

PHYTOPLANKTON DYNAMICS IN A EUTROPHYING SOUTH TEXAS ESTUARY

A Dissertation

by

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

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## ABSTRACT

Low freshwater inflow estuaries are common worldwide, yet data is lacking on phytoplankton dynamics in these systems. This dissertation advances our understanding of phytoplankton dynamics in low-inflow estuaries through analysis of field data collected at multiple temporal scales throughout Baffin Bay, Texas, an estuary that is frequently hypersaline and that has been experiencing symptoms of eutrophication. These symptoms include long-term increases in nutrients and chlorophyll as well as recurring blooms of the “brown tide” phytoplankton, *Aureoumbra lagunensis*.

Variability in phytoplankton biomass and community composition were related to climatic/hydrologic shifts associated with El Niño-Southern Oscillation. During drought conditions, high chlorophyll concentrations were observed ( $25.7 \pm 11.7 \mu\text{g L}^{-1}$ ) and the phytoplankton community consisted of a near monoculture of *A. lagunensis* (87% of phytoplankton biovolume). These results point to the importance of regenerated nutrients in supporting phytoplankton growth during this time. When El Niño conditions developed, high rainfall took place and corresponded with increased dissolved inorganic nitrogen concentrations (ammonium, nitrate + nitrite) in the bay, but chlorophyll concentrations were lower during this time ( $16.2 \pm 14.3 \mu\text{g L}^{-1}$ ). This suggests that the potential stimulatory effects of nutrient pulses were counter balanced by decreased residence times associated with increased inflow.

This study also identified sub-monthly variability as a dominant timescale of chlorophyll variability in Baffin Bay. Wind speed was found to be an important factor related to short-term (timescales of days) bloom events, often positively correlating with chlorophyll concentrations.

Results additionally demonstrate that traditional monitoring frequencies are often are not adequate to capture short-term process and bloom events.

Lastly, this study quantified the distribution of, and potential controls upon, *A. lagunensis* in Baffin Bay. Persistently high abundances of *A. lagunensis* were observed in Laguna Salada, indicating that this tertiary bay may serve as a reservoir for *A. lagunensis* in the system. High abundances of *A. lagunensis* ( $> 1 \times 10^6$  cells mL<sup>-1</sup>) were found at salinities as low as 20, indicating that hypersalinity is not a prerequisite for *A. lagunensis* blooms. Instead, results suggest a variety of physical, chemical and biological factors (top-down controls, nutrient concentrations and forms, salinity) drive *A. lagunensis* population dynamics in the bay.

This research improves our ecological understanding of low-inflow estuaries, specifically pertaining to the ecology of phytoplankton in them. Results also suggest that as climate pressures increase, causing systems like Baffin Bay to become warmer and drier, they will be more conducive for harmful taxa such as *A. lagunensis*. The finding that Laguna Salada may be a reservoir for *A. lagunensis* presents an opportunity for targeted bloom mitigation efforts.

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## CHAPTER I: INTRODUCTION

Estuarine phytoplankton dynamics are complex, due largely to the interactive effects of physical drivers such as freshwater inflow variability, tides and winds (Paerl et al., 2006; Cloern et al., 2014; Dijkstra et al., 2019). These drivers leave a major imprint on the spatial-temporal distribution of phytoplankton biomass and on community composition. Furthermore, their relative influence varies between estuaries, leading to dominant timescales of phytoplankton biomass variability that range from hourly (tidal cycles) to seasonal (temperature and freshwater inflow), and even decadal (climate oscillations that also affect temperature and freshwater inflow; Abreu et al., 2010; Cloern and Jassby, 2010; Winder and Cloern, 2010).

While our understanding of phytoplankton dynamics in “classical,” or river-dominated estuaries has increased greatly over the past three decades (e.g., Cloern, 1996; Pinckney et al., 1999; Smayda and Borkman, 2008; Rothenberger et al., 2009), data is lacking on phytoplankton dynamics in low-inflow estuaries. Low-inflow estuaries are systems that experience minimal freshwater inflows for prolonged periods (Largier, 2010) and thus, from an ecological standpoint, are likely distinct from river-dominated estuaries that have a constant freshwater source. For example, hypersalinity occasionally occurs in low-inflow estuaries due to a lack of freshwater source (Largier, 2010). This salinity stress may select for hypersalinity-tolerant phytoplankton taxa and may negatively affect grazers, leading to distinct phytoplankton communities in low-inflow systems (Buskey et al., 1998; Schapira et al., 2010; Hemraj et al., 2017). Because of the long residence times of many low-inflow estuaries, nutrients can be expected to cycle many times before exiting the system (Dixon et al., 2014). A lack of flushing along with ample regenerated nutrient stocks has been shown to lead to extended periods of elevated phytoplankton biomass in these systems (Hemraj et al., 2017; Barroso et al., 2018).

Further, the long residence times, ample supplies of regenerated nutrients, as well as organic nutrients in some systems create conditions favorable for slower-growing, harmful taxa in low-inflow systems (Smayda and Reynolds, 2001; Sunda et al., 2006).

Factors such as long residence times and pronounced nutrient retention have been associated with eutrophication symptoms in other estuaries (Bricker et al., 2008; Hemraj et al., 2017) and suggest that low-inflow estuaries could be more susceptible to the harmful effects of anthropogenic nutrient loading than river-dominated systems. Aside from being susceptible to nutrient pressures, research suggests that low-inflow estuaries, especially in subtropical regions, may also experience long-term decreases in freshwater inflows due to both climate change and human uses. For example, models project decreasing precipitation with climate change in many subtropical regions worldwide (e.g., Trenberth, 2011), and even point to expansion of semi-arid/arid climates in the future (Chan and Wu, 2015). In many cases, freshwater supplies in these regions are already stressed by human demands. Growing populations are expected to put additional stress on freshwater resources while also exacerbating nutrient loads (Flemer and Champ, 2006; Hallett et al., 2018).

Baffin Bay is a low-inflow, lagoonal estuary that has been experiencing symptoms of eutrophication over the past three decades, namely high and increasing nutrient levels and recurring blooms of the “brown tide” phytoplankton, *Aureoumbra lagunensis* (Wetz et al., 2017). This organism is a mixotroph and can sustain growth in high salinities, suggesting low-inflow estuaries like Baffin Bay may provide optimal conditions for *A. lagunensis* blooms (Buskey et al., 1998; Muhlstein and Villareal, 2007). However, more data is needed on drivers of *A. lagunensis* blooms and overall phytoplankton community structure in this and similar estuaries before generalities can be drawn and extrapolated to future scenarios. Once limited to the Baffin

Bay region, blooms of the *A. lagunensis* organism have recently been identified in other subtropical systems (Gobler et al., 2013; Philips et al., 2015; Hall et al., 2018), indicating a pressing need to better understand *A. lagunensis* dynamics, as well as overall drivers and scales of phytoplankton variability in subtropical systems.

In this study, I conducted a comprehensive investigation of phytoplankton dynamics in Baffin Bay, Texas. With field sampling operating at multiple timescales throughout the bay I characterize the phytoplankton community composition of the system. I also identify spatial patterns of phytoplankton taxa (including *A. lagunensis*) within the bay and describe environmental factors that may drive these trends. Additionally, by incorporating high-frequency data and historical data in this dissertation research, I report on temporal patterns in phytoplankton dynamics across a range of timescales (days-years), and identify that climatic shifts (drought – high rainfall) may dictate the dominance of *A. lagunensis* and overall phytoplankton community structure in the bay. This research identifies opportunities for further study on phytoplankton dynamics in Baffin Bay and other subtropical systems, and may also help inform the design (i.e. sampling frequency) of future monitoring efforts.

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CHAPTER II: PHYTOPLANKTON DYNAMICS IN A LOW-INFLOW ESTUARY (BAFFIN BAY, TEXAS) DURING DROUGHT AND HIGH-RAINFALL CONDITIONS  
CORRESPONDING WITH ENSO

**Abstract**

Low freshwater inflow estuaries are common worldwide, yet our understanding of nutrient-phytoplankton dynamics in these systems is limited. In this study, I examined nutrient-phytoplankton dynamics in Baffin Bay-Upper Laguna Madre, Texas, a low-inflow lagoonal estuary. I combined three years of monthly data with analysis of a lower frequency, multidecadal dataset to describe nutrient-phytoplankton dynamics in the system. During a high salinity period of the field sampling program (corresponding with non-El Niño conditions), phytoplankton community biovolume was high and consisted of a near monoculture of the “brown tide” organism, *Aureoumbra lagunensis*. With the onset of El Niño conditions, rainfall increased and salinity decreased. Other phytoplankton groups became more prevalent, namely planktonic diatoms and the mixotrophic ciliate, *Myrionecta rubra*, while prevalence of *A. lagunensis* declined. While El Niño conditions corresponded with increased inorganic nitrogen concentrations in the bay, this did not lead to an increase in phytoplankton biovolume, indicating that the stimulatory effects of nutrient pulses may have been counter balanced by the decreased residence times associated with increased inflow.

**1. Introduction**

Estuarine phytoplankton dynamics are complex, due largely to the interactive effects of physical drivers such as freshwater inflow variability, tides and winds (Paerl et al., 2006; Cloern et al., 2014; Dijkstra et al., 2019). While our understanding of phytoplankton dynamics in “classical,” or river-dominated estuaries has increased greatly over the past three decades (e.g.,

Cloern, 1996; Pinckney et al., 1999; Smayda and Borkman, 2008; Rothenberger et al., 2009), less is known about low-inflow estuaries. Low-inflow estuaries are systems that experience minimal freshwater inflows for prolonged periods, ranging from seasonal to multiannual timescales (Largier, 2010), and are thus likely distinct from an ecological standpoint compared to river-dominated estuaries that have a constant freshwater inflow. For example, hypersalinity occasionally occurs in low-inflow estuaries due to a lack of freshwater source (Largier, 2010). Because of the long residence times of many low-inflow estuaries, nutrients can be expected to cycle many times before exiting the system (Dixon et al., 2014). A lack of flushing along with ample regenerated nutrient stocks has been shown to lead to extended periods of elevated phytoplankton biomass in these systems (Hemraj et al., 2017; Barroso et al., 2018). These factors suggest that low-inflow estuaries could conceivably be more susceptible to the harmful effects of anthropogenic nutrient loading than river-dominated systems (Bricker et al., 2008; Hemraj et al., 2017).

Aside from being susceptible to nutrient pressures, research suggests that low-inflow estuaries, especially in subtropical regions, may also experience further decreases in inflows due to both climate change and human uses. For example, models project decreasing precipitation with climate change in many subtropical regions worldwide (e.g., Trenberth, 2011), and even point to expansion of semi-arid/arid climates in the future (Chan and Wu, 2015). In many cases, freshwater supplies in these regions are already stressed by human demands. Growing populations are expected to put additional stress on freshwater resources while also exacerbating nutrient loads (Flemer and Champ, 2006; Hallett et al., 2018).

Recognizing that low-inflow/microtidal estuaries are sensitive to large-scale environmental changes and stressors, and may also be at the forefront of climate-induced

precipitation changes (decreases), it is important to begin to develop management strategies to address these challenges. In order to properly manage these systems however, it is necessary to first understand the ecological processes in them, especially those associated with sensitive indicators of environmental change. Phytoplankton biomass (chlorophyll) is a long-held indicator for nutrient pressures, while more recently phytoplankton taxonomic composition has been proposed as an indicator of freshwater inflow extremes in estuaries (e.g., Lemley et al., 2016; Hemraj et al., 2017). From a eutrophication assessment and abatement standpoint, it is also important to understand the role of natural climatic variability and its influence on nutrients and phytoplankton, as phenomena such as El Niño can have a significant influence on inflows and estuarine functioning (e.g., Tolan, 2007). Baffin Bay is a low-inflow, lagoonal estuary that has been experiencing symptoms of eutrophication over the past three decades, namely high and increasing nutrient levels and recurring blooms of the “brown tide” alga, *Aureoumbra lagunensis* (Buskey et al., 2001; Wetz et al., 2017; Cira and Wetz, 2019). In this study, I combined a 3-year temporally and spatially intensive field sampling program with an analysis of a multidecadal historical dataset to describe nutrient-phytoplankton dynamics in the bay, and to put those relationship in the context of large-scale climate variability. I evaluated relationships between phytoplankton community structure and environmental and climatic factors, gaining insight on the role climate patterns have on phytoplankton dynamics in these systems.

## **2. Methods**

### **2.1. Baffin Bay, Texas**

Baffin Bay is a shallow (< 1-3 m average depth), microtidal low-inflow estuary on the South Texas coast. The Baffin Bay watershed is dominated by agriculture (41% of surface area as of 2010; NOAA, 2019), and the climate is semi-arid (Breier et al., 2010). Due to low

freshwater inflow and high rates of evaporation, mean residence time in Baffin Bay is estimated to be > 1 year on average and the system can be hypersaline at times (Breier et al., 2010).

Vertical stratification in the system is rare, and mixing is primarily wind-driven (Orlando et al., 1993; Tunnell, 2002).

## **2.2. Analysis of historic data, 1993 - 2015**

Broad-scale patterns in salinity, total Kjeldahl nitrogen (TKN) and chlorophyll in Baffin Bay and adjacent Upper Laguna Madre were quantified using data from the Texas Commission on Environmental Quality (TCEQ) quarterly water quality monitoring program. Data were assessed for five sites from 1993-2015 (BB3, BB6, LM1, LM2, LM3; Fig. 2.1). Relationships with El Niño-Southern Oscillation (ENSO) conditions were evaluated by classifying the water quality data according to associated El Niño conditions (EN;  $ONI \geq 0.5$ ) or non-El Niño conditions (non-EN;  $ONI < 0.5$ ), as determined using the Ocean Niño Index (ONI, reported by the NOAA Climate Prediction Center). Descriptive statistics (mean  $\pm$  standard deviation) were used to assess spatial trends and compare data between EN and non-EN conditions. TCEQ data that were reported as less than the reporting limit were considered to be one half of the reporting limit for analysis.

## **2.3. Monthly field sampling program, 2013-2016**

Five sites in Baffin Bay were visited monthly from May 2013 – April 2016 (BB1-BB5; Fig. 2.1). At each site, temperature (surface) and salinity (surface and bottom) measurements were taken with a calibrated YSI ProPlus sonde. Additionally, surface water was collected in acid-washed 1 L (for biogeochemical analyses) or 500 mL (for plankton analyses) amber polycarbonate bottles and stored in the dark (the 1 L bottles were also stored on ice) for transport to laboratory for analysis.

Upon return to the laboratory, 1 L bottles were analyzed for inorganic nutrients (silicate, ammonium [NH<sub>4</sub><sup>+</sup>], nitrate + nitrite [N+N], orthophosphate), total dissolved nitrogen (TDN), and dissolved organic carbon (DOC). Bottles were gently inverted and ~50 mL subsamples were filtered through combusted 25 mm GF/F filters (nominal pore size: 0.7 μm). The filtrate was stored frozen (-20 °C) until analysis. For inorganic nutrients, subsamples were thawed to room temperature and analyzed on a Seal QuAAtro autoanalyzer following methods described in Wetz et al. (2017). Additional subsamples were thawed to room temperature and analyzed for DOC and TDN on a Shimadzu TOC-Vs analyzer with nitrogen module (see methods in Wetz et al., 2017). Dissolved inorganic nitrogen (DIN) was calculated as the sum of NH<sub>4</sub><sup>+</sup> and N+N. Dissolved organic nitrogen (DON) was calculated by subtracting DIN from TDN.

*A. lagunensis* and picocyanobacteria were enumerated with flow cytometry. To prepare samples for enumeration, 500 mL bottles were gently inverted and 4 mL subsamples were preserved with 1% glutaraldehyde and stored frozen (-80 °C) until analysis with flow cytometry. Samples were thawed under subdued lighting, then filtered through 20 μm mesh. Subsamples used to enumerate *A. lagunensis* were incubated under subdued lighting with a primary antibody specific to *A. lagunensis* (custom polyclonal antibody from ThermoFisher), followed by a fluorescently labeled secondary antibody (fluorescein isothiocyanate, FITC). Subsamples used to enumerate picocyanobacteria were not fluorescently labeled. Subsamples for *A. lagunensis* and picocyanobacterial abundance were analyzed on an Accuri C6 flow cytometer equipped with an optical filter for detection of FITC (*A. lagunensis*), chlorophyll *a,b* (picocyanobacteria) and side scatter. Accuracy of the cytometer was monitored daily prior to use, and the detection limit for *A. lagunensis* was calculated following Koch et al. (2014) and Cira and Wetz (2019).

Other phytoplankton groups and ciliates were enumerated with light microscopy. To prepare samples for enumeration, 500 mL bottles were gently inverted and 60 mL subsamples were preserved with 3% acid Lugol's solution and stored at room temperature in the dark until analysis. To prepare samples for enumeration, bottles were gently inverted and 5 mL subsamples were poured into Utermöhl chambers and allowed to settle overnight. The subsample volume and settling time were adjusted as needed (i.e. during bloom events), allowing > 1 hr settling time per mL settled. Phytoplankton and ciliate taxa were enumerated and measured at 100 – 600x on an Olympus IX71 inverted microscope. Biovolume was estimated using geometric shapes for each enumerated taxa (Hillebrand et al., 1999; Sun and Liu, 2003). Due to inherent difficulty in differentiating some taxa with light microscopy and acid Lugol's-preserved cells, taxa were grouped as dinoflagellates, diatoms, cryptophytes, chlorophytes, unidentified flagellates, picocyanobacteria, *A. lagunensis*, and the ciliate *Myrionecta rubra* (a mixotrophic ciliate) for analysis. Further, diatoms were categorized as planktonic (e.g., centric and chain forming diatoms such as *Skeletonema*, *Chaetoceros*, *Pseudo-nitzschia*, etc.) or benthic forms (pennate forms such as naviculoids, *Cylindrotheca*, etc.) following categories described in Shaffer and Sullivan (1988) and MacIntyre et al. (2011).

Correlation between phytoplankton groups and environmental variables was assessed using Kendall's tau ( $\alpha = 0.05$ ). Correlation was assessed separately for each phytoplankton group-environmental variable combination. This nonparametric analysis was selected to handle non-normally distributed data and cell counts/nutrient concentrations that were below detection limit (BDL). All analyses were performed in R version 3.3.2 (R Core Team, 2016) using the Kendall package (McLeod, 2011).

Data from the Texas Water Development Board was used to estimate the residence time (monthly freshwater input based on rainfall data/bay volume) of Baffin Bay during 2013 – 2016. To do this, residence time was first estimated as the proportion of monthly modeled freshwater inflow to bay volume using historic data (1977 – 2010). Then, the relationship between residence time and monthly rainfall during that timeframe was estimated. This relationship was then applied to rainfall data from 2013 – 2016 to estimate residence times during that period (See Table 2.1).

### **3. Results**

#### **3.1. Spatial-temporal variability in water quality conditions related to ENSO from long-term time series, 1993 - 2015**

Across all sites, salinity was lower during EN conditions than non-EN conditions (Fig. 2.2A). During EN conditions, salinities were highest at the mouth of Baffin Bay (LM1:  $39.2 \pm 7.6$ ) and lower in both Baffin Bay (BB3:  $31.7 \pm 12.4$ ; BB6:  $33.7 \pm 10.5$ ) and Upper Laguna Madre (LM2:  $33.1 \pm 7.9$ ; LM3:  $31.0 \pm 6.0$ ; Fig. 2.2A). During non-EN conditions, salinity was high and varied little from upper Baffin Bay to the mouth (BB3:  $39.0 \pm 14.4$ ; LM1:  $39.9 \pm 8.6$ ). Slightly lower salinities were observed in Upper Laguna Madre (LM3:  $35.6 \pm 6.6$ ).

TKN concentrations ranged from a low of  $66.7 \pm 29.3 \mu\text{M}$  at LM3 to a high of  $124.4 \pm 45.4 \mu\text{M}$  at BB3. Concentrations were higher and more variable in Baffin Bay than Upper Laguna Madre (Fig. 2.2B). At BB3, BB6 and LM1, TKN concentrations were higher by an average of  $17.6 \mu\text{M}$  during EN conditions than non-EN conditions (Fig. 2.2B). In contrast, TKN concentrations were lower by an average of  $5.7 \mu\text{M}$  during EN conditions compared to non-EN conditions at LM2 and LM3 (Fig. 2.2B).

Average chlorophyll concentrations ranged from  $8.4 \pm 9.1 \mu\text{g L}^{-1}$  at LM3 to a high of  $26.1 \pm 27.5$  at BB3 (Fig. 2.2C), though maximum concentrations reached  $139.0 \mu\text{g L}^{-1}$  at BB3 during non-EN conditions. Chlorophyll concentrations were higher within and at the mouth of Baffin Bay (BB3, BB6 and LM1) than in Upper Laguna Madre (LM2 and LM3) under both EN and non-EN conditions. This difference was more apparent under EN conditions when concentrations in Baffin Bay (BB3:  $25.2 \pm 33.4$ ; BB6:  $22.4 \pm 20.2$ ; LM1:  $22.5 \pm 22.1$ ) were > 2-fold higher than in Upper Laguna Madre (LM2:  $6.6 \pm 7.6$ ; LM3:  $6.6 \pm 5.2$ ; Fig. 2.2C). Within and at the mouth of Baffin Bay, chlorophyll concentrations were similar between EN and non-EN conditions (average concentrations varied by  $< 2.0 \mu\text{g L}^{-1}$ , or  $< 10\%$ ; Fig. 2.2C). In Upper Laguna Madre, chlorophyll concentrations were higher in non-EN conditions by  $2.3 \mu\text{g L}^{-1}$  at LM3, and  $6.5 \mu\text{g L}^{-1}$  at LM2 (which reflect  $\sim 30\%$  and  $\sim 100\%$  increase, respectively; Fig. 2.2C).

### **3.2. Environmental conditions from 2013-2016**

The first two years of monthly sampling were characterized by drought/high salinity conditions (May 2013 – March 2015; Fig. 2.3A) and the last year was characterized by high rainfall/low salinity conditions (April 2015 – April 2016; Fig. 2.3A). This corresponds with a shift from non-EN to EN conditions in November 2014 (Fig 2.3A). From April – June 2015, salinity stratification was observed (Fig. 2.3B) but was generally low on other dates. Temperatures peaked in summer months and were lowest in winter months (Fig. 2.3C). The lowest average winter temperatures progressively increased each year (2013/2014:  $9.9 \pm 0.4 \text{ }^\circ\text{C}$ ; 2014/2015:  $14.0 \pm 0.5 \text{ }^\circ\text{C}$ ; 2015/2016:  $17.7 \pm 0.9 \text{ }^\circ\text{C}$ ; Fig. 2.3C). Average  $\text{NH}_4^+$  and N+N concentrations were almost twice as high from April 2015 onward under low salinity conditions ( $\text{NH}_4^+$ :  $5.6 \pm 6.9 \mu\text{M}$ ; N+N:  $2.9 \pm 7.2 \mu\text{M}$ ) compared to prior high salinity conditions ( $\text{NH}_4^+$ :  $3.0 \pm 3.6 \mu\text{M}$ ; N+N:  $1.5 \pm 4.4 \mu\text{M}$ ; Fig. 2.4A,B). Likewise, orthophosphate concentrations were

higher under low salinity conditions (low salinity:  $1.2 \pm 2.4 \mu\text{M}$ ; high salinity:  $0.7 \pm 1.5 \mu\text{M}$ ) and had distinctive peaks during the spring of 2015 (Fig. 2.4C). Silicate concentrations were lower under low salinity conditions (low salinity:  $54.5 \pm 48.1 \mu\text{M}$ ; high salinity:  $78.3 \pm 16.3 \mu\text{M}$ ; Fig. 2.4D). DOC concentrations were highest in May 2013 ( $> 1500 \mu\text{M}$  at all sites) and decreased throughout the sampling period (Fig. 2.3D). Overall, DOC concentrations were  $1053 \pm 299 \mu\text{M}$  during the high salinity period and  $810 \pm 134 \mu\text{M}$  during the low salinity period (Fig. 2.3D). Lowest DON concentrations occurred during the spring of 2015, reaching a minimum average of  $41 \mu\text{M}$  in May 2015 (Fig. 2.4E). DON was consistently higher than concurrent DIN concentrations throughout the sampling period (Fig. 2.4A,B,E). Overall, there was no clear temporal trend in DON concentrations (Fig. 2.4E). Variability in ciliate biovolume was not aligned with seasonal cycles or interannual shifts in salinity conditions (Fig. 2.5). Ciliate biovolume was typically higher in 2015 than the other years (Fig. 2.5).

From May 2013 through February 2015, residence time was estimated to be  $> 1$  year for all but three months. Residence time was  $< 1$  year from March 2015 through June 2015, reaching  $< 1$  month in May 2015. After June 2015, residence time increased again and was estimated to be  $> 1$  year for all but one month from July 2015 – April 2016 (Table 2.1).

### **3.3. Phytoplankton dynamics from 2013-2016**

Chlorophyll concentrations were lower on average under low (April 2015 – April 2016) compared with high (May 2013 – March 2015) salinity conditions (low salinity:  $16.2 \pm 14.3 \mu\text{g L}^{-1}$ ; high salinity:  $25.7 \pm 11.7 \mu\text{g L}^{-1}$ ; Fig. 2.6). During high salinity conditions, concentrations peaked in summer months, but the seasonal pattern was less pronounced after the onset of low salinity conditions in 2015 (Fig. 2.6). The seasonal trends in chlorophyll, as well as the overall

decrease in chlorophyll associated with the shift from high to low salinity conditions, were reflected by trends in phytoplankton biovolume (Fig. 2.7).

During high salinity conditions from May 2013 – March 2015, the phytoplankton community was dominated by *A. lagunensis*, which accounted for an average of 87% of community biovolume during this period (Fig. 2.7). The second and third most prevalent groups were dinoflagellates and diatoms, only accounting for 9% and 3% of community biovolume, respectively (Fig. 2.7). *A. lagunensis* biovolume peaked in summer months (Fig. 2.7), as did the proportion of *A. lagunensis* in relation to other groups (Fig. 2.7). In contrast, dinoflagellate biovolume peaked in winter months, and diatom biovolume peaked in spring months (Fig. 2.7).

After the onset of low salinity conditions, phytoplankton biovolume decreased by over 40% on average and community composition changed (Fig. 2.7). *A. lagunensis* biovolume decreased sharply across all sites and remained low except at site BB2 (Fig. 2.7). Average dinoflagellate biovolume also decreased from the high to low salinity period (Fig. 2.7). Biovolume of diatoms was higher in low salinity conditions, accounting for an average of 29% of community biovolume (Fig. 2.7). Most diatom biovolume in the high salinity period consisted of benthic taxa (89%), while during the low salinity period planktonic taxa dominated (64%; Fig. 2.8). Benthic taxa were primarily pennate forms, including naviculoids and *Cylindrotheca*. Planktonic diatoms were dominated by *Rhizosolenia*, though *Thalassionema* and *Thalassiosira* were also commonly observed. *Myrionecta rubra* was also more common during the low salinity period, when it was present in 80% of samples (compared with 15% during the high salinity period; Fig. 2.7). Highest *M. rubra* biovolume tended to occur in winter (Fig. 2.7). For example, in winter of 2015/2016, its presence was widespread throughout the bay and it was the primary component of phytoplankton biovolume at all sites except BB2 (Fig. 2.7).

Other phytoplankton groups, including cryptophytes, chlorophytes, picocyanobacteria and unidentified flagellates were a minor component of phytoplankton community biovolume. Among these groups, a clear temporal trend was only identified for picocyanobacteria, the biovolume of which mirrored that of *A. lagunensis* and peaked in summer months (Fig. 2.9). Picocyanobacteria had higher biovolume during the high salinity conditions compared to the low salinity conditions, but consistently accounted for < 1% of phytoplankton biovolume overall (Fig. 2.7).

### **3.4. Phytoplankton composition – relationships with environmental factors from 2013-2016**

Both *A. lagunensis* and picocyanobacterial biovolume were positively correlated with DOC, salinity, and silicate (Table 2.2). Picocyanobacterial biovolume was also positively correlated with temperature (Table 2.2), while that of *A. lagunensis* was negatively correlated with orthophosphate, ciliate biovolume, and  $\text{NH}_4^+$ . Both *A. lagunensis* and picocyanobacterial biovolume were negatively correlated with N+N (Table 2.2). Dinoflagellate biovolume was positively correlated with ciliate biovolume and silicate, and negatively correlated with N+N,  $\text{NH}_4^+$ , salinity and temperature (Table 2.2). *M. rubra* biovolume was positively correlated with N+N,  $\text{NH}_4^+$ , and orthophosphate, and negatively correlated with silicate, DOC and salinity (Table 2.2). Benthic and planktonic diatom biovolume were both negatively correlated with salinity and DOC, and positively correlated with N+N (Table 2.2). Additionally, benthic diatom biovolume was positively correlated with ciliate biovolume and negatively correlated with salinity stratification (Table 2.2), while planktonic diatom biovolume was negatively correlated with silicate and positively correlated with  $\text{NH}_4^+$  and orthophosphate (Table 2.2).

#### 4. Discussion

In this study, I examined nutrient-phytoplankton dynamics in Baffin Bay-Upper Laguna Madre, Texas. Baffin Bay-Upper Laguna Madre experiences a range of salinities from brackish to hypersaline, as captured in this study. This is common in semiarid systems where extended drought can be punctuated by episodic high rainfall (e.g., Norwine, 1978; Barroso et al., 2016). By augmenting an intensive 3-year monthly monitoring program in Baffin Bay with analysis of a decades-long dataset of lower frequency sampling, I was able to examine nutrient-phytoplankton dynamics across a range of salinity conditions and relate those dynamics to large-scale climate patterns. Results from this study increase our understanding of low-inflow estuaries, which are numerically significant on a global basis (e.g., Largier, 2010; Potter et al., 2010), but understudied from an ecosystem dynamics standpoint.

Texas estuaries are characterized by notable interannual variability in freshwater inflow, due in large part to the strong influence of El Niño-Southern Oscillation (ENSO) on regional precipitation patterns (Tolan, 2007). Salinities were found to be lower during El Niño (EN) compared to non-EN conditions due to higher rainfall during the former (see also Tolan 2007). In the 3-year monitoring dataset there was a lag from when ENSO conditions shifted in fall 2014 to when salinity changes were observed in Baffin Bay in spring 2015, similar to the ~ 5 month lag described for the Texas coast by Tolan (2007). Salinity variability was more pronounced in Baffin Bay than in neighboring Upper Laguna Madre, which would be expected given that Upper Laguna Madre is closer to the Gulf of Mexico and would experience water exchange that modulates its salinities (Smith, 1975, 1988).

The effects of ENSO extended beyond the physical conditions in Baffin Bay. During EN conditions, TKN was higher in Baffin Bay and at the mouth of Baffin Bay compared with non-

EN conditions. Similarly, in this monthly sampling program from January 2015, just prior to the first observed EN-related salinity decrease, through April 2016, just prior to the declared end of EN in May 2016, total dissolved nitrogen (TDN) increased by 11  $\mu\text{M}$ . The net increase in nitrogen (as TKN and TDN) during EN conditions in both the long-term and 3-year dataset, as well the observed increase in  $\text{NH}_4^+$  and N+N concentrations concurrent with high rainfall and a decrease in salinity in the 3-year dataset, indicates a watershed source. These findings are consistent with observations of increased nitrogen loadings during high rainfall periods from other estuaries with agriculturally-dominated watersheds (i.e., row crop agriculture; Caffrey et al., 2007; Peierls et al., 2012). Despite the TKN increase in Baffin Bay during EN, no TKN increase was observed at the two Upper Laguna Madre sites during EN conditions. It is unclear why TKN did not increase in Upper Laguna Madre during EN conditions, and in fact appeared to decrease slightly. Further work is clearly needed to understand the sources and drivers of nutrients within and between Baffin Bay and Upper Laguna Madre, as the Upper Laguna Madre contains important seagrass beds that are sensitive to nutrient enrichment (Street et al., 1997; TPWD, 1999).

When considering the ecological effects of freshwater inflow, there is typically a trade-off for phytoplankton between the stimulatory effects of nutrient pulses and the increased flushing associated with inflow events (Peierls et al., 2012; Azevedo et al., 2014). Increased nutrient availability under high inflow conditions may stimulate primary production and has been shown to lead to blooms of fast-growing phytoplankton taxa (e.g., chlorophytes, diatoms; Cloern and Dufford, 2005; Paerl et al., 2014; Carstensen et al., 2015). However, extremely high inflows, such as due to hurricane passage, can lead to reductions in phytoplankton growth and biomass due to light limitation and/or washout effects (Mitrovic et al., 2011; Paerl et al., 2014).

Under low-inflow conditions, nutrient limitation is possible (e.g., Wetz et al., 2011), although in shallow systems, internal nutrient stocks can often sustain phytoplankton growth and allow for biomass accumulation in the absence of significant external inputs (Pinckney et al., 2001; Glibert et al., 2010; Geyer et al., 2018). This appears to be the case in Baffin Bay-Upper Laguna Madre, where chlorophyll/phytoplankton biovolume was generally higher during non-EN conditions despite lower apparent nutrient concentrations. Previous work in Baffin Bay-Upper Laguna Madre has shown that high rates of dissimilatory nitrate reduction to  $\text{NH}_4^+$  are found during higher salinity (i.e., non-EN) conditions, which would provide  $\text{NH}_4^+$  to the phytoplankton (An and Gardner, 2002). A more recent study in Baffin Bay found very high  $\text{NH}_4^+$  concentrations in sediment porewater and argued that fluxes of sediment-derived nutrients can be significant (Lopez et al., 2018). Another recent study found indications of high photoammonification rates in Baffin Bay (Felix and Campbell, 2019), which would be a ready source of nitrogen for phytoplankton during low-inflow conditions given the persistently high ambient dissolved organic matter concentrations (Wetz et al., 2017). In addition, studies have concluded that the dominant phytoplankton taxa during drought/non-EN conditions (*A. lagunensis*) has mixotrophic capabilities and thus maybe able to grow on some fraction of the very high DON in this system (Buskey et al., 1998; Agostoni and Erdner, 2011). Thus, while external nutrient loadings obviously affect nutrient stocks over longer timescales (years-decades) in this system, on timescales relevant to phytoplankton growth, external loadings may be less important for phytoplankton population dynamics than other factors.

In this study, *A. lagunensis* accounted for ~90% of phytoplankton community biovolume during non-EN, high salinity conditions (May 2013 – March 2015). In addition to being mixotrophic, *A. lagunensis* is also adapted to grow in high salinities that are common to Baffin

Bay-Upper Laguna Madre, reaching maximum growth rates of  $\sim 0.6 \text{ d}^{-1}$  at salinities of 30-50 (Buskey et al., 1998). As rainfall increased and salinity decreased in spring 2015 after the onset of EN conditions, *A. lagunensis* biovolume in Baffin Bay dropped sharply while diatoms and other taxa (e.g., the mixotrophic ciliate *M. rubra*) became more prevalent, reflecting an overall increase in phytoplankton diversity as salinity conditions became less harsh (Cornelius, 1984; Schapira et al., 2010). The decline in dominance of *A. lagunensis* during rain events has previously been attributed to less optimal salinities (Buskey et al., 1998). Indeed, at salinities  $< 20$ , similar to those observed here during EN conditions, *A. lagunensis* growth rates decrease to  $< 0.4 \text{ d}^{-1}$  in laboratory studies (Buskey et al., 1998). Although salinity plays an important role in *A. lagunensis* blooms, Hall et al. (2018) pointed to the importance of residence time in facilitating an *A. lagunensis* bloom in Guantánamo Bay, which (residence time) is often conflated with salinity changes. During this 3-year monitoring program, estimates of residence time were  $> 1$  year for most of the study but decreased to  $< 30$  days in May 2015. This coincided with a bay-wide decrease in *A. lagunensis* biovolume. A residence time of  $< 30$  days would account for a dilution loss of  $> 3\%$  ( $\text{d}^{-1}$ ) within Baffin Bay, which could be significant for *A. lagunensis*, particularly given its lower growth rates at low salinities (Buskey et al., 1998).

The decrease in *A. lagunensis* biovolume during the spring of 2015 corresponded with an increase in biovolume of diatoms, a group that is more competitive under high rainfall conditions due to their ability to take advantage of high nutrient concentrations with high growth rates ( $\sim 1\text{-}2 \text{ d}^{-1}$ ; e.g., Shikata et al., 2008; Barroso et al., 2016; Lee, 2017). Prior to 2015, benthic forms (primarily naviculoids) were most prevalent, whereas in 2015, planktonic forms (primarily *Rhizosolenia*, *Thalassionema*) became more prevalent. Vertical stratification is rare in Baffin Bay, thus benthic diatom prevalence during the high salinity period likely reflects resuspension

due to wind-induced water column mixing (Shaffer and Sullivan, 1988; Orlando et al., 1993). The dominance of planktonic diatoms during the low-salinity period is likely driven by freshwater inflow, as many of these taxa are high-nutrient adapted and have high growth rates (Barroso et al., 2016). For example, blooms of *Rhizosolenia* often occur after freshets, suggesting an important role for riverine-derived nutrients and/or lower salinity conditions (e.g., Malej et al., 1995; Buskey et al., 2001; Rothenberger et al., 2009).

It was surprising that picocyanobacterial biovolume and relative importance were low compared to other phytoplankton taxa. In other subtropical systems (e.g., Phlips et al., 1999; Murrell and Lores, 2004; Hall et al., 2018), picocyanobacteria can be a dominant component of the phytoplankton community. This study found a strong temporal coherence between picocyanobacteria and *A. lagunensis*, consistent with prior studies (Kang et al., 2015; Hall et al., 2018). The minor relative importance of picocyanobacteria in Baffin Bay may partially be explained by an allelopathic effect that *A. lagunensis* has been shown to have on competitors, including picocyanobacteria (Kang and Gobler, 2018). Additionally, picocyanobacteria have been shown to be more affected by “top-down” controls than *A. lagunensis* (Buskey et al., 2003). The hypersaline conditions often found in Baffin Bay may intensify preferential grazing on picocyanobacteria because high salinities are associated with increased secretion of a grazer-detering mucus by *A. lagunensis* (Liu and Buskey, 2000), shifting grazing pressure to the picocyanobacteria.

An increase in biovolume of the mixotrophic ciliate, *M. rubra*, also occurred during low salinity conditions. This has been observed elsewhere, such as Chesapeake Bay, where *M. rubra* blooms are generally limited to salinities < 10 (Johnson et al., 2013). Even though *M. rubra* is a mixotroph, nitrate is its primary nitrogen source (Lindholm, 1985) and the organism may require

relatively high nutrient concentrations (Smith and Barber, 1979). Similarly, in this study, *M. rubra* was positively correlated with inorganic nutrients. Highest *M. rubra* biovolume was observed in winter, consistent with findings from other systems showing seasonal peaks in cooler months (Sanders, 1995; Johnson et al., 2013). This has been proposed to be related to a combination of factors such as high nutrient concentrations, low salinities, and low light levels, as well as decreased predation, which create seasonal windows of opportunity for *M. rubra* (Sanders, 1995; Johnson et al., 2013). Taylor et al. (1971) reported that maximum *M. rubra* abundances occurred at temperatures just above 15 °C, which would limit *M. rubra* to the cooler months in Baffin Bay. The combination of lower salinities, greater nutrient availability, and optimal temperatures may explain why highest *M. rubra* biovolume was found in the winter of 2015/2016.

Dinoflagellates were not a major component of the phytoplankton community overall, but for some sampling sites, they did occasionally represent a majority of biovolume in the winter months during non-EN conditions. Seasonal peaks of dinoflagellate biovolume in winter months are a common feature in other coastal systems (Rothenberger et al., 2009; Lee, 2017) and can be explained in part by mixotrophy, a common characteristic among dinoflagellates, which allows them to thrive under low light conditions (Millette et al., 2017). This study did not distinguish mixotrophic from non-mixotrophic taxa, which can be difficult via light microscopy with Lugol's-preserved samples (e.g., Rothenberger et al., 2009). However, this is a future priority given that blooms of harmful taxa (*Pyrodinium bahamense*, *Alexandrium* sp.) have previously been observed in the system.

## **5. Conclusions**

This study highlights the substantial interannual variability in nutrient-phytoplankton dynamics that occurs in Baffin Bay-Upper Laguna Madre, a low-inflow South Texas estuary. Results show that during long residence time, hypersaline conditions that are common during non-EN conditions, phytoplankton biomass was high despite very low inorganic nutrient concentrations, pointing to the importance of regenerated nutrients or DON uptake. The high phytoplankton biomass was composed of a near monoalgal bloom of the harmful “brown tide” organism *A. lagunensis*. In contrast, during higher inflow conditions, the estuary behaved similarly to a “classical” estuary (Olli et al., 2019), with a more diverse phytoplankton community. These findings are consistent with those from other systems showing that decreases in freshwater inflows, as well as associated increases in residence times and salinities, can lead to increased phytoplankton biomass and decreased phytoplankton diversity (Schapira et al., 2010; Barroso et al., 2016; Hemraj et al., 2017). If broadly applicable, the implication of this is that with future expansion of arid/semiarid regions and/or increasing human freshwater demands, susceptible estuaries will experience lower inflows, more pronounced hypersalinities and presumably less diverse communities. The question is – will these communities be dominated by harmful taxa such as seen here, or non-harmful taxa? It is possible that Baffin Bay represents an extreme case, where a combination of nutrient pollution and low inflows have pushed the system to dominance by a harmful taxon. Additional data is needed from other similar systems to determine if findings presented here are broadly applicable to low-inflow estuaries.

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reduce estuarine primary productivity with cascading effects on higher trophic levels.

*Limnol. Oceanogr.* 56, 627-638.

## Figures



Figure 2.1. Five Baffin Bay water quality monitoring stations (visited monthly, May 2013 – April 2016; BB1 – BB5) and five TCEQ monitoring stations (visited quarterly, 1993 – 2015; BB3, BB6, LM1, LM2, LM3).

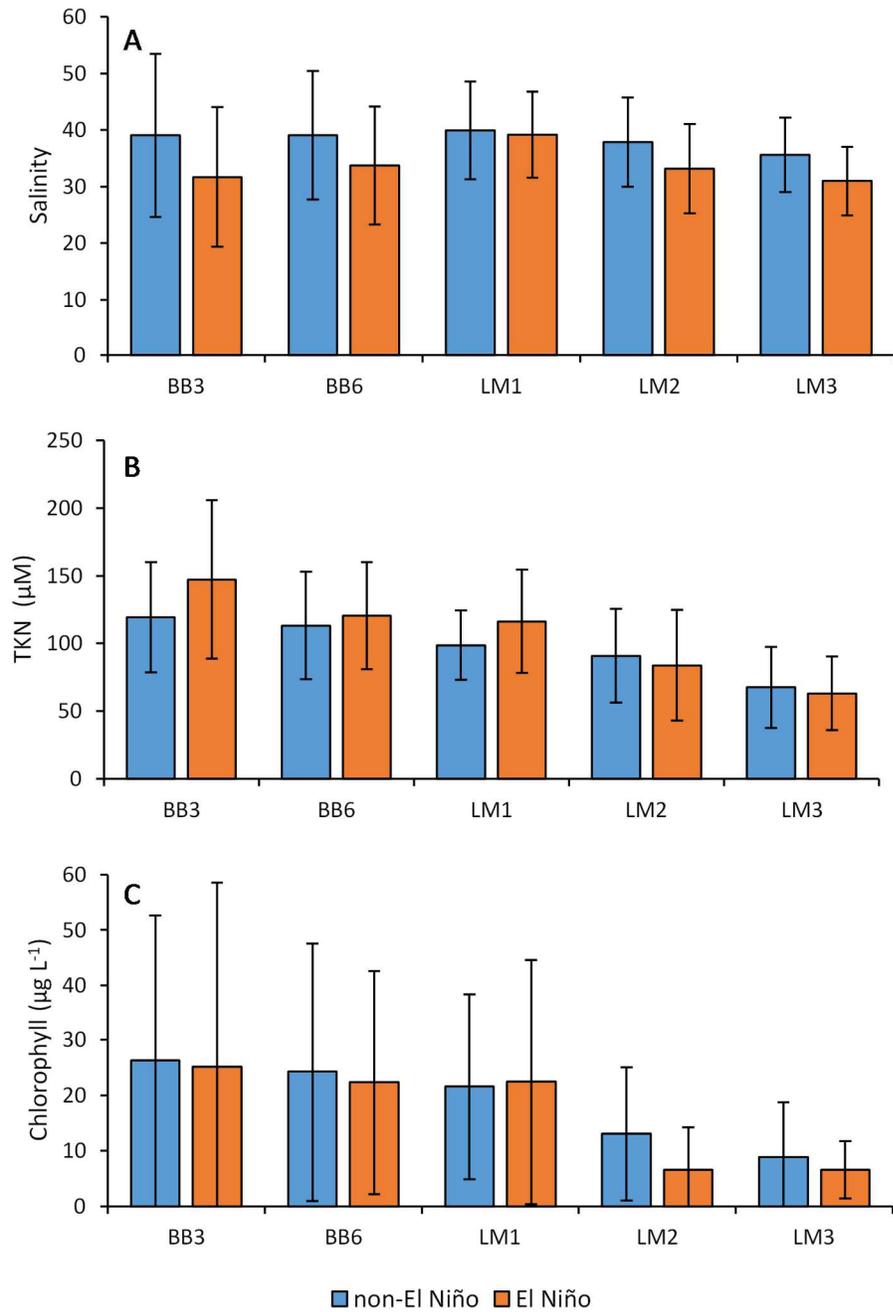


Figure 2.2. Average ( $\pm$  standard deviation) A) salinity, B) TKN ( $\mu\text{M}$ ), and C) chlorophyll ( $\mu\text{g L}^{-1}$ ) for five TCEQ sites in Baffin Bay and Upper Laguna Madre during non-El Niño conditions and El Niño conditions from 1993 – 2015.

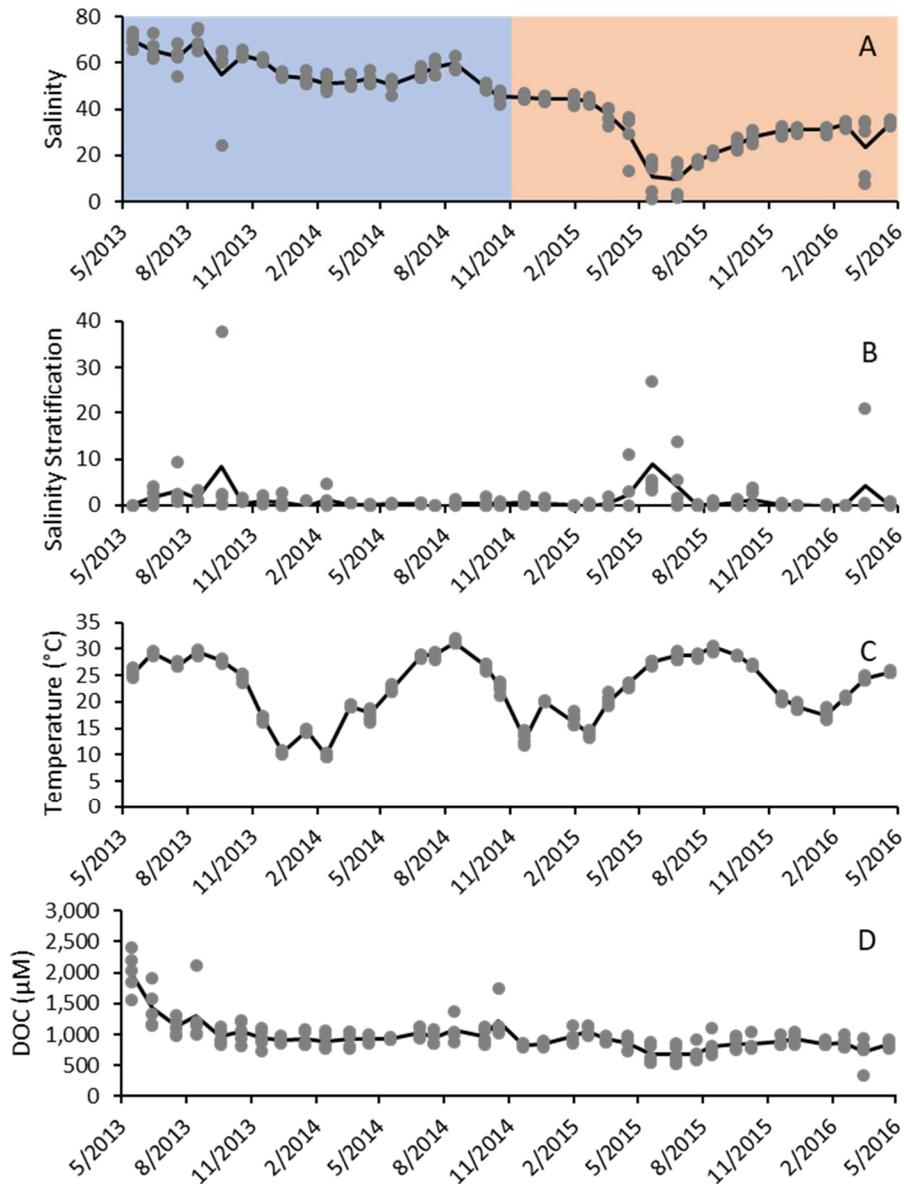


Figure 2.3. Average (black line; values at each of five sites represented by gray points) A) salinity, B) salinity stratification, C) temperature (°C), and D) DOC concentrations (μM) from May 2013 – April 2016. Shaded area in panel A depicts non-El Niño (blue) and El Niño (orange) conditions.

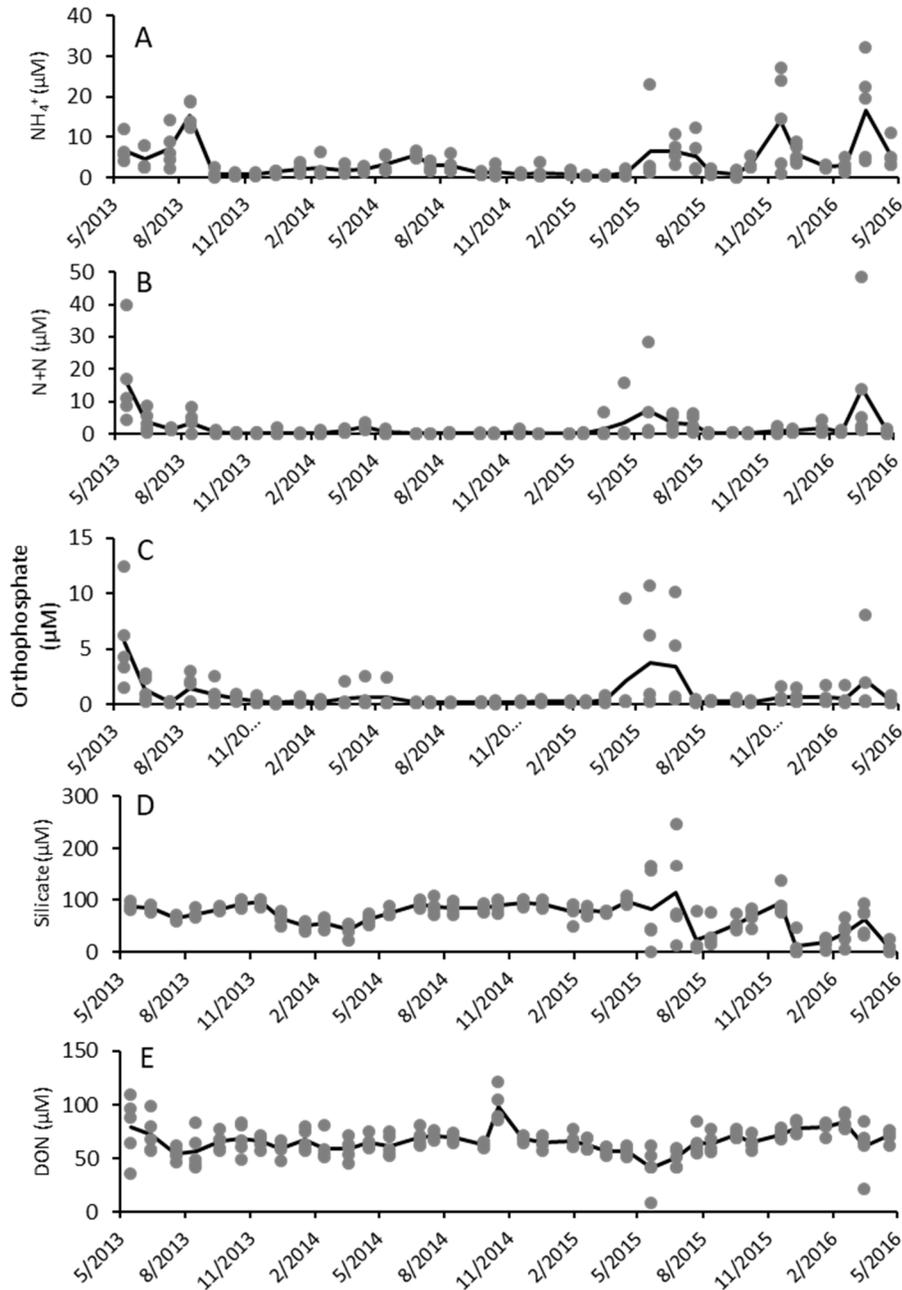


Figure 2.4. Average (black line; values at each of five sites represented by gray points) A)  $\text{NH}_4^+$ , B) N+N, C) orthophosphate, D) silicate, and E) DON concentrations ( $\mu\text{M}$ ) from May 2013 – April 2016.

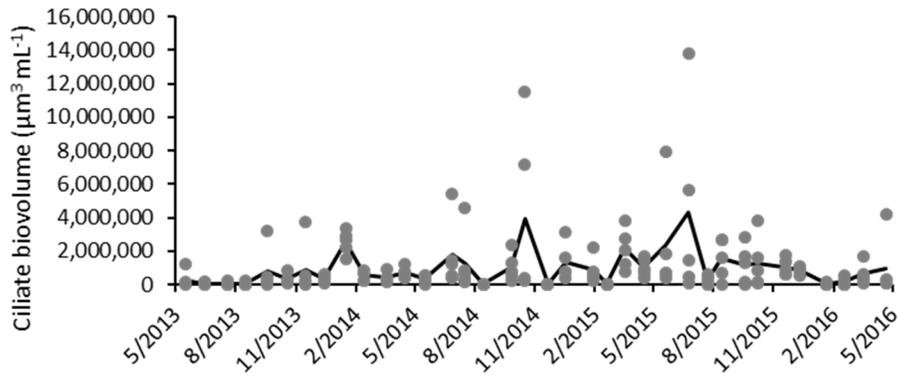


Figure 2.5. Average (black line; values at each site represented by gray points) ciliate biovolume at five Baffin Bay water quality monitoring stations from May 2013 – April 2016.

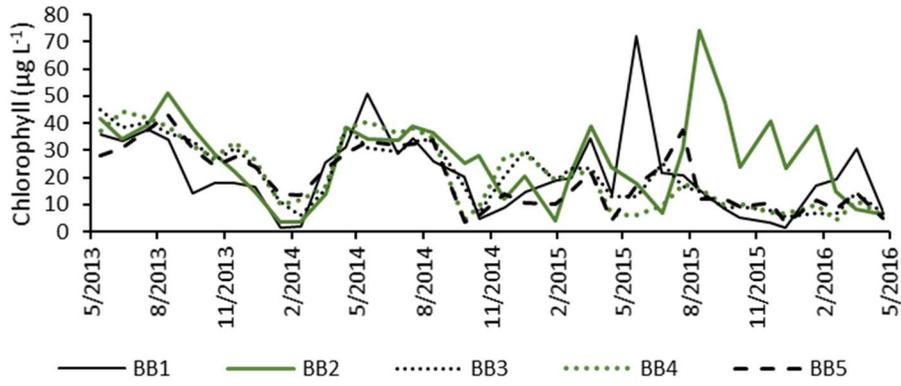


Figure 2.6. Chlorophyll concentrations at five Baffin Bay water quality monitoring stations from May 2013 – April 2016.

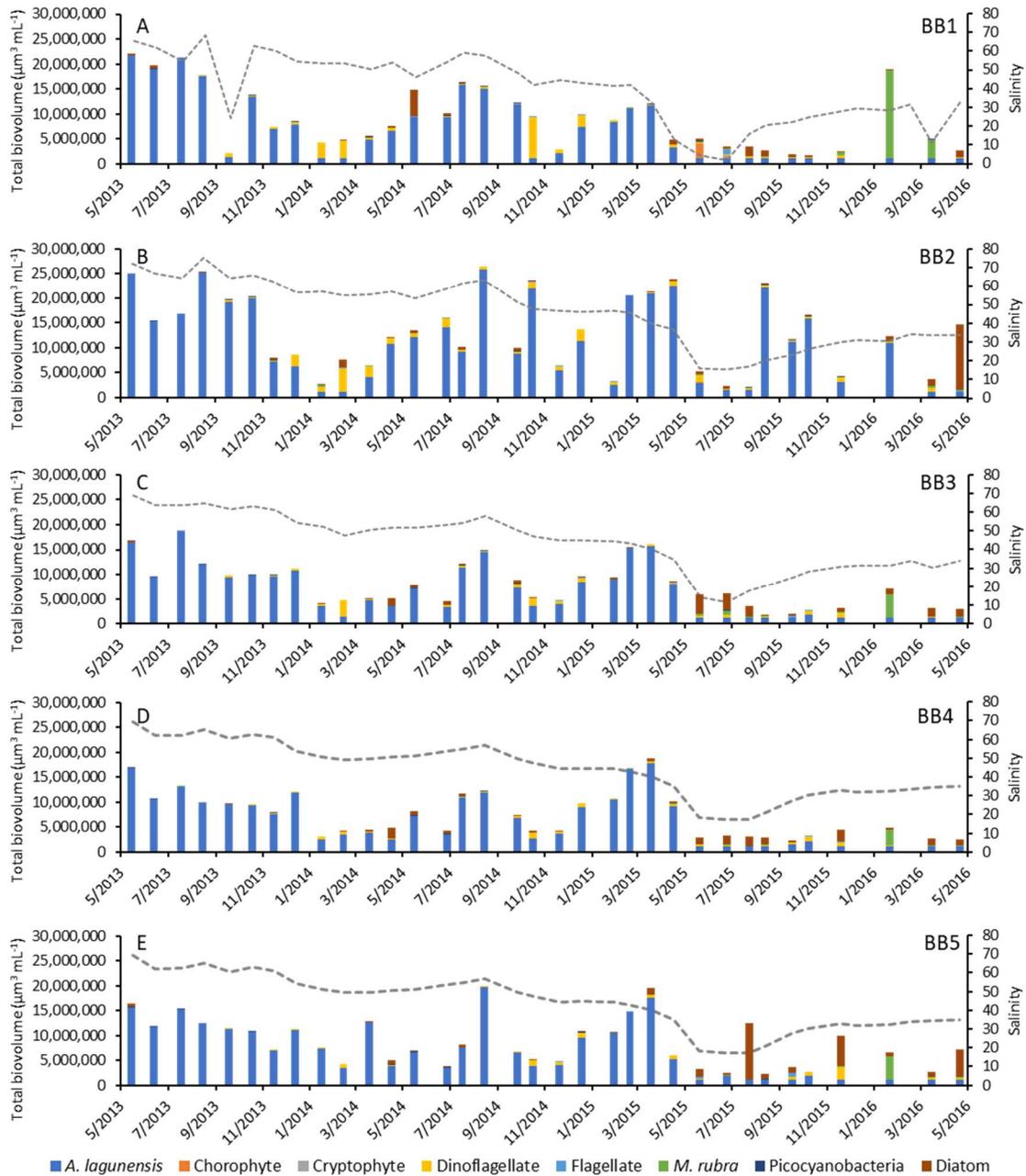


Figure 2.7. Biovolume of phytoplankton groups at five monitoring stations in Baffin Bay, A) BB1, B) BB2, C) BB3, D) BB4, E) BB5, from May 2013 – April 2016. When *A. lagunensis* was BDL, biovolume was calculated using  $40,000 \text{ cells mL}^{-1}$ , 0.5 of the detection limit for the fluorometric enumeration method. Salinity for each site is included as a dashed gray line.

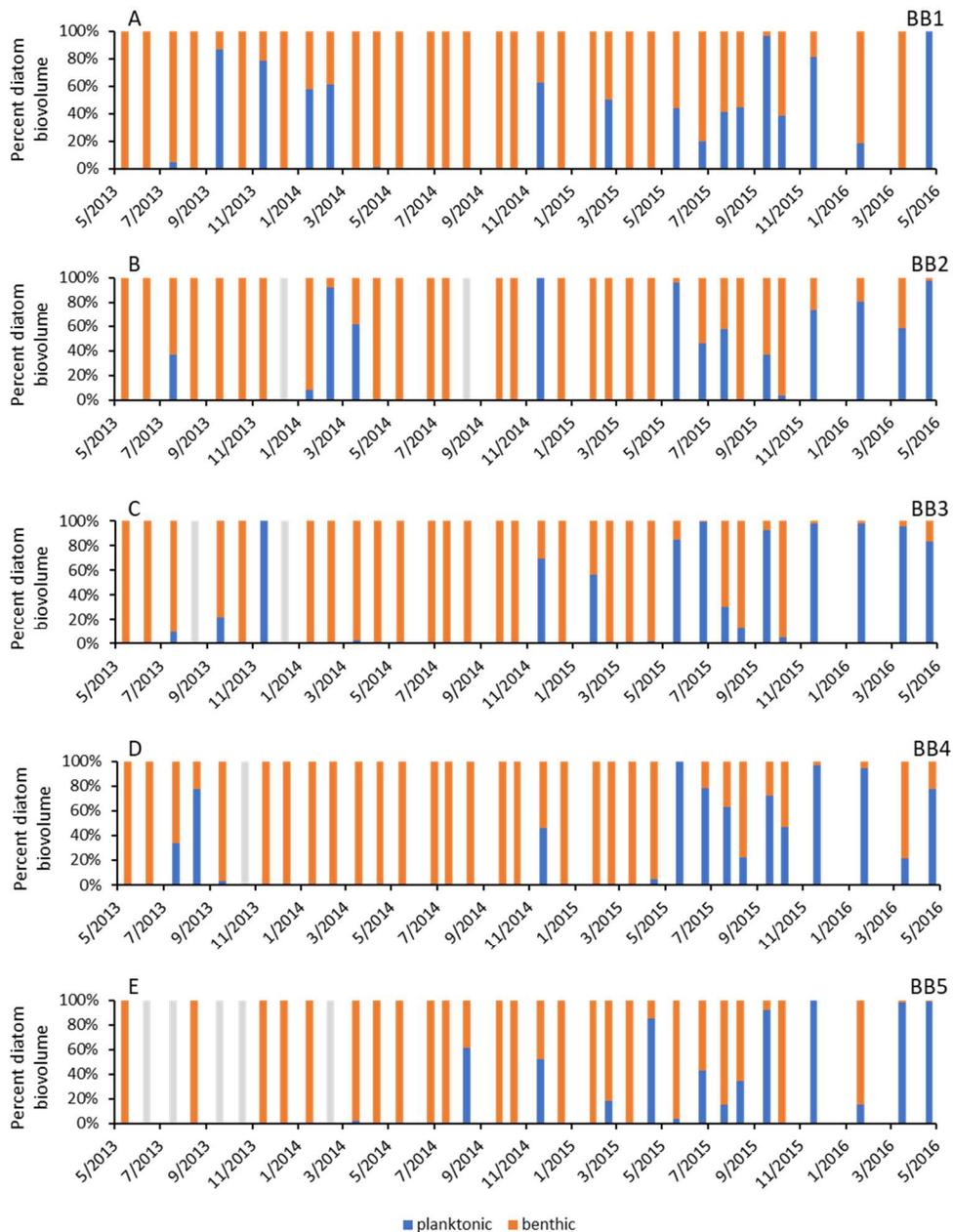


Figure 2.8. Diatom composition, comparing percent diatom biovolume of planktonic and benthic forms, at five monitoring stations in Baffin Bay, A) BB1, B) BB2, C) BB3, D) BB4, E) BB5, from May 2013 – April 2016. Gray bars represent sampling events when no diatoms were enumerated in phytoplankton samples. Refer to Fig. 2.7 for total diatom biovolume.

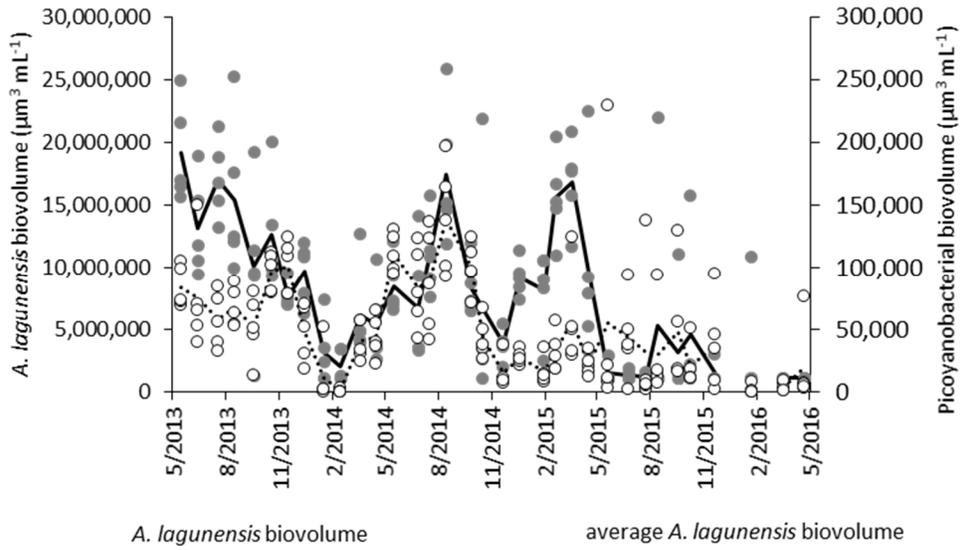


Figure 2.9. Average (black line; values at each site represented by gray points) *A. lagunensis* biovolume and average (dashed line; values at each site represented by white points) picocyanobacterial biovolume at five Baffin Bay water quality monitoring stations from May 2013 – April 2016.

## Tables

Table 2.1. Estimated monthly residence times of Baffin Bay during field sampling program from TWDB rainfall data (2013 – 2016).

year	month	monthly rainfall (inches) <sup>1</sup>	residence time (months) <sup>2</sup>
2013	5	1.62	32.6
2013	6	1.45	35.0
2013	7	2.84	19.7
2013	8	1.79	30.4
2013	9	6.87	3.8
2013	10	1.62	32.6
2013	11	2.95	18.9
2013	12	0.71	47.4
2014	1	0.64	48.8
2014	2	0.44	53.0
2014	3	1.5	34.3
2014	4	0.29	56.3
2014	5	4.43	10.3
2014	6	0.86	44.6
2014	7	1.09	40.5
2014	8	2.19	25.8
2014	9	8.22	2.2
2014	10	3.34	16.1
2014	11	3.79	13.4
2014	12	1.58	33.1
2015	1	2.06	27.2
2015	2	1.59	33.0
2015	3	5.59	6.4
2015	4	5.16	7.6
2015	5	10.63	0.8
2015	6	4.78	8.9
2015	7	1.77	30.7
2015	8	0.72	47.2
2015	9	4.04	12.1
2015	10	5.39	6.9
2015	11	1.4	35.7
2015	12	0.82	45.3
2016	1	2.34	24.3
2016	2	0.06	61.9
2016	3	3.93	12.6
2016	4	1.03	41.6

<sup>1</sup> As reported by TWDB for Quad ID 1010, [waterdatafortexas.org/lake-evaporation-rainfall](http://waterdatafortexas.org/lake-evaporation-rainfall), accessed 11/01/2019

<sup>2</sup> Estimated by exponential trendline fit with historical data:  
residence time (months) =  $63.455 * e^{-0.411 * \text{monthly rainfall}}$

Table 2.2. Kendall's tau correlation coefficients between phytoplankton groups and environmental variables ( $\alpha = 0.05$ ), assessed separately for each phytoplankton group-environmental variable combination. Significant correlations ( $p$ -value  $< 0.05$ ) are indicated by red and green for negative and positive correlations, respectively.

	Picocyanobacteria		<i>A. lagunensis</i>		Dinoflagellates		<i>M. rubra</i>		Planktonic diatoms		Benthic diatoms	
	tau	p-value	tau	p-value	tau	p-value	tau	p-value	tau	p-value	tau	p-value
Temperature (°C)	0.225	<0.001	0.043	0.414	-0.190	<0.001	0.028	0.624	0.030	0.585	0.087	0.086
Salinity	0.352	<0.001	0.470	<0.001	-0.138	0.006	-0.405	<0.001	-0.455	<0.001	-0.199	<0.001
Salinity Stratification	0.010	0.851	-0.030	0.582	0.058	0.259	-0.024	0.674	0.019	0.731	-0.226	<0.001
NH <sub>4</sub> <sup>+</sup> (μM)	-0.062	0.231	-0.178	<0.001	-0.148	0.003	0.167	0.003	0.190	<0.001	0.088	0.082
N+N (μM)	-0.113	0.030	-0.159	0.003	-0.232	<0.001	0.198	<0.001	0.266	<0.001	0.134	0.008
Orthophosphate (μM)	-0.067	0.203	-0.132	0.014	-0.064	0.206	0.136	0.016	0.204	<0.001	0.040	0.437
Silicate (μM)	0.315	<0.001	0.257	<0.001	0.101	0.046	-0.226	<0.001	-0.338	<0.001	-0.086	0.090
DON (μM)	0.085	0.102	0.037	0.485	0.096	0.058	0.105	0.063	0.055	0.319	0.019	0.712
DOC (μM)	0.344	<0.001	0.491	<0.001	-0.094	0.063	-0.257	<0.001	-0.338	<0.001	-0.125	0.014
Ciliate biovolume (μm <sup>3</sup> mL <sup>-1</sup> )	-0.029	0.576	-0.157	0.003	0.312	<0.001	0.011	0.848	0.015	0.780	0.151	0.003

# CHAPTER III: TIMESCALES AND DRIVERS OF CHLOROPHYLL VARIABILITY IN BAFFIN BAY, TEXAS

## **Abstract**

Little is known about the role of short-term (hourly to daily) processes on estuarine phytoplankton dynamics, though these are often important timescales of variability in coastal systems. This study coupled high-frequency (daily) data (2015 – 2016) with a lower frequency dataset (2014 – 2018) to investigate timescales of chlorophyll variability, and drivers of blooms in subtropical Baffin Bay, Texas. Sub-monthly variability was high in the system, which I show would have been missed with traditional (monthly, quarterly) sampling efforts. From bloom events identified in the high frequency dataset, wind was a predominant factor related to short-term (daily resolution) bloom events, often positively correlated with chlorophyll concentrations. Results expand upon the currently limited knowledge of short-term chlorophyll variability in subtropical, lagoonal systems. Additionally, findings also offer insight into the proper design of sampling programs in similar systems.

## **1. Introduction**

Estuaries are dynamic systems, defined by dominant modes of environmental variability that range from hourly (tidal cycles) to seasonal (temperature and freshwater inflow), and even decadal (climate oscillations that also affect temperature and freshwater inflow). Monitoring programs in a number of estuaries (e.g., San Francisco Bay, Chesapeake Bay, Neuse River Estuary; Cloern and Dufford, 2005; Rothenberger et al., 2009; Harding et al., 2019) have greatly improved our understanding of seasonal and interannual variability in estuarine phytoplankton population dynamics. However, while variability on short-term (hourly to daily) timescales has been shown to be important aspect of phytoplankton variability in many aquatic and marine

systems, it is not captured with traditional monitoring frequencies (Abreu et al., 2010; Cloern and Jassby, 2010; Côté and Platt, 1983; Litaker et al., 1993). Furthermore, the role of short-term processes (e.g., wind, tides) on phytoplankton dynamics has received little attention, limiting our ability to understand phytoplankton dynamics, and their environmental drivers, in coastal systems (Harris, 1980; Wetz et al., 2006).

Our understanding of estuarine phytoplankton dynamics is further complicated by differences in timescales of phytoplankton variability among estuaries worldwide (Cloern and Jassby, 2010; Winder and Cloern, 2010). Low-latitude systems tend to have less seasonal variability in light and temperature than is found in temperate systems, and as a result, phytoplankton seasonal patterns in low-latitude systems are generally depressed and more irregular than in temperate systems (Cushing, 1959; Winder and Cloern, 2010). This suggests that generalizations about predominant drivers and scales of phytoplankton dynamics may not be transferable across estuaries occupying different latitudinal bands or climatic regimes. Low latitude tropical and subtropical systems have generally received little research interest to date (Murrell et al., 2007), limiting our understanding of phytoplankton dynamics in them.

The goal of this study was to characterize chlorophyll at high temporal resolution (daily) in Baffin Bay, Texas. In addition, relevant environmental data were analyzed to assess drivers of short-term variability in chlorophyll. Results improve our understanding of timescales of phytoplankton variability in the estuarine environment and complement other chapters to provide a better understanding of phytoplankton population dynamics in a subtropical estuary (Baffin Bay, Texas). Additionally, by simulating various monitoring frequencies, I was able to demonstrate the effects of lower sampling frequency on the characterization of phytoplankton population dynamics.

## **2. Methods**

### **2.1. Baffin Bay, Texas**

Baffin Bay is a shallow (average depth  $\sim 1$  m) estuary located in a semi-arid region of the South Texas coast (Diener, 1975; Breier et al., 2010). Because there is no major river discharge to Baffin Bay and evaporation frequently exceeds precipitation, Baffin Bay is often hypersaline (*see* Chapter II). This, as well as minimal tidal influence ( $\leq 10$  cm on average), results in a long residence time on average (*see* Chapter II). Mixing within the bay is primarily wind-driven (Tunnell, 2002).

### **2.2. Monthly sampling to assess scales of chlorophyll variability**

Data from a monthly monitoring program (2014 – 2018) was used to assess variability in chlorophyll concentrations. As part of this sampling program, surface water was collected at site BB3 (Fig. 3.1), and extracted chlorophyll was determined fluorometrically as described in Wetz et al. (2016). Chlorophyll variability was assessed with a multiplicative decomposition model using the `decompTS` function from the `wql` package in R (Jassby et al. 2017). Output from this function was used to compare the relative magnitude of annual, monthly and sub-monthly variability during the 5-year sampling period (2014 – 2018), expressed as the standard deviation of each timescale component (Cloern, 2019).

### **2.3. High temporal resolution sampling program, 2015 - 2016**

Water temperature, salinity, and chlorophyll (as in vivo fluorescence) were monitored at 15-minute intervals using Hydrolab DS5X sondes deployed at  $\sim 0.5$  m depth at sites BB3 and Cayo (Fig. 3.1). Data collected at 15-minute intervals was subsequently converted to daily averages to remove diel signatures. Missing datapoints were filled by linear interpolation prior to taking the daily average, and a day was omitted if more than one consecutive hour of data was

missing within that 24-hour period. Gaps in data represent days when conductivity and/or chlorophyll sensors were not functioning or did not pass appropriate post-deployment checks, according to manufacturer's recommendations. The chlorophyll probe was calibrated with rhodamine dye, and was analyzed as reported by the sonde, in  $\mu\text{g L}^{-1}$ .

Bloom events were identified as chlorophyll increases of  $50 \mu\text{g L}^{-1}$  within a four-day period, which represents an approximate doubling of the mean chlorophyll concentration during the entire time series for both sites. When a bloom event was identified, sonde data from up to 14 days before and after the bloom were used to establish correlations between chlorophyll and environmental variables. Multiple blooms occurring within a 14-day period were combined and analyzed as one bloom event. Also note that a pair of back-to-back bloom events in spring 2015 at BB3 were combined for analysis. Statistical analyses were conducted on bloom events that coincided with continuous coverage of water temperature (from sondes), wind (from Kingsville Naval Air Station, Station USW00012928; Fig. 3.1) and rain (averaged from three sites in the Kingsville area: US1TXKL0011, USC00414810, USW00012928; Fig. 3.1; retrieved from the National Climatic Data Center), resulting in six blooms that were used for analysis. Wind data was assessed as average daily wind speed ( $\text{m s}^{-1}$ ) and the maximum daily wind speed (maximum wind speed sustained for 2-minute period,  $\text{m s}^{-1}$ ).

To identify explanatory variables for chlorophyll during each bloom event, additive linear models were explored using the dredge function (MuMIn package; Barton, 2018). The potential need for incorporation of one-day time-lagged variables was assessed with cross correlation functions. Models were compared with AICc (Corrected Akaike Information Criterion; MuMIn package; Barton, 2018) and the quality of models was assessed through diagnostic plots showing normality and model fit. Models were assessed to remove collinear variables and were

simplified using backwards regression to remove non-significant terms and create a significant model ( $\alpha = 0.05$ ). Note that during one bloom event (BB3 on 7/10/15 – 7/22/15), no rain occurred so it was not included in the analysis. Analyses were performed in R version 3.3.2 (R Core Team, 2016). To supplement interpretation of bloom event analysis, monthly discrete sample data (temperature, salinity, ammonium  $[\text{NH}_4^+]$ , nitrate + nitrite  $[\text{N+N}]$ , silicate, orthophosphate, phytoplankton community composition) from two adjacent sites, BB1 and BB3 (Fig. 3.1) were assessed (see methods in Cira and Wetz, 2019).

## **2.4. Effect of sampling frequency on chlorophyll estimates**

To determine the effects of different sampling frequencies on chlorophyll estimates, I utilized the 2015 daily sonde chlorophyll dataset from site BB3 and simulated the effects of two lower sampling frequencies (monthly, quarterly). The raw dataset had 171 days of useable chlorophyll data and was treated as one “year” of data (one “year” = 171 days). To mimic monthly or quarterly sampling of this “year” of data, the raw dataset was first divided into quarters ( $171/4 = 42.75$ ; n of each quarter = 42 or 43) and months ( $171/12 = 14.25$ ; n of each month = 14 or 15). Then, for each sampling frequency (quarterly and monthly), 1,000 random resampling simulations were conducted in which one random sample was collected for each quarter or month, resulting in 1,000 sets of 4 samples (quarterly sampling) or 12 samples (monthly sampling). Descriptive statistics (annual mean, minimum, maximum) were used to compare the resampled sets to the raw dataset.

## **3. Results**

### **3.1. Timescales of chlorophyll variability (2014 – 2018)**

From the decomposition model output, there was an overall decrease in annual chlorophyll coefficients from 2014 to 2018 (Fig. 3.2A). Seasonal trends are visible, with a

chlorophyll peak in summer months (Fig. 3.2B). The standard deviations of the decomposition model coefficients are representative of the variability contained in each model component (annual, seasonal, sub-monthly; error bars in Fig. 3.2). The standard deviation of the seasonal component (0.21) was less than that of the annual component (0.30), indicating the magnitude of interannual variability was larger than that of seasonal variability during the 5-year sample period (2014 – 2018; Fig. 3.2A,B). The standard deviation of the residual component (0.37) reflects variability not captured in the annual and monthly variation, and likely relates to short-term (sub-monthly) variability (Fig. 3.2C). The standard deviation of this component was greater than the seasonal and the annual components, reflecting the relative importance of short-term variability in the chlorophyll dynamics in Baffin Bay from 2014 to 2018.

### **3.2. Effects of different sampling frequencies on simulated annual chlorophyll concentrations**

Chlorophyll concentrations at BB3 averaged  $69.7 \mu\text{g L}^{-1}$  and ranged from  $8.2 \mu\text{g L}^{-1}$  to  $305.9 \mu\text{g L}^{-1}$  in 2015 ( $n=171$ ; Figs. 3.3A,B, 3.4). The distribution of chlorophyll measurements was skewed right (Fig. 3.3A,B); while the majority of measurements were  $< 40 \mu\text{g L}^{-1}$ , some reached  $> 300 \mu\text{g L}^{-1}$ . Measurements  $> 100 \mu\text{g L}^{-1}$  were all from the spring 2015.

The average of the annual chlorophyll means calculated from the monthly ( $69.5 \mu\text{g L}^{-1}$ ) and quarterly ( $69.0 \mu\text{g L}^{-1}$ ) simulations did not differ from that of the raw dataset ( $69.7 \mu\text{g L}^{-1}$ ; Table 3.1), though the variability of the calculated annual means differed between the resampling frequencies. The annual means calculated using quarterly sampling ranged from  $28.3 \mu\text{g L}^{-1}$  to  $117.5 \mu\text{g L}^{-1}$ , while those calculated using monthly sampling spanned from  $54.3 \mu\text{g L}^{-1}$  to  $95.1 \mu\text{g L}^{-1}$  (Table 3.1; Fig. 3.3A,B). Additionally, the characterization of the distribution of chlorophyll measurements varied between the sampling methods. The range of chlorophyll

concentrations in the raw data was from  $8.2 \mu\text{g L}^{-1}$  to  $305.9 \mu\text{g L}^{-1}$  (Fig. 3.3A,B). With quarterly sampling, the maximum concentration reported for each simulated year was, on average,  $174.6 \mu\text{g L}^{-1}$ ,  $\sim 131 \mu\text{g L}^{-1}$  less than the raw data maximum (Fig. 3.3A). The minimum concentration captured with quarterly sampling was, on average,  $24.9 \mu\text{g L}^{-1}$ ,  $\sim 17 \mu\text{g L}^{-1}$  higher than the raw data minimum. With monthly sampling, the maximum concentration averaged  $260.4 \mu\text{g L}^{-1}$  ( $\sim 46 \mu\text{g L}^{-1}$  lower than raw data maximum) and the minimum concentration averaged  $17.2 \mu\text{g L}^{-1}$  ( $\sim 9 \mu\text{g L}^{-1}$  higher than the raw data minimum; Fig. 3.3B, Table 3.1).

### **3.3. Spatial and temporal distribution of chlorophyll and environmental factors (2015 – 2016)**

At both sonde deployment sites, water temperature followed a consistent seasonal trend, peaking at just over  $30 \text{ }^{\circ}\text{C}$  in summer months and decreasing to near  $10 \text{ }^{\circ}\text{C}$  in the winter months (Fig. 3.5). Variability in temperature was higher in the winter/spring months, with temperature shifts of  $5\text{-}10 \text{ }^{\circ}\text{C}$  noted over short timescales ( $< 3 \text{ d}$ ), while in summer months temperatures remained constant (Fig. 3.5). No clear seasonal trend in salinity was observed (Fig. 3.5). Instead, salinity was characterized by an extended increase, punctuated by sharp decreases due to rain events (Fig. 3.5). Salinities ranged from  $\sim 10$  to  $\sim 45$  at both sites (Fig. 3.5).

Chlorophyll concentrations did not exhibit clear seasonal trends. Concentrations peaked in early spring 2015 at both sonde deployment sites (BB3 and Cayo; Fig. 3.5). Overall, concentrations were slightly higher and more variable at BB3 than Cayo ( $51.6 \pm 61.3 \mu\text{g L}^{-1}$ ,  $47.2 \pm 47.9 \mu\text{g L}^{-1}$ , respectively), though temporal coverage was also higher at BB3 ( $n = 309$ ) than Cayo ( $n = 235$ ). Bloom events were identified at both sites, across years and seasons (Figs. 3.5, 3.6). Blooms were often ephemeral, lasting  $< 3$  days, though many bloom events also

consisted of multiple chlorophyll peaks leading up to the day with maximum chlorophyll (day 0 on Fig. 3.6).

### 3.4. Short-term drivers of blooms (2015 – 2016)

In spring 2015, bloom events were identified at both BB3 and Cayo. The phytoplankton community was dominated by *A. lagunensis* during this time (see Chapter II). An extended bloom event occurred at BB3 from 2/20 to 3/17 (BB3-A; Fig. 3.7A). Based on the linear model, over half (adjusted  $r^2 = 0.56$ ) of the chlorophyll variability during this time can be explained by inverse relationships with average wind speed and temperature (Table 3.2). On 2/19, leading up to this bloom event, salinity was 43.2,  $\text{NH}_4^+$  concentration was  $0.44 \mu\text{M}$ , N+N concentration was  $0.46 \mu\text{M}$ , orthophosphate concentration was  $0.25 \mu\text{M}$ , and silicate concentration was  $83.9 \mu\text{M}$  (Table 3.3). After the event (on 3/18), orthophosphate and  $\text{NH}_4^+$  concentrations increased (to  $0.52 \mu\text{M}$  and  $0.69 \mu\text{M}$ , respectively), while N+N and silicate concentrations were slightly lower ( $0.02 \mu\text{M}$  and  $79.1 \mu\text{M}$ , respectively) than on 2/19 (Table 3).

Later in spring 2015, there was a bloom at Cayo from 4/1 – 4/10 (Cayo-A; Fig. 3.8A). Sonde coverage did not capture the decline of the bloom. In contrast to the spring bloom at BB3, temperature was positively related to chlorophyll and, along with rain, explained almost half of the variability in chlorophyll (adjusted  $r^2 = 0.45$ ; Table 3.4). Salinities at both of the adjacent sites decreased from before (3/18) to after (4/16) the bloom event, though the decrease at BB1 was more pronounced (Tables 3.5, 3.6). The phytoplankton community biovolume at both nearby sites decreased from 3/18 to 4/16. *A. lagunensis* dominated community biovolume at both sites on both dates, but at BB1 there was a noticeable increase in diatom and dinoflagellate biovolume from 3/18 to 4/16 (see Chapter II).  $\text{NH}_4^+$ , N+N, and orthophosphate concentrations at BB1 increased by orders of magnitude from 3/18 to 4/16 ( $\text{NH}_4^+$ :  $0.78 \mu\text{M}$  to  $2.30 \mu\text{M}$ ; N+N: 0.01

$\mu\text{M}$  to  $15.92 \mu\text{M}$ ; orthophosphate:  $0.81 \mu\text{M}$  to  $9.57 \mu\text{M}$ ), while concentrations at BB3 remained low (Tables 3.5, 3.6).

In contrast to the spring, the phytoplankton community was more diverse during summer 2015, with diatoms accounting for the largest fraction of community biovolume at BB1 and BB3 (see Chapter II). The summer 2015 bloom event at BB3 (BB3-B), occurred from 7/10 to 7/22 (Fig. 3.7B). Sonde coverage did not capture the bloom decline. Maximum wind speed was positively correlated with chlorophyll during this event, explaining 36% of the variation in chlorophyll (Table 3.2). Temperature was invariant throughout the bloom (Fig. 3.7), while salinity increased from before to after the bloom (6/24 to 7/23; Table 3.3). Silicate concentration decreased sharply, from  $68.5 \mu\text{M}$  to  $11.6 \mu\text{M}$  (Table 3.3). N+N and orthophosphate concentrations also decreased, while  $\text{NH}_4^+$  concentration increased ( $5.79 \mu\text{M}$  to  $12.41 \mu\text{M}$ ; Table 3.3). There was no rain during this period, and the most recent rain event was noted over a week prior to the bloom event, on 7/2/2015 (data not shown).

A summer 2015 bloom event at Cayo (Cayo-B) occurred from 7/24 to 8/12 (Fig. 3.8B). Based on the linear model, there was a significant positive relationship between chlorophyll and average wind speed, with an adjusted  $r^2$  of 0.43 (Table 3.4). Temperature remained constant for a large portion of the bloom, with only a slight increase in temperature noted in early August. Salinity increased from before (7/23) to after (8/13) the bloom at both BB1 (15.9 to 20.5) and BB3 (17.8 to 20.4; Tables 3.5, 3.6).  $\text{NH}_4^+$  and N+N concentrations decreased over that time period at both BB1 ( $\text{NH}_4^+$ :  $2.40 \mu\text{M}$  to  $0.61 \mu\text{M}$ ; N+N:  $0.65 \mu\text{M}$  to  $0.19 \mu\text{M}$ ) and BB3 ( $\text{NH}_4^+$ :  $12.41 \mu\text{M}$  to  $1.62 \mu\text{M}$ ; N+N:  $5.07 \mu\text{M}$  to  $0.27 \mu\text{M}$ ), while silicate concentrations increased at both sites (BB1:  $15.9 \mu\text{M}$  to  $27.4 \mu\text{M}$ ; BB3:  $11.6 \mu\text{M}$  to  $21.5 \mu\text{M}$ ; Tables 3.5, 3.6).

Orthophosphate concentrations had mixed trends (BB1: 0.44 to 0.26  $\mu\text{M}$ ; BB3: 0.23  $\mu\text{M}$  to 0.36  $\mu\text{M}$ ; Tables 3.5, 3.6).

Winter blooms were observed at both BB3 and Cayo, though in different years. The Cayo winter bloom was observed from 11/21/15 - 11/30/15 (Cayo-C; Fig. 3.8C). Based on cell count data from BB1 and BB3 on 11/19 and phytoplankton live screens from 12/10, the community during this bloom consisted mainly of dinoflagellates, *M. rubra*, *A. lagunensis*, and planktonic, chain-forming diatoms (*see* Chapter II). During this bloom, chlorophyll was positively correlated with one-day lagged average wind speed, explaining 61% of the variation in chlorophyll (Table 3.4). From before (11/15) to after (12/10) the bloom event, there were decreases in orthophosphate and silicate concentrations at both BB1 and BB3 (Tables 3.5, 3.6). The decrease in silicate was sharp, from 81.3  $\mu\text{M}$  to 9.1  $\mu\text{M}$  at BB1, and from 89.1  $\mu\text{M}$  to 0.4  $\mu\text{M}$  at BB3 (Tables 3.5, 3.6). DIN concentrations increased at BB1 ( $\text{NH}_4^+$ : 3.59  $\mu\text{M}$  to 7.49  $\mu\text{M}$ ; N+N: 0.35  $\mu\text{M}$  to 0.53  $\mu\text{M}$ ) and decreased at BB3 ( $\text{NH}_4^+$ : 14.49  $\mu\text{M}$  to 3.46  $\mu\text{M}$ ; N+N: 1.12  $\mu\text{M}$  to 0.59  $\mu\text{M}$ ; Tables 3.5, 3.6).

A winter bloom was observed at BB3 from 12/14/16 to 12/28/16 (BB3-C; Fig. 3.7C). Although I do not have cell counts from this time, phytoplankton live screens indicated a mix of diatoms, dinoflagellates, and small flagellates. From the linear model, both average wind speed and one-day lagged average wind speed were significantly related to chlorophyll, together explaining 79% of variability in chlorophyll during the event (Table 3.2). On 12/14, at the beginning of this bloom event, salinity was 43.2, silicate was high (139.3  $\mu\text{M}$ ), and  $\text{NH}_4^+$  and N+N were 8.65  $\mu\text{M}$  and 3.73  $\mu\text{M}$ , respectively (Table 3.3). Temperature did fluctuate throughout the bloom event (Fig. 3.7), though it did not correlate to chlorophyll (Table 3.2). No

post-bloom environmental data from January 2017 is available, as sampling was prevented due to poor weather.

#### **4. Discussion**

In this study I combined two years of high-frequency data with an extended dataset from a monthly sampling program to investigate timescales of chlorophyll variability and drivers of blooms in Baffin Bay, Texas. Results show that event-scale (i.e., sub-monthly) chlorophyll variability was higher than variability associated with lower frequency timescales (i.e., seasonal, interannual), which is common in coastal systems (Cloern and Jassby, 2010). I was also able to elucidate drivers of short-term variability in phytoplankton population dynamics, which is sorely lacking because many sampling programs are unable to sample relevant variables (including chlorophyll) at high frequencies due to monetary or logistical concerns. Results presented expand upon the currently limited knowledge of short-term chlorophyll variability in subtropical, lagoonal estuarine systems. Findings also offer insight into the proper design of sampling programs in similar systems.

##### **4.1. Timescales of chlorophyll variability (2014 – 2018)**

The magnitude of short-term (sub-monthly) variability was higher than that of monthly and interannual variability in Baffin Bay. High short-term variability in phytoplankton biomass is common in coastal systems (Cloern and Jassby, 2010), and may reflect factors affecting phytoplankton growth or biomass distribution that occur on timescales of hours-days (e.g., tides, advection; Wetz et al., 2006; Pannard et al., 2008), as well as episodic changes in phytoplankton biomass due to ephemeral climatic events (Litaker et al., 1993; MacIntyre and Cullen, 1996; Winder and Cloern, 2010). Based on a similar analysis conducted by Cloern and Jassby (2010) on coastal systems worldwide, in which the median sub-monthly variability among 84 datasets

was found to be 0.59, the sub-monthly variability in Baffin Bay is relatively low (0.37). This may be explained by the absence of a tidal influence in Baffin Bay, in contrast to estuaries such as the Matanzas River Estuary (Florida; Dix et al., 2013) or North Inlet (South Carolina; Wetz et al., 2006) where tides have a strong influence on phytoplankton biomass. It may also be explained by the long-residence time of Baffin Bay, which would allow for extended effects of high rainfall periods, in contrast to systems with rapid flushing that would return conditions to baseline quickly (Rhode River subestuary, Chesapeake Bay; St. Lucie Estuary, Florida; Gallegos and Neale, 2015; Philips et al., 2020). As discussed later, the sub-monthly variability in Baffin Bay likely reflects the relative importance of short-timescale processes such as wind and localized, ephemeral rain events (MacIntyre and Cullen, 1996; Lucas and Cloern, 2002; Abreu et al., 2010). For example, wind was implicated as an important driver of short-term chlorophyll dynamics in nearby San Antonio Bay (MacIntyre and Cullen, 1996) and in other systems worldwide (e.g., Pannard et al. 2008; Abreu et al. 2010).

While not as large in magnitude as sub-monthly variability, there was also significant variability in chlorophyll at interannual timescales in Baffin Bay. During 2014-2018, effects of El Niño Southern Oscillation (ENSO), through both non-El Niño (drought) and El Niño (high rainfall) conditions, were observed and are a primary cause of the high interannual phytoplankton variability in chlorophyll (*see* Chapter II). Climatic phenomena such as the Pacific Decadal Oscillation and North Atlantic Oscillation have been associated with interannual variability in other subtropical and temperate coastal systems (Miller and Harding, 2007; Abreu et al., 2010; Cloern and Jassby, 2010). In Texas, El Niño conditions lead to high rainfall and low salinities in the coastal zone (Tolan, 2007). The periodicity of ENSO along the Texas coast is

estimated to be 4-5 years (Tolan, 2007), so this interannual variability can be expected to have a recurring imprint on phytoplankton dynamics in Baffin Bay and other Texas estuaries.

Seasonal timescales contributed the least to variability in chlorophyll in Baffin Bay. A similar depressed seasonal pattern in the Patos Lagoon Estuary, Brazil, a subtropical, microtidal lagoon, is thought to be caused by the absence of a consistent bloom season (Abreu et al., 2010; Cloern and Jassby, 2010). In contrast, in many temperate river-dominated estuarine systems phytoplankton dynamics exhibit pronounced seasonal trends (e.g., Chesapeake Bay; Malone et al., 1988). Overall, the distinction between sub-tropical systems like Baffin Bay and temperate systems is consistent with the positive relationship between seasonal variability and latitude demonstrated by Cloern and Jassby (2010).

#### **4.2. Effects of sampling frequency**

Monthly and quarterly sampling are common frequencies for water quality monitoring programs, and both frequencies have been used to sample Baffin Bay. Most bloom events identified with the high-frequency sampling in this study lasted less than three days, so these blooms would likely not be captured by traditional (monthly, quarterly) sampling approaches. This effect was seen in sampling simulations as a reduction in the maximum chlorophyll concentration captured with either (monthly, quarterly) sampling approach. Compared with the raw dataset, the maximum chlorophyll concentration was reduced by 15% in monthly sampling simulations and by 43% in quarterly sampling simulations. Similar relationships between sampling frequencies and chlorophyll variability have been reported elsewhere (Baltic Sea, Rantajarvi et al. 1998), highlighting the limitations of traditional sampling frequencies in capturing short-term chlorophyll variability.

The appropriate sampling resolution depends on chlorophyll variability in the system (Rantajärvi et al., 1998). As noted here, inadequate sampling frequency may cause blooms to be missed, or lead to an incomplete/inaccurate understanding of drivers of phytoplankton dynamics (Rantajärvi et al., 1998; Abreu et al., 2010). However, depending on available resources and research goals, sampling at a high frequency may not always be recommended. For example, MacIntyre and Cullen (1996) found that daily productivity in San Antonio Bay, Texas, could be reasonably estimated from one discrete midday sample. Thus, to maximize resources, they suggest future monitoring efforts limit sampling to once daily and focus on characterizing day-to-day, rather than within-day, variability in productivity. In short, sampling frequency should be aligned with research needs. If the specific goal is to capture bloom events in Baffin Bay that develop and decline on timescales of days, monthly or quarterly sampling is clearly inadequate, and daily resolution sampling may be needed. However, if the goal is to describe interannual or long-term trends, then monthly scales may be a preferred frequency because, as shown here, they may adequately capture the annual mean chlorophyll without the need for more labor intensive, costlier higher frequency sampling. As done in this study, a combination of monitoring methods may be an acceptable approach to balance data needs and resource limitations.

#### **4.3. Linking environmental drivers to blooms**

Bloom events were identified across seasons and years at both sites, corresponding with a range of temperature and salinity conditions. Wind-related variables (average speed, maximum speed, one-day lagged average wind speed) were significant factors related to chlorophyll in five of the six bloom events assessed, indicating that wind is an important driver of phytoplankton dynamics in Baffin Bay. High wind may inject nutrients from sediment porewater into the water column while also resuspending sediments that may release nutrients (Morin and Morse, 1999;

Giffin and Corbett, 2003), stimulating phytoplankton growth in surface waters (Valiela et al., 1998; Lawrence et al., 2004; Yeager et al., 2005). High wind may also resuspend phytoplankton cells, directly increasing phytoplankton biomass in the surface waters (Demers et al. 1987; Millet and Cecchii 1992; Garstecki et al. 2002). Wind has been linked to short-term chlorophyll variability in nearby San Antonio Bay (MacIntyre and Cullen, 1996) and in other systems worldwide (Pannard et al. 2008; Abreu et al. 2010). It is not surprising that wind-driven mixing affects phytoplankton dynamics in Baffin Bay because of its shallow depth (Diener, 1975). Likewise, wind-driven mixing has been recently demonstrated to be an important driver of suspended sediment dynamics in nearby Corpus Christi Bay (Reisinger et al., 2017).

During the summer blooms, wind was the only factor related to chlorophyll, and wind alone predicted ~40% of chlorophyll variability during both events. Summer tends to be a dry period in South Texas, with relatively little rainfall and high rates of evaporation (Breier et al., 2010; TWDB, 2011). These conditions were reflected by salinity increases at BB1 and BB3 over the course of both bloom events and the complete absence of rain during one event. Without external nutrient inputs during the summer months, wind-driven resuspension of nutrients may be an important source of nutrient flux into the surface water. The increase in  $\text{NH}_4^+$  from before to after the bloom event at BB3 reflects a wind-driven release of  $\text{NH}_4^+$  from sediments (Morin and Morse, 1999), while the simultaneous decrease in silicate is consistent with uptake by diatoms, which may have been resuspended by wind. The surface water diatom community at BB3 during July and August 2015 was primarily benthic taxa (Naviculoids and *Cylindrotheca*; see Chapter II), supporting this interpretation of the data. While the bloom decline was not captured in the BB3 bloom event, it was captured during the Cayo bloom. The positive correlation between wind and chlorophyll for the duration of the bloom indicates that not only

was high wind associated with bloom initiation, but also that relaxation of wind was associated with bloom decline. This could either be due to a cessation of nutrient flux or sedimentation of diatoms cells (Garstecki et al., 2002). On the two days following peak chlorophyll, concentrations decreased by 26% and 57% each day. Based on sinking velocities described by Durante et al. (2019) for simple, elongated cells, the sinking rate of the dominant benthic diatom group enumerated (Naviculoids of length  $\sim 30 \mu\text{m}$ ) would be  $\sim 0.6 \text{ m day}^{-1}$ . Thus, in the absence of turbulence these cells could be completely removed from the surface water within one day. However, average wind speeds were  $> 5 \text{ m s}^{-1}$  even at the end of the bloom. This suggests that the decrease in chlorophyll was not driven solely by sedimentation, as wind speeds of similar magnitudes are associated with resuspension of benthic particles (sediments and/or phytoplankton cells) in other shallow, coastal systems (e.g., Millet and Cecchi, 1992; Arfi et al., 1994; Booth et al., 2000). Instead, horizontal dispersion due to wind may have contributed to the bloom demise (Millet and Cecchi, 1992). Additionally, biological processes like grazing and benthic filter feeders were not explored here, but are known to play a role in short-term phytoplankton dynamics (Litaker et al., 1993; Thompson et al., 2008), particularly in summer months, and should be considered in future studies addressing the decline of blooms in this system.

As during summer, there was also a significant relationship between chlorophyll dynamics and wind during winter. A key difference however was that there was a one-day time lag between wind speed increases and chlorophyll increases during the winter months. I suspect that this is due to the slower phytoplankton growth rates seen in colder months (Côté and Platt, 1983; Litaker et al., 1993). The presence of a time lag also suggests that the increase in chlorophyll is due to phytoplankton growth rather than merely resuspension of phytoplankton

cells. Benthic phytoplankton biomass tends to be lower in winter months than during spring or summer (MacIntyre and Cullen, 1996), suggesting that overall, wind-driven resuspension of phytoplankton cells may be less important in winter months compared with other times of year. Furthermore, the plankton community during this time consisted primarily of planktonic rather than benthic diatom taxa.

Wind was not the only environmental factor found to correlate with bloom formation in the bay. In the spring of 2015, blooms occurred at BB3 and Cayo despite negative (BB3) or non-existent (Cayo) relationships between wind and chlorophyll. One aspect of these blooms that was different from the aforementioned summer and winter blooms was the high abundance of *A. lagunensis*. For the Cayo spring bloom, chlorophyll was positively correlated with temperature and rain. There are two possibilities behind the positive relationship between temperature and chlorophyll, and they are not mutually exclusive. The first is simply that phytoplankton growth tends to increase with increasing temperatures (Eppley, 1972), which (temperature increase) in this case would have also corresponded to increasing daylength and light availability. The combination of these factors has long been known to lead to classic spring blooms in oceanic systems (Cushing, 1959). Another possibility is that the increased temperature stimulated nutrient regeneration, which is temperature-dependent (Kemp and Boynton, 1984). Indeed, DIN concentrations were low prior to the bloom, and N:P ratios were indicative of N-limiting conditions. Thus factors increasing N-availability would likely have had a positive impact on phytoplankton growth. This may also explain the positive relationship between chlorophyll and rain, which would have supplied additional nutrients to the system. In contrast to the spring bloom event at Cayo, the spring bloom event at BB3 was negatively correlated with both wind and temperature. Late winter/spring is characterized by the passage of northerly fronts in ~ 5 day

intervals, associated with wind speeds  $> 15 \text{ m s}^{-1}$ , an abrupt shift in wind direction from the southeast to the north, and a drop in air temperature (Morgan et al., 1975; Buskey et al., 1997; Ward, 1997; Reisinger et al., 2017). The environmental variability at this time, combined with the lag in phytoplankton response identified during the winter blooms (though not explicitly identified in the spring), complicates our ability to link these factors directly with a biologic response. However, instances of wind speeds  $> 15 \text{ m s}^{-1}$  were followed by an increase in chlorophyll at two times throughout the BB3 spring bloom event, suggesting chlorophyll increases after passage of northerly fronts. Springtime blooms in other systems have been associated with periods of strong wind followed by a relaxation of wind (Tian et al., 2011). MacIntyre et al. (2004) describe high wind events as triggering formation of *Aureococcus anophagefferens* blooms by creating conditions favorable for its growth (high turbidity/low light, high organic nutrients). Because of its slow growth rate, bloom formation after these conditions were created would not be immediate. A similar relationship is expected to exist for *A. lagunensis* because it is adapted to the high turbidity/low light conditions that may be caused by wind (Buskey et al., 1998; Ong et al., 2010), can utilize organic nitrogen forms (e.g., Muhlstein and Villareal, 2007), and has relatively slow growth (Buskey et al., 1998). The negative relationship between chlorophyll and temperature may also be an artifact of the passage of cold fronts, which are typically followed by depressed temperatures (Ward, 1997). This is demonstrated by the initial chlorophyll increase during the BB3 spring bloom event, which corresponded to both a decrease in temperature as well as a relaxation of wind speed.

While the analysis of high frequency data here highlights the importance of wind to short-term phytoplankton dynamics in Baffin Bay, it is important to reiterate that many other factors such as nutrient concentrations and grazing pressure have been shown to play significant

roles in bloom dynamics. Short-term nutrient addition bioassays conducted at a similar time as this analysis (2015) demonstrate a stimulatory effect of nitrogen on phytoplankton growth in Baffin Bay, suggesting that nitrogen concentration may be an important driver of phytoplankton dynamics in the bay on daily timescales (Wetz et al., 2017). Additionally, on longer timescales, a disruption in grazing pressure is thought to have contributed to a previous bloom in the system (Buskey, 1997). These factors are more onerous to assess on hourly-daily timescales, but knowledge of them would be needed to comprehensively assess drivers of bloom dynamics in the system.

## **5. Conclusions**

As demonstrated here, wind is a prevailing driver of phytoplankton population dynamics on daily time scales in Baffin Bay, influencing chlorophyll variability that is likely missed by coarse monitoring programs. This study suggests a variety of mechanisms by which wind can influence the phytoplankton community in Baffin Bay, such as by resuspending phytoplankton cells from the sediments, stimulating cell growth, and potentially even influencing the composition of the phytoplankton community. These results are important locally given that wind speeds along the Texas coast are projected to increase due to climate change (McInnes et al., 2011).

The short-timescale variability (e.g., daily) seen here represents a large portion of chlorophyll variability in many systems worldwide (Côté and Platt, 1983; Anderson, 2009; Cloern and Jassby, 2010; Martin-Platero et al., 2018). Unfortunately most sampling programs do not operate at these high frequency timescales and consequently relatively little is still known about the role of short-term processes on estuarine phytoplankton ecology (Harris, 1980; Wetz et al., 2006; Pannard et al., 2008). Nonetheless, it is important to acknowledge that drivers of

phytoplankton variability occur on a continuum of scales (Cloern, 2019), and quantification of scales of variability will help distinguish phytoplankton responses to short-term drivers from those attributable to long-term, lower-frequency factors like climate change and eutrophication (Cloern and Jassby, 2008; Li et al., 2010).

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## Figures

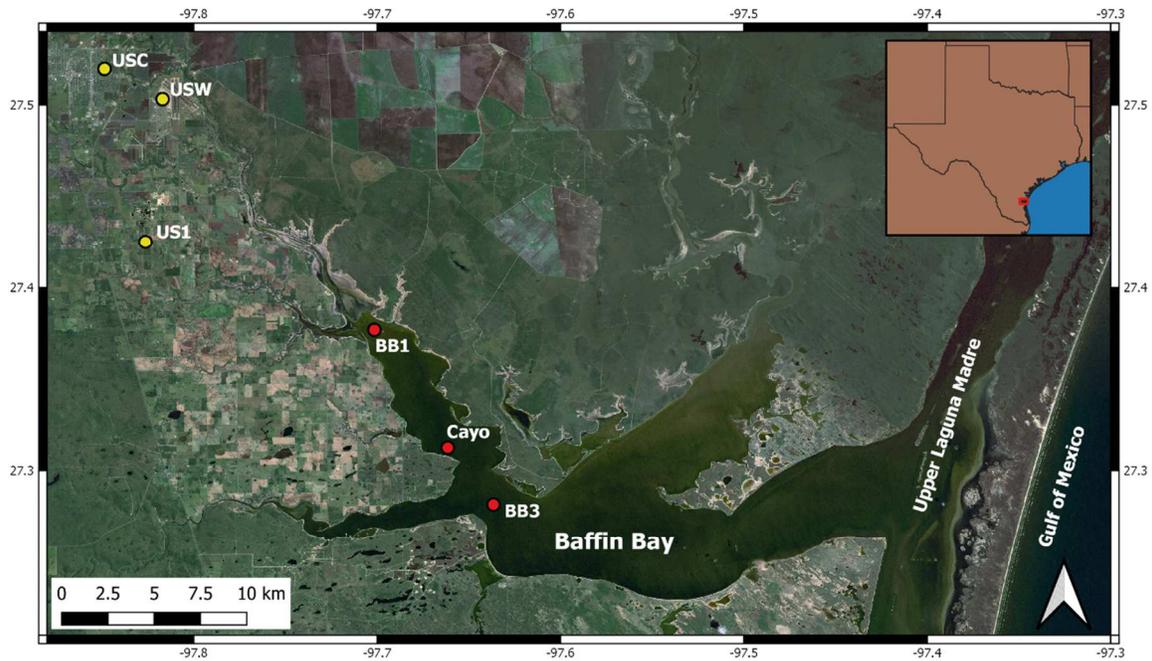


Figure 3.1. Map of Baffin Bay, Texas. Red circles indicate Baffin Bay monthly water quality sampling stations (BB1, BB3) or sonde deployment sites (Cayo, BB3). Yellow circles indicate stations where wind data and rainfall data were collected, with labels taken from the first three letters of the station names.

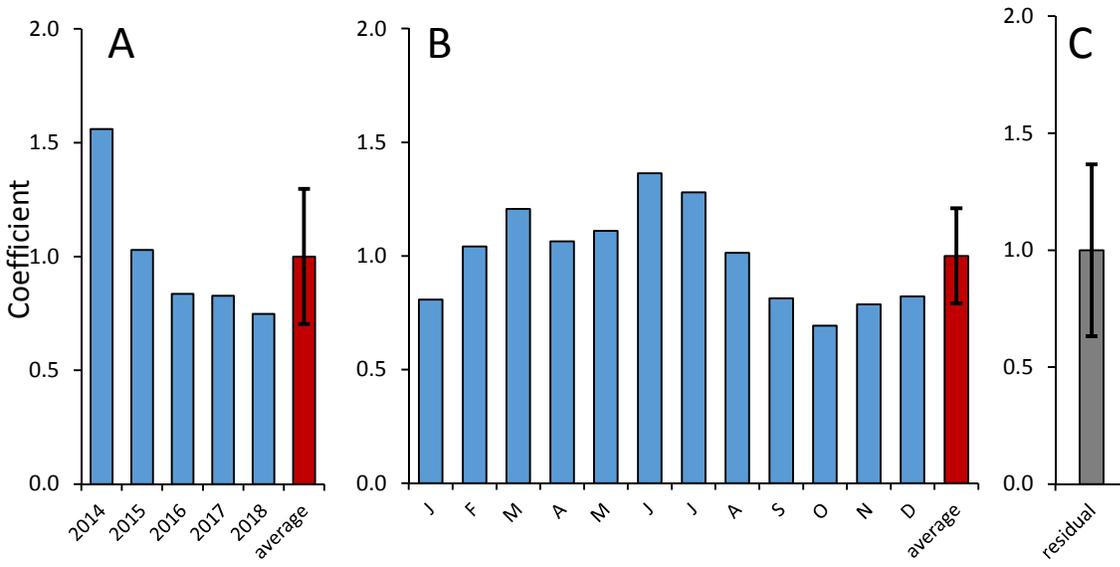


Figure 3.2. Annual (A), monthly (B), and residual (C) coefficients for chlorophyll from the decomposition model. For annual and monthly coefficients, individual coefficients are in blue, and the average is in red. The average residual (sub-monthly) coefficient is in gray. Error bars represent standard deviation for the average annual, monthly, and residual coefficients.

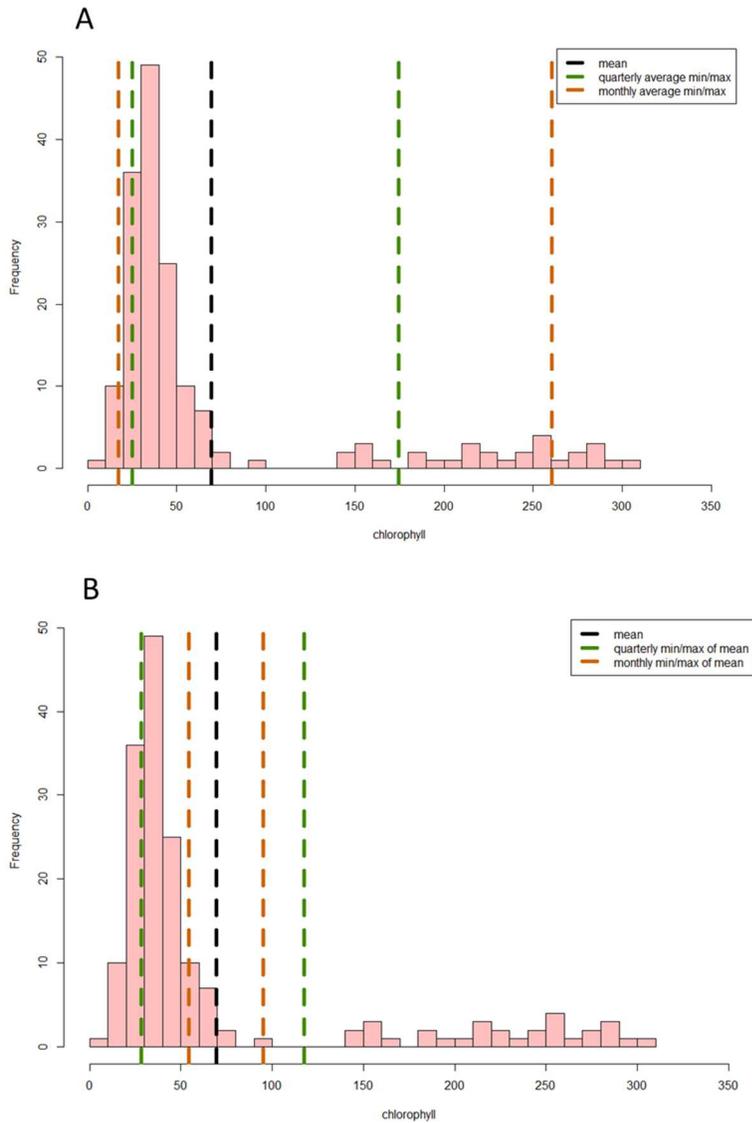


Figure 3.3. Histograms of raw dataset (n=171; peach bars) overlaid with with mean chlorophyll concentrations (black lines). Summary statistics from quarterly (green lines) and monthly (brown lines) resampling simulations show: A) the average minimum and maximum chlorophyll concentrations reported with quarterly and monthly sampling simulations, and; B) the range (minimum and maximum) of annual chlorophyll means calculated with quarterly and monthly sampling simulations.

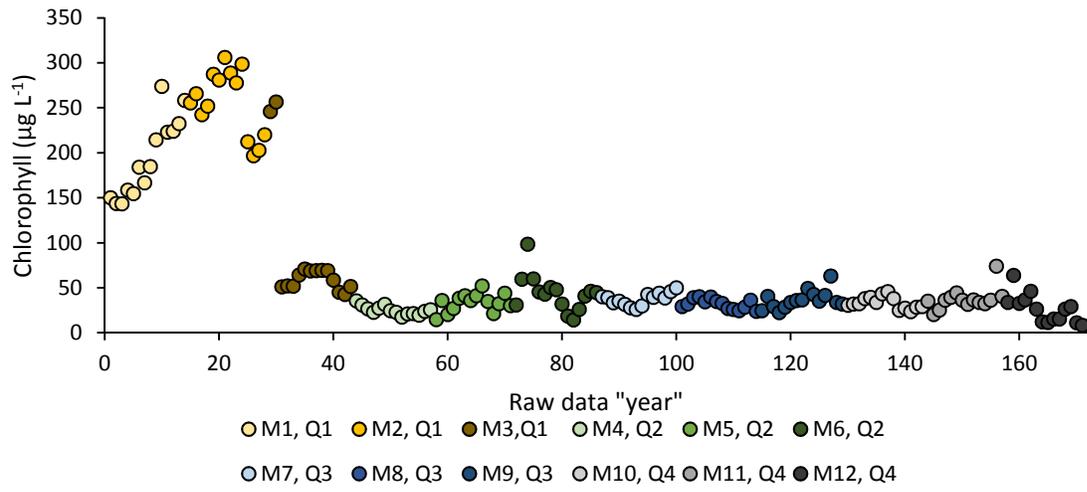


Figure 3.4. Raw dataset “year” (n=171) used in the resampling simulations, color-coded based on the month (M) or quarter (Q) each datapoint was grouped in for the resampling simulations.

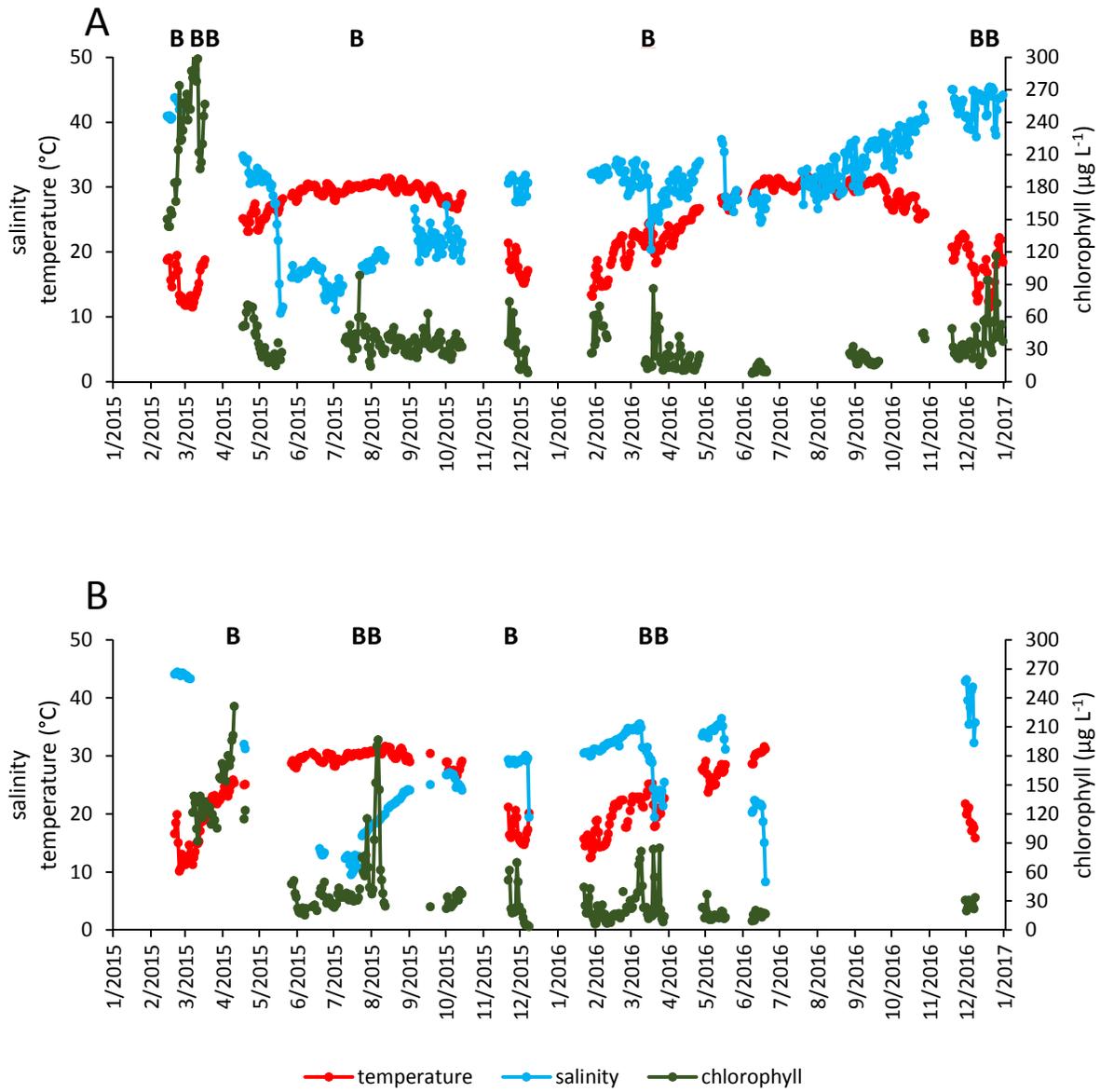


Figure 3.5. Daily averaged salinity, water temperature (°C) and chlorophyll ( $\mu\text{g L}^{-1}$ ) from continuous sonde deployments at two sites in Baffin Bay, A) BB3 and B) Cayo. Bloom events are indicated by a “B” along the top of each panel.

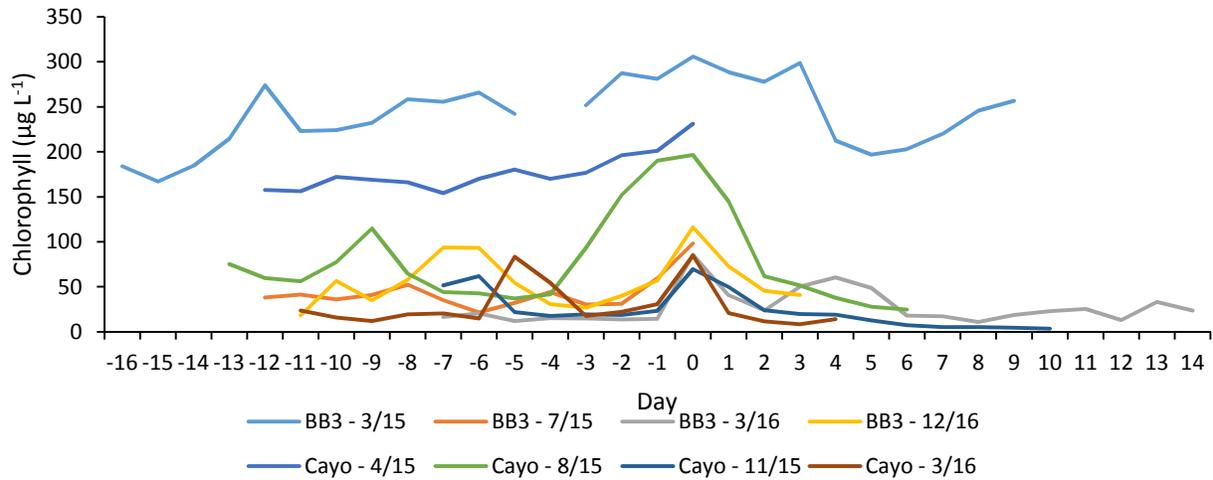


Figure 3.6. All identified bloom events by month/year of occurrence. Bloom events are plotted with the maximum chlorophyll concentrations ( $\mu\text{g L}^{-1}$ ) aligned with day 0 along the x-axis, with the extent of data coverage showing the chlorophyll concentrations on days leading up to, and after, the chlorophyll peak.

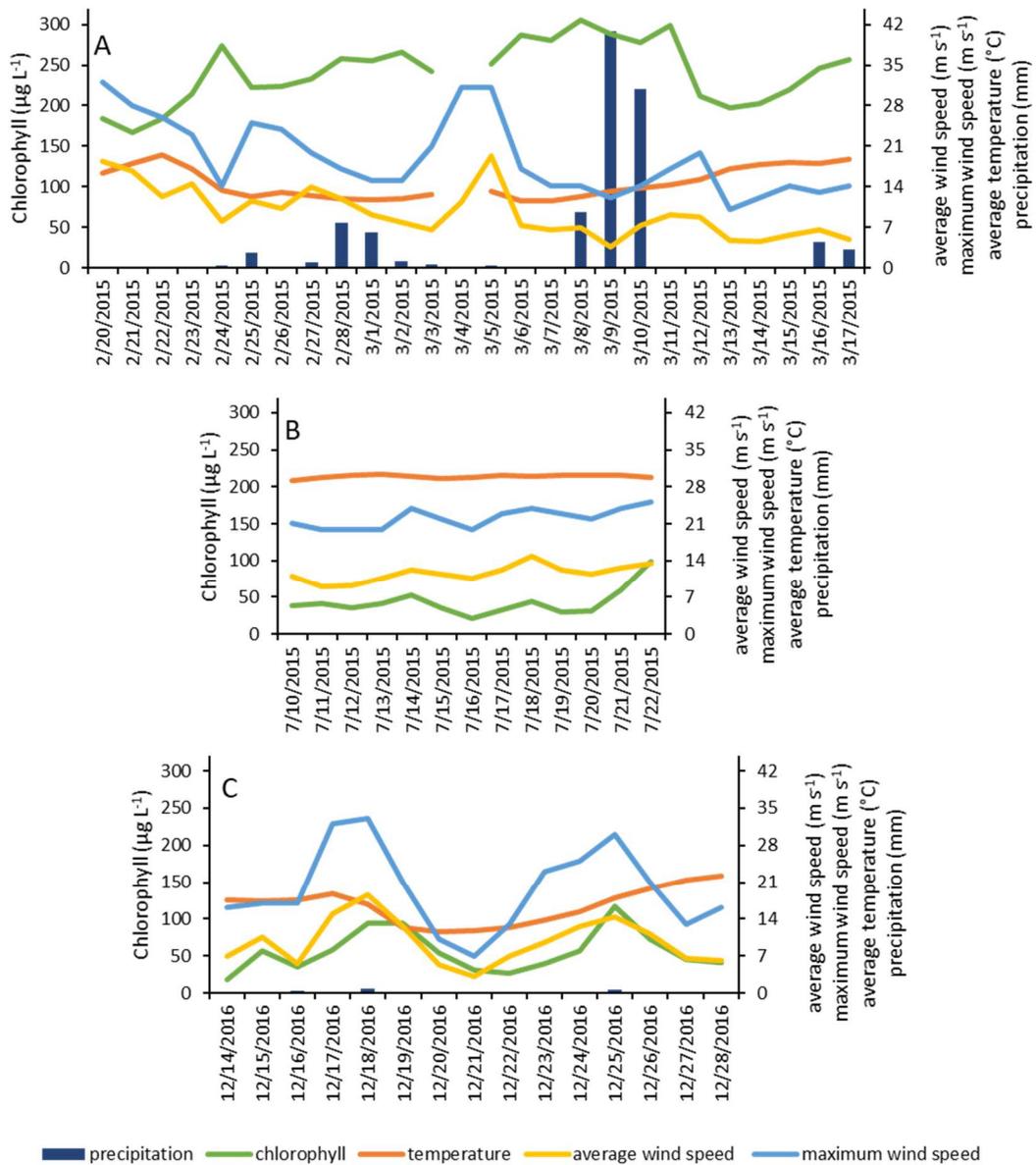


Figure 3.7. Chlorophyll ( $\mu\text{g L}^{-1}$ ), temperature ( $^{\circ}\text{C}$ ), average daily wind speed ( $\text{m s}^{-1}$ ), maximum 2-minute sustained daily wind speed ( $\text{m s}^{-1}$ ) and rainfall amount ( $\text{mm day}^{-1}$ ) for three bloom events analyzed at BB3. Bloom event names, dates, and sample sizes are as follows and correspond to panels in figure: A) BB3-A, 2/20/15-3/17/15,  $n = 25$ ; B) BB3-B, 7/10/15 -7/22/15,  $n = 13$ ; C) BB3-C, 12/14/16 - 12/28/16,  $n = 15$ .

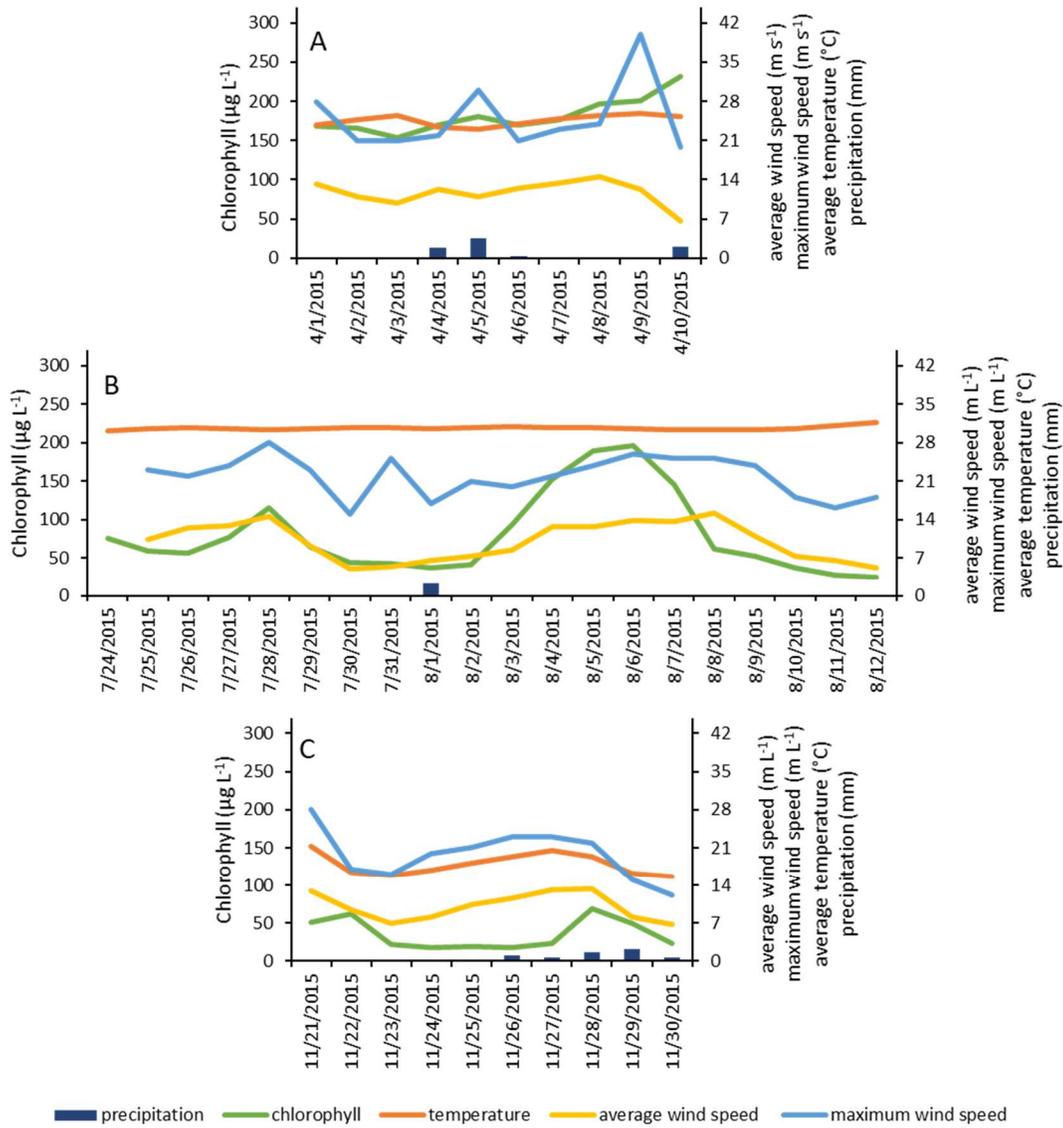


Figure 3.8. Chlorophyll ( $\mu\text{g L}^{-1}$ ), temperature ( $^{\circ}\text{C}$ ), average daily wind speed ( $\text{m s}^{-1}$ ), maximum 2-minute sustained daily wind speed ( $\text{m s}^{-1}$ ) and rainfall amount ( $\text{mm day}^{-1}$ ) for three bloom events analyzed at Cayo. Bloom event names, dates, and sample sizes are as follows, and correspond to panels in figure: A) Cayo-A, 4/1/15 - 4/10/15,  $n = 10$ ; B) Cayo-B, 7/24/15 - 8/12/15,  $n = 20$ ; C) Cayo-C, 11/21/15 - 11/30/15,  $n = 10$ .

## Tables

Table 3.1. Descriptive statistics for chlorophyll measurements during the simulated year of sampling, for quarterly and monthly sampling simulations.

	Quarterly sampling	Monthly sampling
average annual mean chlorophyll ( $\mu\text{g L}^{-1}$ )	69.0	69.5
minimum annual mean chlorophyll ( $\mu\text{g L}^{-1}$ )	28.3	54.3
maximum annual mean chlorophyll ( $\mu\text{g L}^{-1}$ )	117.5	95.1
average chlorophyll minimum ( $\mu\text{g L}^{-1}$ )	24.9	17.2
average chlorophyll maximum ( $\mu\text{g L}^{-1}$ )	174.6	260.4

Table 3.2. Additive linear model coefficients for environmental factors explaining chlorophyll during select bloom events at BB3 from 2015 – 2016 (BB3-A: 2/20/15-3/17/15, n = 25; BB3-B: 7/10/15 -7/22/15, n = 13; BB3-C: 12/14/16 - 12/28/16, n = 15). Overall model p-value and adjusted  $r^2$  are in the bottom rows for corresponding bloom events.

Environmental parameter	BB3-A 2/20/15-3/17/15		BB3-B 7/10/15 -7/22/15		BB3-C 12/14/16 - 12/28/16	
	coefficient	p-value	coefficient	p-value	coefficient	p-value
Average wind speed ( $\text{m s}^{-1}$ )	-3.64	0.006			3.37	0.002
Average wind speed – 1 day lag ( $\text{m s}^{-1}$ )					3.28	0.002
Maximum speed ( $\text{m s}^{-1}$ )			6.68	0.018		
Temperature ( $^{\circ}\text{C}$ )	-9.14	<0.001				
Rain amount ( $\text{mm day}^{-1}$ )						
Model adjusted $r^2$	0.56		0.36		0.79	
Model p value	<0.001		0.018		<0.001	

Table 3.3. Environmental conditions before and after the bloom events BB3-A, BB3-B, and BB3-C, from monthly water quality monitoring samples collected at BB3. All parameters reported (including temperature and salinity) are from monitoring data. No post-BB3-C data is reported because sampling was not conducted in January 2017.

	Pre – BB3-A	Post – BB3-A	Pre – BB3-B	Post – BB3-B	Pre – BB3-C
Date	2/19/2015	3/18/2015	6/24/2015	7/23/2015	12/14/2016
Temperature (°C)	14.2	19.6	28	29	17.3
Salinity	43.2	40.1	11.7	17.8	43.2
NH <sub>4</sub> <sup>+</sup> (μM)	0.44	0.69	5.79	12.41	8.65
N+N (μM)	0.46	0.02	5.58	5.07	3.73
DON (μM)	58.1	55.1	41.9	67.7	97.8
Silicate (μM)	83.9	79.1	68.5	11.6	139.3
DOC (μM)	1019	845	647	605	1121
Orthophosphate (μM)	0.25	0.52	0.69	0.23	0.42

Table 3.4. Additive linear model coefficients for environmental factors explaining chlorophyll during select bloom events at Cayo from 2015 – 2016 (Cayo-A: 4/1/15 - 4/10/15, n = 10; Cayo-B: 7/24/15 - 8/12/15, n = 20; Cayo-C: 11/21/15 - 11/30/15, n = 10). Overall model p-values and adjusted  $r^2$  are in the bottom rows for corresponding bloom events.

Environmental parameter	Cayo-A 4/1/15 - 4/10/15		Cayo-B 7/24/15 - 8/12/15		Cayo-C 11/21/15 - 11/30/15	
	coefficient	p-value	coefficient	p-value	coefficient	p-value
Average wind speed ( $\text{m s}^{-1}$ )			10.54	0.001		
Average wind speed – 1 day lag ( $\text{m s}^{-1}$ )					6.73	0.008
Maximum wind speed ( $\text{m s}^{-1}$ )						
Temperature ( $^{\circ}\text{C}$ )	19.55	0.024				
Rain amount ( $\text{mm day}^{-1}$ )	13.90	0.037				
Model adjusted $r^2$	0.45		0.43		0.61	
Model p value	0.050		0.001		0.008	

Table 3.5. Environmental conditions before and after the bloom events Cayo-A, Cayo-B, and Cayo-C, from monthly water quality monitoring samples collected at BB3. All parameters reported (including temperature and salinity) are from monitoring data.

	Pre – Cayo-A	Post – Cayo-A	Pre – Cayo-B	Post – Cayo-B	Pre – Cayo-C	Post – Cayo-C
Date	3/18/2015	4/16/2015	7/23/2015	8/13/2015	11/19/2015	12/10/2015
Temperature (°C)	19.6	23.5	29	30.3	20.7	18.5
Salinity	40.1	34.6	17.8	20.4	30.9	31.5
NH <sub>4</sub> <sup>+</sup> (μM)	0.69	1.14	12.41	1.62	14.49	3.46
N+N (μM)	0.02	0.16	5.07	0.27	1.12	0.59
DON (μM)	55.1	57.8	67.7	55.6	72.0	73.0
Silicate (μM)	79.1	93.4	11.6	21.5	89.1	0.4
DOC (μM)	845	919	605	712	867	896
Orthophosphate (μM)	0.52	0.28	0.23	0.36	0.57	0.23

Table 3.6. Environmental conditions before and after the bloom events Cayo-A, Cayo-B, and Cayo-C, from monthly water quality monitoring samples collected at BB1. All parameters reported (including temperature and salinity) are from monitoring data.

	Pre – Cayo-A	Post – Cayo-A	Pre – Cayo-B	Post – Cayo-B	Pre – Cayo-C	Post – Cayo-C
Date	3/18/2015	4/16/2015	7/23/2015	8/13/2015	11/19/2015	12/10/2015
Temperature (°C)	21.8	22.7	28.4	29.3	19.9	19.8
Salinity	32.5	13.0	15.9	20.5	28.0	29.3
NH <sub>4</sub> <sup>+</sup> (μM)	0.78	2.30	2.40	0.61	3.59	7.49
N+N (μM)	0.01	15.92	0.65	0.19	0.35	0.53
DON (μM)	62.2	51.7	60.0	68.2	69.6	73.6
Silicate (μM)	75.1	106.7	15.9	27.4	81.3	9.1
DOC (μM)	879	739	686	792	839	844
Orthophosphate (μM)	0.81	9.57	0.44	0.26	1.64	1.56

CHAPTER IV: SPATIAL-TEMPORAL DISTRIBUTION OF *AUREOUMBRA LAGUNENSIS*  
 (“BROWN TIDE”) IN BAFFIN BAY, TEXAS<sup>1</sup>

**Abstract**

Once limited to the Laguna Madre of Texas, blooms of the brown tide organism, *Aureoumbra lagunensis*, have recently been reported elsewhere. Previous studies have focused on the role of extreme hypersalinity and lack of grazing pressure as facilitators of brown tide blooms. However, development of blooms in systems that are not experiencing extreme hypersalinity, and also that are undergoing eutrophication, suggests that our understanding of *A. lagunensis* bloom dynamics requires additional refinement. The goal of this study was to quantify the spatial-temporal distribution of, and potential controls upon, *A. lagunensis* in Baffin Bay, Texas. Five sites were sampled monthly over a three-year period, encompassing nearly two years of drought and hypersaline conditions, followed by a high rainfall, lower salinity period. *A. lagunensis* abundances were higher during drought in May 2013 – March 2015 compared to the higher rainfall period of April 2015 – April 2016. Abundances typically peaked in summer months, though the seasonal pattern was disrupted in 2015 during the shift from high to low salinity conditions. Persistently high abundances of *A. lagunensis* were observed in the Laguna Salada tributary of Baffin Bay, which typically has higher dissolved organic nitrogen concentrations and may be less well flushed than other parts of Baffin Bay. Thus this location may serve as a reservoir for *A. lagunensis* in the system. Overall, *A. lagunensis* abundance was positively correlated with DOC and salinity, and negatively correlated with ammonium, orthophosphate, and ciliate biovolume. These results suggest a variety of physical, chemical and

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<sup>1</sup> A version of this chapter was originally published as: Cira, E.K., Wetz, M.S., 2019. Spatial-temporal distribution of *Aureoumbra lagunensis* (“brown tide”) in Baffin Bay, Texas. *Harmful Algae* 89, 101669.

biological factors affect *A. lagunensis* population dynamics and stress the need for more research on nutrient-*A. lagunensis* relationships.

## **1. Introduction**

Harmful algal blooms (HABs) can have negative effects on fisheries, tourism, and coastal ecosystems through toxin production, triggering of low dissolved oxygen conditions, or disruption of food webs (Zingone and Enevoldsen, 2000; Hoagland et al., 2002; Berdalet et al., 2016). HABs are a global concern, with analyses showing increases in the number of waterbodies affected by them over the past half century (Hallegraeff et al., 2003; Heisler et al., 2008; Anderson et al., 2012). In order to develop potential HAB mitigation strategies, it is critical to understand the relationship between HABs and environmental drivers (GEOHAB, 2001; Sellner et al., 2003; Anderson, 2009; Glibert et al., 2010; Paerl et al., 2018). These relationships are often complex and require intensive research using field, laboratory and modeling studies to fully elucidate (Zingone and Enevoldsen, 2000; GEOHAB, 2001).

While eutrophication is believed to be a primary driver, there are many other physical, chemical, and biological factors that modulate the effects of increased nutrient loading on HAB population dynamics (Cloern, 2001; Heisler et al., 2008). For example, the importance of nutrient form (i.e., inorganic versus organic) is now widely recognized (Glibert et al., 2006). Physical factors such as lack of flushing are also recognized as promoting HABs (e.g., Ryan et al., 2008; Ralston et al., 2012). Likewise, there is growing recognition of the role that “top down” biological controls (or lack thereof) may have in HAB population dynamics (Buskey, 2008; Smayda, 2008; Stoecker et al., 2008).

Harmful blooms of the brown tide organism, *Aureoumbra lagunensis*, were once limited to the Laguna Madre of South Texas, where the first *A. lagunensis* bloom was identified in 1989

(Buskey et al., 2001, Villareal et al., 2004). In the past decade however, *A. lagunensis* blooms have been observed in Indian River Lagoon, Florida, and Guantánamo Bay, Cuba (Gobler et al., 2013; Koch et al., 2014; Hall et al., 2018). Previous studies have focused on the role of hypersalinity and lack of grazing pressure as facilitators of blooms (e.g., Buskey et al., 1998), but the development of blooms in systems that are not experiencing extreme hypersalinity (Gobler et al., 2013; Koch et al., 2014; Hall et al., 2018), and also that are undergoing eutrophication (Phlips et al., 2015; Wetz et al., 2017), suggests that our understanding of *A. lagunensis* bloom dynamics requires additional refinement. Data from sustained monitoring can provide information on environmental conditions that are conducive to HABs in general while also informing future targeted studies of bloom dynamics. Here I present data from three years of monthly field monitoring of *A. lagunensis* abundance in Baffin Bay, Texas, which has experienced persistent blooms of that organism since 1990. The goal of this study was to quantify the spatial-temporal distribution of, and potential controls upon, *A. lagunensis* in Baffin Bay, Texas.

## **2. Materials and methods**

### **2.1. Site description**

Baffin Bay is a shallow (average depth ~1 m) estuary located in a semi-arid region of the South Texas coast (Diener, 1975; Breier et al., 2010). Separated from the Gulf of Mexico by Padre Island, there is limited water exchange with the Gulf of Mexico. This, as well as minimal tidal influence ( $\leq 10$  cm on average), results in a long residence time on average ( $\sim > 1$  year; An and Gardner, 2000, 2002; Simms et al., 2010). Mixing within the bay is primarily wind-driven (Tunnell, 2002). Baffin Bay has three tertiary bays (Laguna Salada, Cayo del Grullo, and Alazan Bay) which are fed by intermittent streams. Because there is no major river discharge to Baffin

Bay and evaporation exceeds precipitation (An and Gardner, 2002), Baffin Bay is often hypersaline and can behave as a reverse estuary (Buskey et al., 2001; Cira and Wetz unpubl. data). However, during El Niño conditions that cause high rainfall on the Texas coast (Tolan, 2007), a traditional salinity gradient (lower in the upper estuary, higher downstream) can also occur (Cira and Wetz unpubl. data).

## **2.2. Sampling program**

Five sites in Baffin Bay were visited monthly from May 2013 – April 2016 (Fig. 4.1). One site was located in each tertiary bay (Laguna Salada, Cayo del Grullo, and Alazan Bay) and two were in the main channel. Temperature (surface) and salinity (surface and bottom) were measured at each site with a calibrated YSI ProPlus sonde. Surface water was collected in acid-washed 1 L (for biogeochemical analyses) or 500 mL amber polycarbonate bottles (for plankton analyses). Bottles were stored in the dark (the 1 L bottle was also stored on ice) for transport to a shore-based laboratory.

## **2.3. Chemical analysis**

Upon return to the laboratory, 1 L bottles were gently inverted and ~50mL subsamples were filtered through combusted 25mm GF/F filters (nominal pore size: 0.7  $\mu\text{m}$ ). The filtrate was stored frozen (-20°C) until analysis. After thawing to room temperature, the filtrate was analyzed for inorganic nutrients on a Seal QuAAtro autoanalyzer following methods described in Wetz et al. (2017). Additional subsamples were thawed to room temperature and analyzed for dissolved organic carbon (DOC) and total dissolved nitrogen (TDN) on a Shimadzu TOC-Vs analyzer with nitrogen module (see methods in Wetz et al., 2017). Dissolved inorganic nitrogen (DIN) was calculated by adding ammonium and nitrate + nitrite (N+N). Dissolved organic

nitrogen (DON) was calculated by subtracting DIN from TDN. Analysis of DON and DOC were omitted for BB5 on 11/2014 and BB3 on 1/2016 due to quality control concerns.

#### **2.4. *Aureoumbra lagunensis* and ciliate enumeration**

Upon return to the laboratory, 500 mL bottles were gently inverted and a 4 mL subsample was preserved with 1% glutaraldehyde and stored frozen (-80 °C) until analysis with flow cytometry. Samples were thawed under subdued lighting, then filtered through 20 µm mesh. Samples were incubated under subdued lighting with a primary antibody specific to *A. lagunensis* (custom polyclonal antibody from ThermoFisher), followed by a fluorescently labeled secondary antibody (fluorescein isothiocyanate, FITC). After labeling, samples were analyzed on an Accuri C6 flow cytometer equipped with an optical filter for detection of FITC fluorescence and side scatter. The detection limit (80,000 cells mL<sup>-1</sup>) was calculated following Koch et al. (2014), using unstained *A. lagunensis* cultures and field samples in which *A. lagunensis* was known to be absent. Note that samples for flow cytometric analysis were not collected on 12/2015 and 2/2016.

For ciliate enumeration, 60 mL subsamples were preserved with 3% acid Lugol's solution and stored at room temperature in the dark. Bottles were gently inverted and a 5 mL subsample poured into Utermöhl chambers and allowed to settle overnight. The subsample volume and settling time were adjusted as needed (i.e. during bloom events), allowing > 1 h settling time per mL settled. Ciliates were enumerated and measured at 100 – 600x on an Olympus IX71 and total ciliate biovolume was estimated using associated geometric shapes for each enumerated group (Hillebrand et al., 1999; Sun and Liu, 2003).

## 2.5. Statistical analysis

Differences in *A. lagunensis* abundances and environmental variables among the five sampling sites were tested using Kruskal-Wallis test ( $\alpha=0.05$ ) followed by Dunn's multiple comparison test with a Bonferroni adjustment ( $\alpha=0.1$ ). The environmental factors assessed include salinity (measured at the surface), salinity stratification (calculated by subtracting surface salinity from bottom salinity for each sampling event), temperature, ammonium, orthophosphate, DON, DOC, and ciliate biovolume.

Correlation between *A. lagunensis* abundance and environmental factors were assessed using Kendall's tau ( $\alpha=0.05$ ). Nonparametric analyses were selected to handle non-normally distributed data and cell counts/nutrients that were below detection limit (BDL; note BDL measurements were considered to be at the detection limit value for analysis). All analyses were performed in R version 3.3.2 (R Core Team, 2016) using the Kendall (McLeod, 2011) and `dunn.test` (Dinno, 2017) packages.

## 3. Results

### 3.1. Spatial-temporal distribution of *A. lagunensis* and supporting environmental variables

*A. lagunensis* abundances ranged from BDL (80,000 cells mL<sup>-1</sup>) to  $> 1 \times 10^6$  cells mL<sup>-1</sup> throughout the sampling period (Fig. 4.2A). *A. lagunensis* abundances typically peaked in summer months, though the seasonal pattern was disrupted in 2015 when the system shifted from a low rainfall, high salinity regime to a high rainfall, lower salinity regime (Fig. 4.2A, B). Overall, *A. lagunensis* abundances were higher in May 2013 – March 2015 than in April 2015 – April 2016 (Fig. 4.2A). Over the three-year sampling period, abundances were highest at BB2 on average. This relationship was significant ( $p < 0.1$ ) in comparison with BB1, and borderline significant with BB3 and BB4 ( $p = 0.12$ ; Fig. 4.2A). The spread of *A. lagunensis* abundances

was also highest at BB2, with an interquartile range about twice that of the other sites (Fig. 4.2A).

The shift from low to high rainfall in early 2015 was the dominant feature in the temporal trends of many of the environmental variables as well. For example, hypersaline conditions were in place prior to spring 2015, but salinity rapidly dropped thereafter, reaching  $< 10$  at BB1 and BB5 (Fig. 4.2B). After summer 2015, salinity began to increase throughout the bay, reaching  $\sim 35$  at all sites by spring 2016 (Fig. 4.2B). Salinity stratification was generally low in Baffin Bay due to strong winds, but stratification briefly increased in spring 2015 (Fig. 4.2C). Temperature was comparable among the sampling sites and peaked in summer months. The highest summer temperature was consistent among the sampling years, but the lowest winter temperature progressively increased each winter (2013/2014:  $\sim 10$  °C, 2014/2015:  $\sim 14$  °C, 2015/2016:  $\sim 18$  °C; Fig. 4.2D). Ammonium concentrations showed no significant differences among sampling sites but were generally higher during summer. Ammonium concentrations increased from spring 2015 to the end of the study period, and occasionally exceeded  $5 \mu\text{M}$  (Fig. 4.3A). DON concentrations were rarely  $< 40 \mu\text{M}$  and occasionally exceeded  $100 \mu\text{M}$  (Fig. 4.3B). Highest DON concentrations were recorded at BB2, and DON concentrations were significantly higher ( $p < 0.1$ ) at BB2 than at BB3, BB4, and BB5 (Fig. 4.3B) and significantly higher ( $p < 0.1$ ) at BB1 than at BB3 and BB4. No clear seasonal or interannual patterns in DON were observed. Orthophosphate concentrations were significantly higher at BB1 compared to the other sites ( $p < 0.1$ ; Fig. 4.3C). Orthophosphate was typically highest during summer and ephemeral increases to  $> 5 \mu\text{M}$  were observed at BB1 and BB5 in spring 2015 and early 2016 (Fig. 4.3C). DOC concentrations were often higher at BB2 than the other sites, with significant differences ( $p < 0.1$ ) found in comparison with BB3, BB4, and BB5 (Fig. 4.3D). No clear

seasonal trend was apparent but DOC decreased throughout the sampling period (Fig. 4.3D).

There were no significant spatial trends in ciliate biovolume though it tended to be lower in the main channel sites (BB3, BB4) than the tributary sites (Fig. 4.3E). While no seasonal trends in ciliate biovolume were observed, it was generally lower during the drought period (May 2013 – March 2015) than the higher rainfall period (April 2015 – April 2016; Fig. 4.3E).

### **3.2. Relationship between *A. lagunensis* and environmental variables**

*A. lagunensis* abundance was positively correlated with salinity and DOC, and negatively correlated with ammonium, orthophosphate, and ciliate biovolume (Table 4.1). Using data from all sites, the relationship between abundance and water temperature was not significant ( $p > 0.05$ ). However at BB2, where the lower salinity conditions were less pronounced (Fig. 4.2B) and *A. lagunensis* persisted through 2015 and 2016, there was a positive correlation with water temperature (Kendall's tau=0.253,  $p= 0.038$ ). Likewise, as January water temperatures increased from 14.3 °C (2014) to 17.0 °C (2015) to 18.2 °C (2016) at BB2, *A. lagunensis* abundances increased from BDL (2014) to 177,000 cells mL<sup>-1</sup> (2015) to 768,000 cells mL<sup>-1</sup> (2016).

## **4. Discussion**

In light of the appearance of harmful *A. lagunensis* blooms outside of Texas, namely in Indian River Lagoon, Florida and Guantánamo Bay, Cuba (Gobler et al., 2013; Phlips et al., 2015; Hall et al., 2018), there is an urgent need to understand environmental drivers of these blooms. Early studies on *A. lagunensis* in Texas focused on hypersalinity and low inorganic nutrient concentrations as overarching features of the environment that promote the blooms (Buskey et al., 1998). More recent work in Guantánamo Bay suggests that extreme hypersalinity is not necessarily a prerequisite for blooms (Hall et al., 2018). Recent studies have also shown potential for blooms to occur in systems experiencing nutrient pollution, particularly under

conditions of high reduced nitrogen (ammonium, organic nitrogen) relative to nitrate availability (e.g., Kang et al., 2015; Wetz et al., 2017). The goal of this study was to quantify the spatial-temporal distribution of, and potential controls upon, *A. lagunensis* in Baffin Bay, Texas, a system that has undergone eutrophication in recent decades (Besonen et al., 2016; Wetz et al., 2017) and that has experienced recurring *A. lagunensis* blooms since 1990.

At the beginning of this study, when hypersalinity was noted, bloom-level abundances of *A. lagunensis* ( $> 500,000$  cells  $\text{mL}^{-1}$ ) were in place at all sampling sites. There are a number of possible explanations for this. At a basic level, this may reflect biomass accumulation facilitated by increased residence time during drought conditions. Others have postulated that *A. lagunensis* may simply be better able to tolerate these harsh salinity conditions compared to other phytoplankton (Buskey et al., 1998). This is a difficult hypothesis to test without additional data on the salinity tolerance of other endemic phytoplankton taxa, but field data does indicate that the *A. lagunensis* blooms were near mono-specific (Cira and Wetz unpubl. data). Previous studies have also shown weaker top-down controls on *A. lagunensis* during hypersalinity (Buskey et al., 1998; Phlips et al., 2015). Lower ciliate biovolume was found during the high salinity, high *A. lagunensis* abundance conditions compared to the low salinity period in this study, consistent with this hypothesis. Possibilities for this include negative effects of salinity on the ciliates (e.g., Buskey et al., 1998) and/or production of harmful substances by *A. lagunensis*. In regards to the latter, previous work in the laboratory has shown that *A. lagunensis* produces a thick mucus layer, particularly at salinities  $> 50$ , that deters microzooplankton grazers (Liu and Buskey, 2000a, b). I found a positive correlation with DOC, which may serve loosely as a proxy for mucus given that it has been shown to be carbon rich and contribute to marine DOC pools (Decho and Lopez, 1993; Aluwihare et al., 1997; Bhaskar and Bhosle, 2005). Unfortunately, I

only have data on ciliates and not other microzooplankton grazers (e.g., dinoflagellates, Buskey et al., 1998), limiting the scope of inferences that can be drawn regarding top down controls.

During the heavy rainfall period in spring 2015, *A. lagunensis* abundances decreased precipitously at all sampling sites. Similar phenomena have been identified before; Buskey et al. (2001) noted that a 7-year bloom of *A. lagunensis* in the Laguna Madre ended following a period of heavy rainfall, and Philips et al. (2015) found that an *A. lagunensis* bloom in Indian River Lagoon subsided after the passage of a tropical storm. Hypotheses for this pattern have included increased flushing and higher grazing pressure. Higher flushing rates could certainly have accompanied the sharp salinity decreases that were observed in spring 2015. *A. lagunensis* has a relatively slow growth rate at salinities  $< 20$  ( $\mu < 0.4 \text{ day}^{-1}$ ) compared to salinities between  $\sim 20$ – $75$  ( $\mu \sim 0.55$ – $0.65 \text{ day}^{-1}$ , Buskey et al., 1998), which may make it less competitive under high flushing rates. Enhanced grazing has also been proposed as a factor that limits *A. lagunensis* biomass accumulation in low salinity conditions (Buskey et al., 1998). In support of this, I found higher ciliate biovolume during the low salinity period and an overall statistically significant inverse correlation between ciliate biovolume and *A. lagunensis* abundance, suggesting a predator-prey relationship.

After cessation of the heavy rainfall period in spring 2015, *A. lagunensis* abundances increased again at BB2 in the summer but remained low elsewhere. The lowest surface salinity recorded at BB2 in spring 2015 was 17, higher than the other two tributary sites. Thus, this tributary was less affected by the otherwise heavy rainfall in the region. This is consistent with climatological precipitation data, which indicate that the southern/western reaches of Baffin Bay (including Laguna Salada and its drainage basin) receive lower precipitation on average than the tributaries in the northern part of the bay (TWDB, 2011).

While my results add to the growing amount of evidence that high salinity may play a role in enhancing the potential for *A. lagunensis* blooms, I also found high *A. lagunensis* abundances ( $> 1 \times 10^6$  cells mL<sup>-1</sup>) at salinities as low as 20. In Baffin Bay, 41% all of salinity measurements from a state water quality monitoring program from 1985 to 2016 fell within the salinity range of 20–40 (Wetz, unpubl. data). Recent *A. lagunensis* blooms in other systems have occurred at salinities of 35–40 (Koch et al., 2014; Kang et al., 2017; Hall et al., 2018). This suggests that factors other than salinity also affect *A. lagunensis* population dynamics. This study has not identified those factors, though the inverse correlation with ammonium and phosphate, indicative of a drawdown effect as biomass increases, as well as overall high DON concentrations, points to the importance of nutrients. As this has bloom management implications, more work is clearly needed to understand the conditions (incl. nutrients) leading to *A. lagunensis* blooms in Baffin Bay and elsewhere.

On seasonal timescales, *A. lagunensis* abundance typically peaked in the summer months and declined in winter months, though this pattern was interrupted by the high rainfall in spring 2015. Across all sites, I found no statistically significant relationship between *A. lagunensis* abundance and water temperature, despite the seasonal patterns found in the earlier part of the record (i.e., May 2013 – early 2015). I suspect this relationship was weakened due to inclusion of data from mid-2015 to early 2016, when *A. lagunensis* was virtually absent due to unsuitable salinity conditions, except at BB2. Nonetheless, the BB2 data showed a statistically significant relationship between abundance and water temperature. Likewise, *A. lagunensis* abundances at BB2 increased progressively during January of each year corresponding with increased water temperatures. These results are broadly consistent with laboratory-based results from Buskey et al. (1998), which demonstrated a strong temperature effect on *A. lagunensis* growth, especially at

temperatures less than 25 °C. Climate projections predict that air and water temperatures in South Texas may increase by 3–7 °C by the end of the century (Walsh et al., 2014). These findings suggest that as winters become milder, conditions may become more conducive for *A. lagunensis* growth year-round assuming other environmental conditions (salinity, light, nutrients) are adequate. Aside from future climate projections, there are already indications of long-term water temperature changes in Baffin Bay. Analysis of historical water temperatures indicate that spring and summer water temperatures have warmed in Baffin Bay over the last half century (Bugica et al., 2020), which may a) lead to stronger and/or earlier spring blooms if the trend continues, and b) intensify nutrient regeneration in both spring and summer to further support *A. lagunensis* bloom development and persistence. Research on temperature-spring bloom dynamics in Baffin Bay is currently underway.

The most striking pattern observed in this study was the persistently high abundance of *A. lagunensis* in the Laguna Salada tributary (site BB2) of Baffin Bay. This was noted in both 2013 and 2014 but was most pronounced relative to the other sites in 2015 after the heavy rainfall period. Based on the data available in this study, the cause(s) behind the higher *A. lagunensis* abundances at BB2 remain enigmatic. For example, during spring 2015, *A. lagunensis* abundances plummeted at BB2 along with the other sites in the bay, but by summer 2015, abundances had increased again in Laguna Salada. Salinity at BB2 during this time was ~20, meaning that despite low salinities, conditions in Laguna Salada may support development of *A. lagunensis* blooms. On average, salinity was slightly higher at BB2 compared to the other sites, but from mid-2015 onward, after *A. lagunensis* abundance had rebounded in Laguna Salada, there was no clear salinity difference among sites. Likewise, ciliate biovolume was only slightly higher at BB2, but was also quite variable. The only obvious difference was higher DON

concentrations on average at BB2 compared to the other sites. In a more recent survey, DON concentrations averaged  $223 \pm 76 \mu\text{M}$  from February 2017 – November 2018 at a site just 8 km upstream of BB2, further highlighting the enrichment of this tributary with DON (Hayes and Wetz, unpubl. data). Unlike with DOC, there was no significant correlation between *A. lagunensis* and DON, suggesting that the high concentrations of DON at BB2 were likely not derived from *A. lagunensis*. High concentrations of DON may support growth high abundances of *A. lagunensis* in Laguna Salada because the organism is known to use organic nitrogen compounds such as urea (Muhlstein and Villareal, 2007). However, given the complex chemical nature and variable lability of estuarine DON depending on the source (Bronk et al., 2007; Petrone et al., 2009; Osburn et al., 2016), more work is clearly needed to determine if nutrient (nitrogen) availability and/or greater lability of DON at BB2 is a factor explaining the higher *A. lagunensis* abundances there.

In summarizing findings on the spatial distribution of *A. lagunensis* in Baffin Bay from both this study as well as previous work by Rhudy et al. (1999), an emerging theme is that the Laguna Salada tributary may serve as a reservoir of *A. lagunensis* cells and seed stock for the rest of Baffin Bay and the neighboring Laguna Madre. From an environmental standpoint, the Laguna Salada has unique features that may facilitate its role as an incubator. These include relatively high DON concentrations and, during otherwise “wet” conditions at a regional scale, lower rainfall and higher salinities on average compared to other parts of the bay. While conditions may not be continuously favorable for *A. lagunensis* in Laguna Salada, the organism has been shown to produce resting cells, withstanding unfavorable environmental conditions for months at a time (Kang et al., 2017). This may contribute to its persistence in Laguna Salada and may facilitate bloom formation in other parts of the bay as well. More research is clearly

needed to determine which unique characteristics of the Laguna Salada contribute to *A. lagunensis* persistence, as identification of this “incubator” for *A. lagunensis* within the larger system presents a unique opportunity for bloom mitigation. Theoretical laboratory research has shown that chemical and biological controls may be effective on mature “brown tide” blooms (Gastrich et al., 2004; Randhawa et al., 2012), although these techniques have not been employed in the natural environment. Future rerouting of highly treated municipal wastewater effluent into the tributary to increase flushing and reduce salinity may be possible, though organic N removal from wastewater is often limited (e.g., Bratby et al., 2008). Thus the effects of increased flushing versus increased nutrient loads would need to be weighed carefully. Within the larger Baffin Bay system, stakeholder-led efforts are now underway to reduce nutrient loads to Baffin Bay through watershed management and restoration activities, with a goal of reducing the extent and duration of future algal blooms.

## **5. Conclusions**

This study adds to our understanding of *A. lagunensis* population dynamics in Baffin Bay, Texas, which has experienced prolonged blooms since 1990. I show that a tributary of Baffin Bay, the Laguna Salada, may serve as a reservoir for cells during conditions that are hostile to the organism throughout the rest of the bay. This is likely due to the geographic and environmental uniqueness of the Laguna Salada and is currently the subject of additional studies. I also found considerable seasonal and interannual variability in *A. lagunensis* abundance, tied to large-scale rainfall patterns. *A. lagunensis* population dynamics were observed under salinity conditions ranging from near fresh to extreme hypersaline. Results show that while salinity is indeed an important aspect of *A. lagunensis* dynamics overall, other factors (e.g., nutrients) may be as important and require additional study.

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### Figures

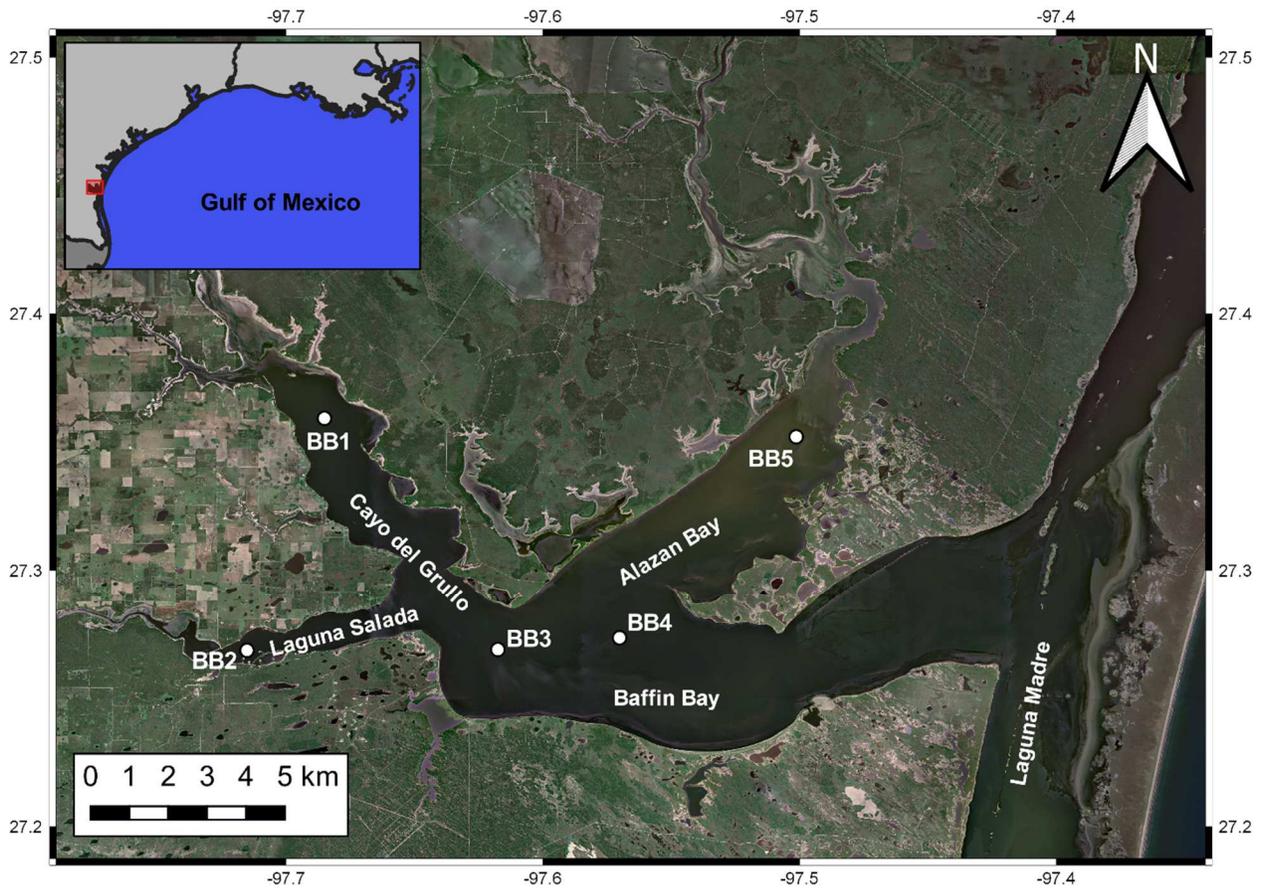


Figure 4.1. Water quality sampling stations visited monthly, May 2013 – April 2016, in Baffin Bay, Texas.

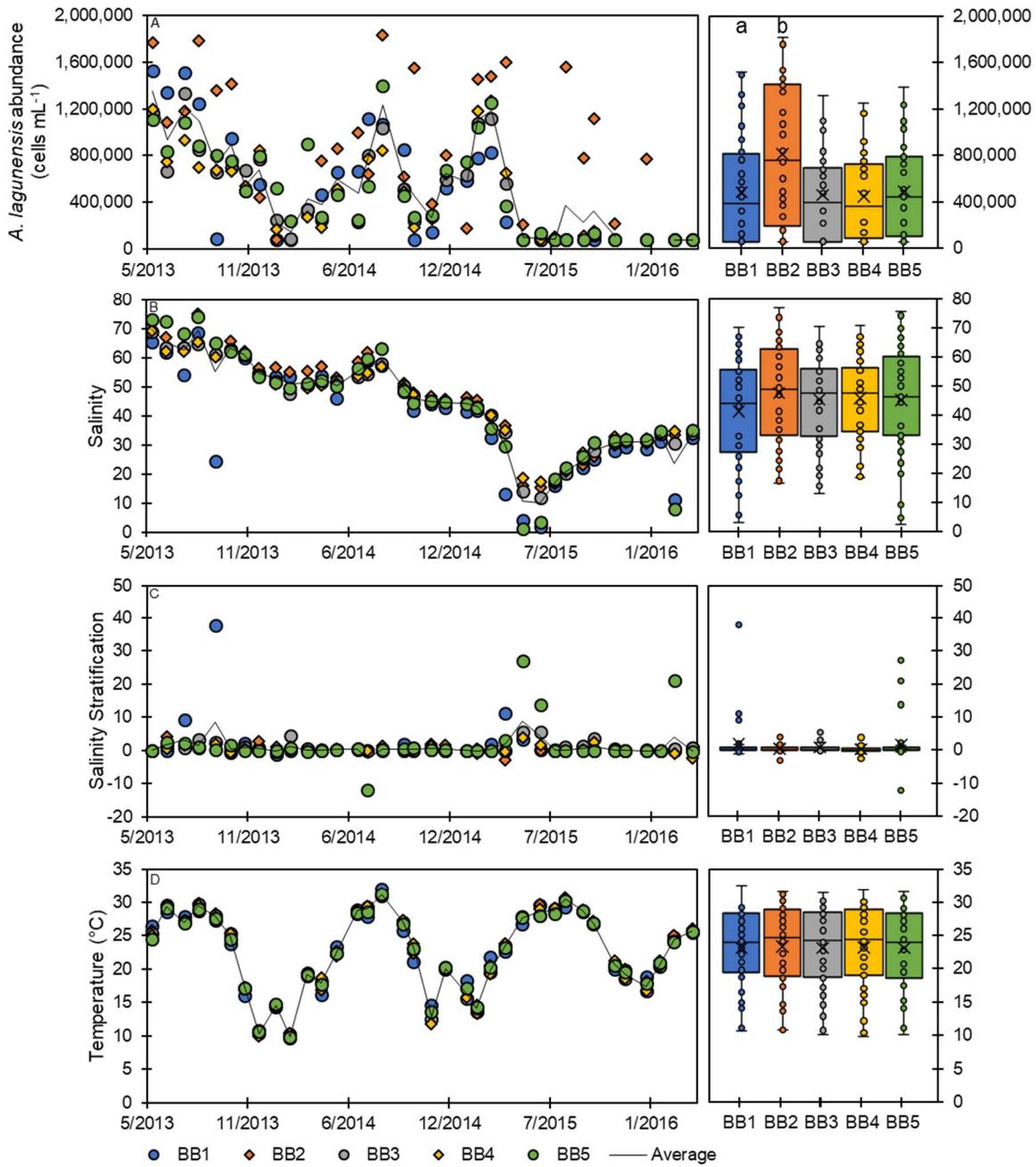


Figure 4.2. *A. lagunensis* abundance (A), surface salinity (B), salinity stratification (C), and temperature (D) at the five sampling locations for the sampling period. Different letters (a, b) above columns indicate significant differences between sites. Sites that share a common letter are not statistically different.

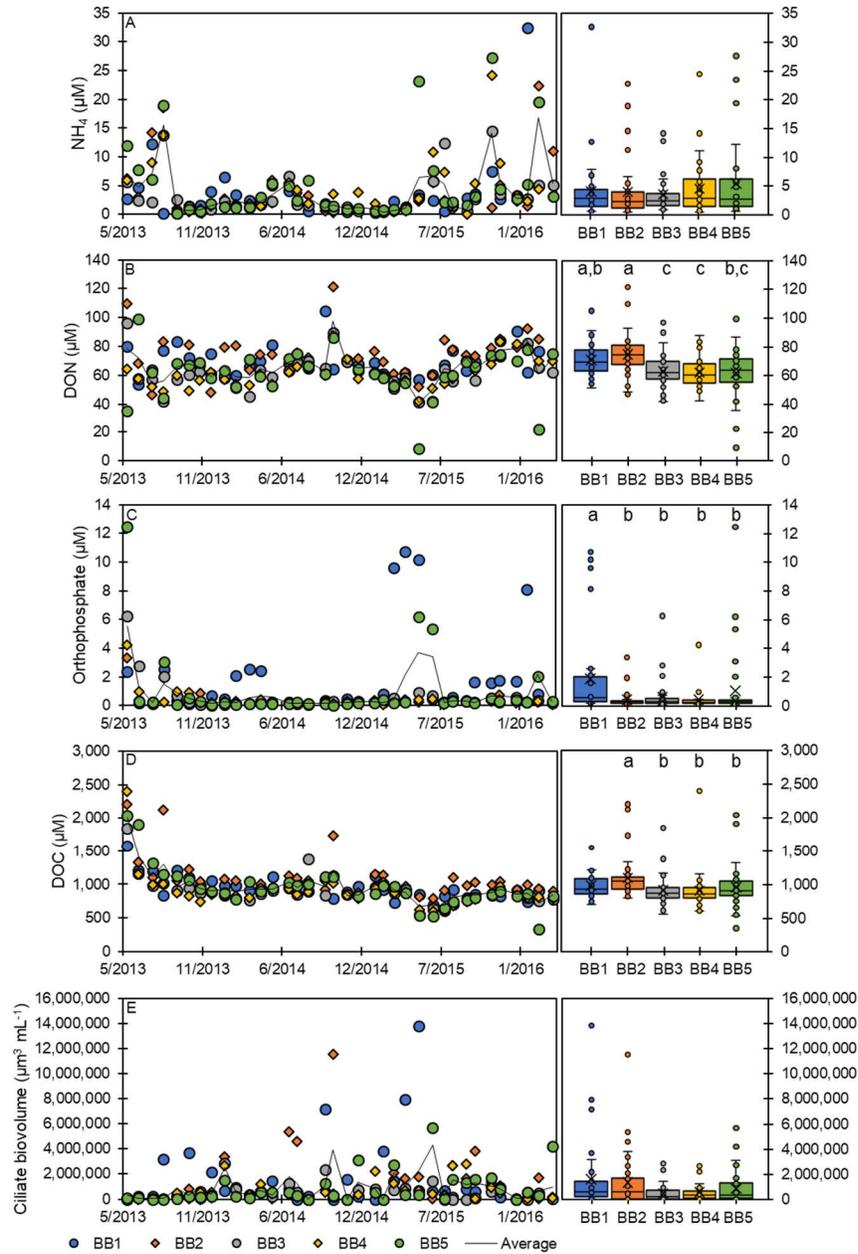


Figure 4.3.  $\text{NH}_4^+$  (A), DON (B), orthophosphate (C), DOC (D) concentrations and ciliate biovolume (E) at the five sampling locations for the sampling period. Different letters (a, b, c) above columns indicate significant differences between sites. Sites that share a common letter are not statistically different

## Tables

Table 4.1. Kendall's tau and p-values for correlations between *A. lagunensis* abundance and environmental variables. Significant correlations ( $\alpha=0.05$ ) and corresponding p-values are in bold.

Environmental variable	Kendall's tau	p-value
Salinity	<b>0.470</b>	<b>&lt;0.001</b>
Salinity stratification	-0.032	0.567
Water temperature (°C)	0.043	0.414
Ammonium ( $\mu\text{M}$ )	<b>-0.178</b>	<b>&lt;0.001</b>
Orthophosphate ( $\mu\text{M}$ )	<b>-0.132</b>	<b>0.014</b>
DON ( $\mu\text{M}$ )	0.038	0.480
DOC ( $\mu\text{M}$ )	<b>0.491</b>	<b>&lt;0.001</b>
Ciliate biovolume ( $\mu\text{m}^3 \text{mL}^{-1}$ )	<b>-0.157</b>	<b>0.003</b>

## CHAPTER V: CONCLUDING SUMMARY

Estuarine phytoplankton dynamics are inherently complex, shaped by interacting environmental factors on multiple timescales. While our understanding of phytoplankton dynamics in river-dominated estuaries has advanced in recent decades, data is lacking on phytoplankton dynamics in low-inflow systems. Research suggests that low-inflow estuaries may be more susceptible to environmental changes and anthropogenic stressors (e.g., nutrient loading, water diversion) than “classical” systems because of a general lack of flushing. In some regions, low-inflow conditions are expected to become more extreme (drier) due to climate change and growing human water demands. Thus, there is a pressing need to understand phytoplankton dynamics in low-inflow systems in order to inform management efforts and project future ecological changes. This dissertation research adds to our currently limited knowledge of phytoplankton dynamics in low-inflow estuaries by quantifying the spatial-temporal distribution of phytoplankton and environmental drivers of phytoplankton biomass and taxonomic composition in Baffin Bay, Texas.

This research highlighted substantial interannual variability in nutrient-phytoplankton dynamics in Baffin Bay-Upper Laguna Madre, corresponding with the El Niño Southern Oscillation (ENSO). During high-rainfall (El Niño) conditions, the phytoplankton community in Baffin Bay was relatively diverse with a prevalence of diatoms. Despite the relatively high inorganic nutrient concentrations during this time, however, overall community biovolume was low; this reflects the trade-off between nutrient inputs and flushing rates on phytoplankton dynamics described in many river-dominated systems. During drought (non-El Niño) conditions however, the system was characterized by high phytoplankton biovolume and a near monoalgal bloom of *A. lagunensis*. These results point to the importance of regenerated nutrients in the

bay, capable of supporting high phytoplankton biomass during times of low freshwater inflow and low external nutrient inputs. Additionally, the extended residence times during drought conditions create conditions favorable to *A. lagunensis* growth and accumulation in the system. The implications of this are that with future expansion of arid/semiarid regions and/or increasing human freshwater demands, susceptible estuaries may experience lower flows, more pronounced hypersalinity, presumably less diverse phytoplankton communities, and potentially dominance by harmful taxa such as *A. lagunensis* that thrive under stagnant conditions with ample regenerated and/or organic nutrient availability. More research is needed in other systems to determine if findings presented here are broadly applicable to low-inflow estuaries.

This study also investigated timescales of chlorophyll variability and drivers of blooms in Baffin Bay, identifying short-term (sub-monthly) variability as a dominant timescale of variability in the system. Wind was found to be an important driver of day-to-day phytoplankton population dynamics in the bay, influencing chlorophyll variability through potential mechanisms such as resuspension of phytoplankton cells from the sediments and stimulation of growth via nutrient release from sediments. Short-term variability represents a large portion of chlorophyll variability in many systems worldwide, and this study demonstrates that traditional monitoring frequencies are not adequate to assess short-term processes.

With a focused investigation on *A. lagunensis* dynamics, this study quantified its spatial-temporal distribution and potential drivers of biomass variability in Baffin Bay. Results identified a seasonal trend, with *A. lagunensis* abundance peaking in summer months. Additionally, this study found that while salinity has an important influence on *A. lagunensis* population dynamics, other factors (e.g., top-down controls, temperature,  $\text{NH}_4^+$ , phosphate, DON) are also important. As this has bloom management implications, more work is clearly

needed to understand the conditions leading to *A. lagunensis* blooms in Baffin Bay, particularly given the increasing nutrient concentrations in the bay and the projections for increased temperatures in South Texas. Results also suggest that a tertiary bay of the system, Laguna Salada, may serve as a reservoir for *A. lagunensis* cells when conditions are hostile to the organism throughout the rest of the bay. This is likely due to the geographic and environmental uniqueness of the Laguna Salada and is currently the subject of additional studies.

Overall, results from this dissertation improve our understanding of spatial-temporal phytoplankton variability in Baffin Bay, Texas. Results also highlight the potential implications of intensifying anthropogenic and climate pressures on phytoplankton dynamics in Baffin Bay and other low-inflow estuaries, though more comprehensive research is needed before generalizations can be drawn from this research and extrapolated to future scenarios. This research sets the foundation for future research, such as intensive field- and lab-based studies to establish causal linkages between environmental variables (wind, nutrient concentration and form, top-down controls) and phytoplankton dynamics in Baffin Bay or other low-inflow estuaries.