 (shade is 95% confidence interval).



Figure 12. Ammonium gradient moving away from river mouth.



Figure 13. Mean orthophosphate from November 2019-October 2021 (shade is 95% confidence interval).



Figure 14. Orthophosphate gradient across sites moving away from river mouth.



Figure 15. Mean orthophosphate versus discharge for all dates.



Figure 16. Mean DIN:DIP ratio from November 2019-October 2021 (shade is 95% confidence interval).



Figure 17. Mean silicate from November 2019-October 2021 (shade is 95% confidence interval).



Figure 18. Silicate gradient across sites moving away from river mouth.



Figure 19. Mean silicate versus discharge for all dates.



Figure 20. Mean silicate versus mean temperature for all sites and dates.





Figure 21. PCA by season.



Site ▲ A1 ▼ A2 ■ A4 ◆ A6 ● A9 + MAD

Figure 22. PCA by site.



Figure 23. Mean chlorophyll (a) concentration from November 2019-October 2021 (shade is 95% confidence interval).



Figure 24. Chlorophyll gradient moving away from river mouth.



Figure 25. Total biovolume over time.


Figure 26. Site A1 functional group biovolume over time.



Figure 27. A2 functional group biovolume over time.



Figure 28. A4 functional group biovolume over time.



Figure 29. A6 functional group biovolume over time.



Figure 30. A9 functional group biovolume over time.



Figure 31. MAD functional group biovolume over time.

Table 1. Kruskall-Wallis test for environmental factors and each site (adjusted p-values for multiple comparisons with Dunn Test). Shared letters/colors signify no significant difference between two sites.

Site	I	41	Μ	AD	A	12		A	4	А	.6	A	9
Chlorophyll (mg/L)	a		a		a		a			a	b	b	
N+N (µM)	a		a		a	b	b			b		b	
Orthophosphate (µM)	a		a	d	b	d	b		С	b	с	с	
Salinity	a		а	b	a	b	b		с	с	d	d	
Ammonium (µM)	a		а		a		a			a		a	
Silicate (µM)	а		а		a	b	a	b	С	b	С	c	
DIN:DIP (µM)	а	b	а	b	a	b	b			a	b	а	
DIN:Si (µM)	a		а		a		а			a		a	
Secchi depth (m)	a		a		a	b	b		С	b	С	с	
Total biovolume (microns/mL)	a		a		a		а			a		a	
Diatom biovolume (microns/mL)	а		a		a		а			a		a	
Euglenoid biovolume (microns/mL)	a		a		a		а			a		a	
Dinoflagellate biovolume (microns/mL	a		a	b	a	b	b			a	b	a	b

Site	A1		MAD		A2	A4		A6		A9	
Cryptophyte biovolume (microns/mL)	a		a		a	a		a		a	
Picocyanobacteria (cells/mL)	a		a		а	a		a		a	
Picoeukaryotes (cells/mL)	a	b	b	С	a	a	С	a	С	b	

Table 1. continued

Table 2. Kendall's tau correlation results between chlorophyll and environmental variables, as well as biovolume for all sites. Highlighted variables indicate significant correlations (α =0.05).

	Chlorophyll					
	p-value	tau				
Salinity	< 0.01	-0.40				
Ammonium (µM)	0.27	-0.08				
N+N (μ M)	0.73	-0.02				
$PO_4(\mu M)$	0.02	0.17				
Silicate (µM)	0.05	0.14				
DO (µM)	0.81	-0.01				
Temperature (°C)	<0.01	0.22				
Discharge (m/s)	0.08	0.11				
Secchi depth (m)	< 0.01	-0.34				
Total biovolume (microns ³ /mL)	<0.01	0.23				

	Crypt	ophyte	Eugl	enoid	Diatom		Dinoflagellat e		Picocyanobac- teria		picoeukaryote s		Total biovolume	
	tau	p- value	tau	p- value	tau	p- value	tau	p- value	tau	p- value	tau	p- value	tau	p- value
Salinity	-0.26	<0.00 1	-0.04	0.61	0.13	0.05	0.20	0.004	0.14	0.04	< 0.01	0.89	0.08	0.25
Ammoniu m	0.13	0.06	0.09	0.17	-0.28	<0.0 1	- 0.20	0.004	-0.22	< 0.01	0.13	0.06	-0.27	<0.01
N+N	0.02	0.78	0.02	0.73	-0.06	0.38	- 0.18	0.009	-0.21	< 0.01	-0.14	0.04	-0.07	0.31
PO ₄	-0.05	0.47	-0.05	0.47	0.05	0.42	- 0.05	0.44	0.02	0.75	0.10	0.14	0.11	0.10
Silicate	-0.13	0.06	-0.05	0.48	0.02	0.77	- 0.04	0.57	< 0.01	0.97	0.11	0.12	0.03	0.64
Temp	-0.42	<0.00 1	-0.11	0.09	0.09	0.17	0.15	0.03	027	< 0.01	0.33	< 0.01	0.15	0.03
Discharge	0.25	<0.00 1	0.06	0.41	-0.01	0.94	- 0.01	0.89	0.09	0.22	0.04	0.59	0.03	0.63
Secchi depth	0.06	0.42	0.07	0.37	0.12	0.11	0.09	0.20	0.09	0.20	-0.12	0.11	0.05	0.47

Table 3. Kendall's tau correlation results between phytoplankton total and functional group biovolume and environmental variables. Highlighted variables indicate significant correlations (α =0.05).

Table 4. Kendall's tau correlation results between HAB biomass/*Dinophysis* and environmental variables. Highlighted variables indicate significant correlations (α =0.05).

	Dinop	ohysis
	tau	p-value
Salinity	0.20	0.33
Ammonium (µM)	0.05	0.82
N+N (μM)	0.42	0.04
PO4 (µM)	0.02	0.94
Silicate	0.39	0.06
DIN:DIP	0.20	0.33
Si:DIN	-0.48	0.03
Temperature	-0.23	0.12
Discharge	0.32	0.12