



Phytoplankton Dynamics in a Low-Inflow Estuary (Baffin Bay, TX) During Drought and High-Rainfall Conditions Associated with an El Niño Event

Emily K. Cira^{1,2} · Terence A. Palmer² · Michael S. Wetz²

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Abstract

Low freshwater inflow estuaries are common worldwide, yet our understanding of phytoplankton dynamics in these systems is limited compared to river-influenced estuaries. Combining 3 years of monthly sampling data with analysis of a lower frequency, multidecadal dataset, we examined nutrient-phytoplankton dynamics in Baffin Bay-Upper Laguna Madre, TX (USA), a low-inflow lagoonal estuary. During a low rainfall, high salinity period (corresponding with non-El Niño conditions), phytoplankton community biovolume was high and consisted of a near monoculture of the harmful “brown tide” organism, *Aureoombra lagunensis*. With the onset of El Niño conditions, rainfall increased and salinity decreased. Other phytoplankton groups became more prevalent, namely diatoms and the mixotrophic ciliate, *Mesodinium* sp., while prevalence of *A. lagunensis* declined. Although El Niño conditions corresponded with increased inorganic nitrogen concentrations, this did not lead to a near-term (weeks-months) increase in phytoplankton biovolume, indicating that the stimulatory effects of nutrient pulses may have been countered by the decreased residence times associated with increased inflow. Overall, results demonstrate that low freshwater inflows, as well as high residence times and salinities, can lead to increased phytoplankton biomass and decreased phytoplankton diversity, despite relatively low external nutrient loadings. With future expansion of arid/semiarid regions and/or increasing human freshwater demands, Baffin Bay and similar systems may experience lower inflows, more pronounced hypersalinity, and presumably less diverse phytoplankton communities, potentially dominated by harmful taxa as seen here.

Keywords Freshwater inflow · Phytoplankton · Nutrients · Estuary · ENSO · *Aureoombra lagunensis*

Introduction

Estuarine phytoplankton population dynamics are complex, due in part 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), research on phytoplankton dynamics has lagged in many low-inflow estuaries despite their broad distribution worldwide (reviewed in Largier 2010). 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, hypersaline conditions that are stressful to many estuarine organisms occasionally occur in low-inflow estuaries due to a lack of freshwater source (Largier 2010; Tweedley et al. 2019). A prolonged lack of riverine-derived nutrient loads could lead to nutrient limitation of phytoplankton growth and biomass accumulation (Wetz et al. 2011; Philips et al. 2020), but intense nutrient recycling under the long residence time conditions that would be expected in many low-inflow estuaries may alleviate nutrient limitation (Cloern 2001; Pinckney et al. 2001). In fact, several studies have demonstrated that poor flushing, along

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✉ Emily K. Cira
emily.k.cira@gmail.com

¹ Department of Physical, Environmental and Natural Sciences, Texas A&M University-Corpus Christi, 6300 Ocean Dr., Unit 5802, Corpus Christi, TX 78412, USA

² Harte Research Institute for Gulf of Mexico Studies, Texas A&M University-Corpus Christi, 6300 Ocean Dr, Corpus Christi, TX 78412, USA

with ample regenerated nutrient stocks, leads to extended periods of elevated phytoplankton biomass in these systems (Knoppers et al. 1991; Hemraj et al. 2017; Barroso et al. 2018). These factors suggest that low-inflow, long-residence time 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; Warwick et al. 2018).

Aside from being susceptible to nutrient pressures, research suggests that low-inflow estuaries in some regions may also experience decreases in inflow 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 estuaries may be sensitive to large-scale environmental changes and stressors, and that some are at the forefront of climate-induced precipitation changes (decreases), it is important to develop management strategies to address these challenges. To do this, 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 of nutrient pressures, while phytoplankton taxonomic composition has been proposed as an indicator of freshwater inflow extremes and nutrient pressures in estuaries (e.g., Paerl et al. 2010; Paerl et al. 2014; Lemley et al. 2016; Hemraj et al. 2017).

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* (Wetz et al. 2017; Cira and Wetz 2019). Blooms of this organism have been associated with ecosystem disruptive effects such as loss of seagrass due to shading, reductions in zooplankton biomass, and decreased diversity of benthic invertebrates (Buskey and Hyatt 1995; Onuf 1996; Ward et al. 2000). Efforts are now underway to seek solutions to the excessive nutrient loads that have affected Baffin Bay, namely by quantifying nutrient load sources and by establishing nutrient load reduction targets. In order to gauge the effectiveness of nutrient load reductions, it is important to understand and account for the role of natural variability in indicators such as phytoplankton biomass. Likewise, for these efforts to be effective from an ecosystem health standpoint, it is necessary for ecosystem/nutrient management efforts to account for conditions favoring blooms of harmful taxa including *A. lagunensis* as opposed to ecologically “healthy” taxa such

as diatoms. In this study, we combined 3 years of monthly monitoring data with data from a multidecadal quarterly sampling program to quantify nutrient-phytoplankton dynamics in the bay, and to put those relationships in the context of large-scale climate variability.

Methods

Baffin Bay, TX

Baffin Bay is a shallow (< 1–3 m average depth), microtidal (0.5 m tidal range) low-inflow estuary on the South Texas coast (Diener 1975). 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 Jr. et al. 1993; Tunnell Jr 2002).

Analysis of Historic Data, 1993–2015

Broadscale 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’s (TCEQ) quarterly water quality monitoring program. Data were assessed for five sites from 1993 to 2015 (BB3, BB6, LM1, LM2, LM3; Fig. 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, a rolling 3-month mean sea surface temperature anomaly in the east-central tropical Pacific, NOAA Climate Prediction Center). Descriptive statistics (mean \pm standard deviation) were used to assess spatial trends and to 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. This occurred in <1% of TKN samples and ~20% of chlorophyll samples.

Monthly Field Sampling Program, 2013–2016

Five sites in Baffin Bay were visited monthly for a 3-year period, from May 2013 to April 2016 (BB1–BB5; Fig. 1). At each site, vertical profiles of temperature and salinity were taken with a calibrated YSI ProPlus sonde. Salinity stratification was calculated by subtracting surface salinity from near bottom salinity. Surface water was collected in acid-washed 1

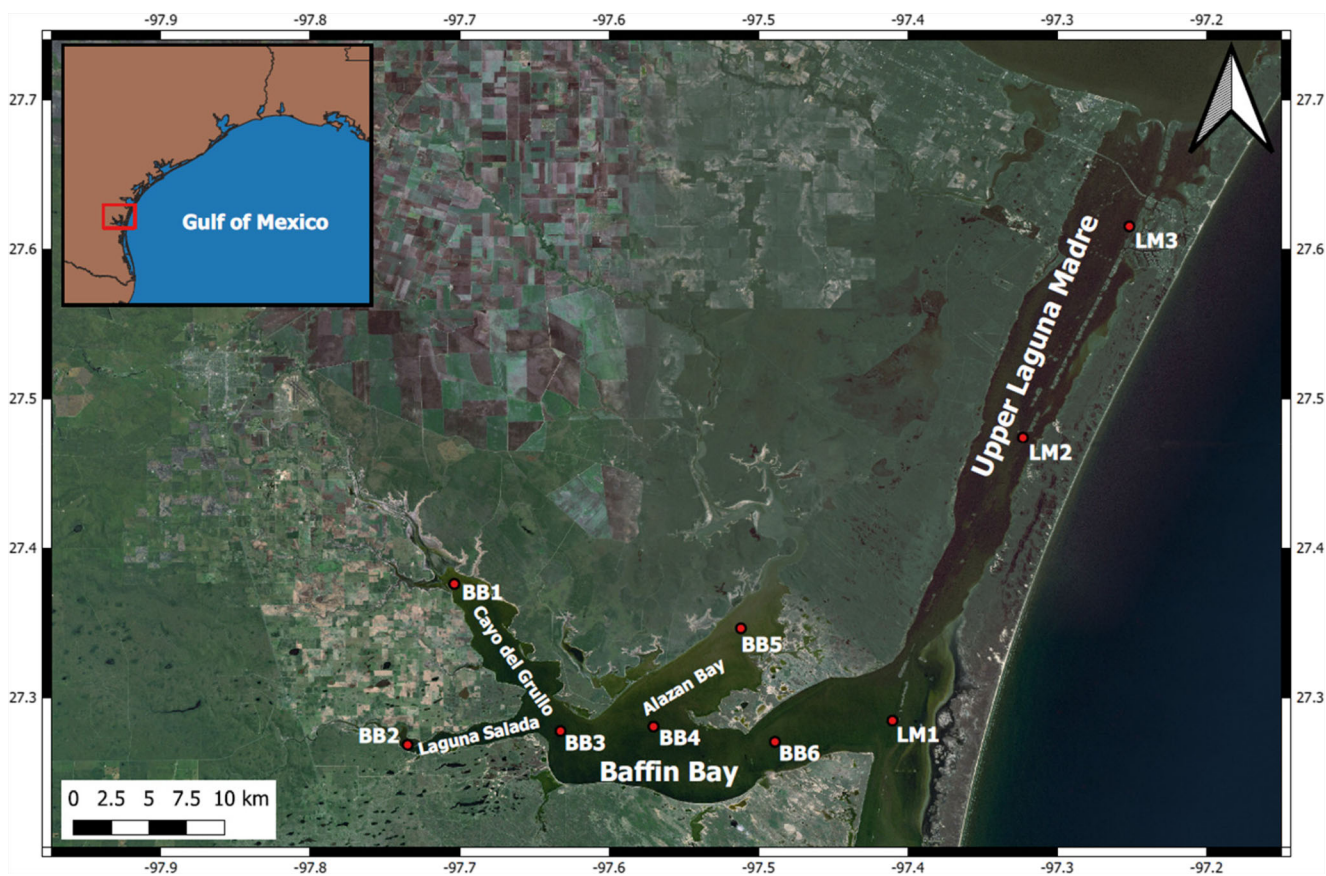


Fig. 1 Five Baffin Bay water quality monitoring stations (visited monthly, May 2013–April 2016; BB1–BB5) and five TCEQ monitoring stations (visited quarterly, 1993–2015; BB3, BB6, LM1, LM2, LM3)

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 the laboratory for analysis. Near bottom samples were not collected for phytoplankton or nutrients because of the shallow water column and pervasive well-mixed conditions.

Upon return to the laboratory, samples from the 1 L bottles were analyzed for inorganic nutrients (silicate, ammonium $[\text{NH}_4^+]$, nitrate + nitrite $[\text{N}+\text{N}]$, 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. The filtrate was stored frozen ($-20\text{ }^\circ\text{C}$) 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_4^+ and $\text{N}+\text{N}$. 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 ($-80\text{ }^\circ\text{C}$) 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. Upon return to the laboratory, 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 h settling time per mL settled. Phytoplankton and ciliate taxa were enumerated and measured at $\times 100$ – $\times 600$ 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 *Mesodinium* sp. (a mixotrophic ciliate) for analysis. Diatoms were further categorized as planktonic (e.g., *Skeletonema*, *Chaetoceros*, *Pseudo-nitzschia*) or benthic forms (e.g., naviculoids, *Cylindrotheca*) following categories described in Shaffer and Sullivan (1988) and MacIntyre et al. (2011).

Spatiotemporal differences in water quality were determined using principal components analysis (PCA) on \log_e -transformed data. Spatiotemporal differences in planktonic community composition were characterized using non-metric multi-dimensional scaling (nMDS) on $\log_e(x+1)$ biovolume data. PCA and nMDS analyses were conducted using PRIMER 7 software (Clarke et al. 2014).

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. Finally, this relationship was applied to rainfall data from 2013–2016 to estimate residence times during that period (more information provided in the Electronic Supplementary Material; ESM 1, ESM 2).

Results

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. 2a). During EN conditions, salinities were highest at the mouth of Baffin Bay (LM1, 39.2 ± 7.6) and lower in both Baffin Bay (BB3, 31.7 ± 12.4 ; BB6, 33.7 ± 10.5) and Upper Laguna Madre (LM2, 33.1 ± 7.9 ; LM3, 31.0 ± 6.0 ; Fig. 2a). During non-EN conditions, salinities were high and varied little from upper Baffin Bay to the mouth (BB3, 39.0 ± 14.4 ; LM1, 39.9 ± 8.6). Slightly lower salinities were observed in Upper Laguna Madre (LM3, 35.6 ± 6.6 ; Fig. 2a).

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. 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. 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. 2b).

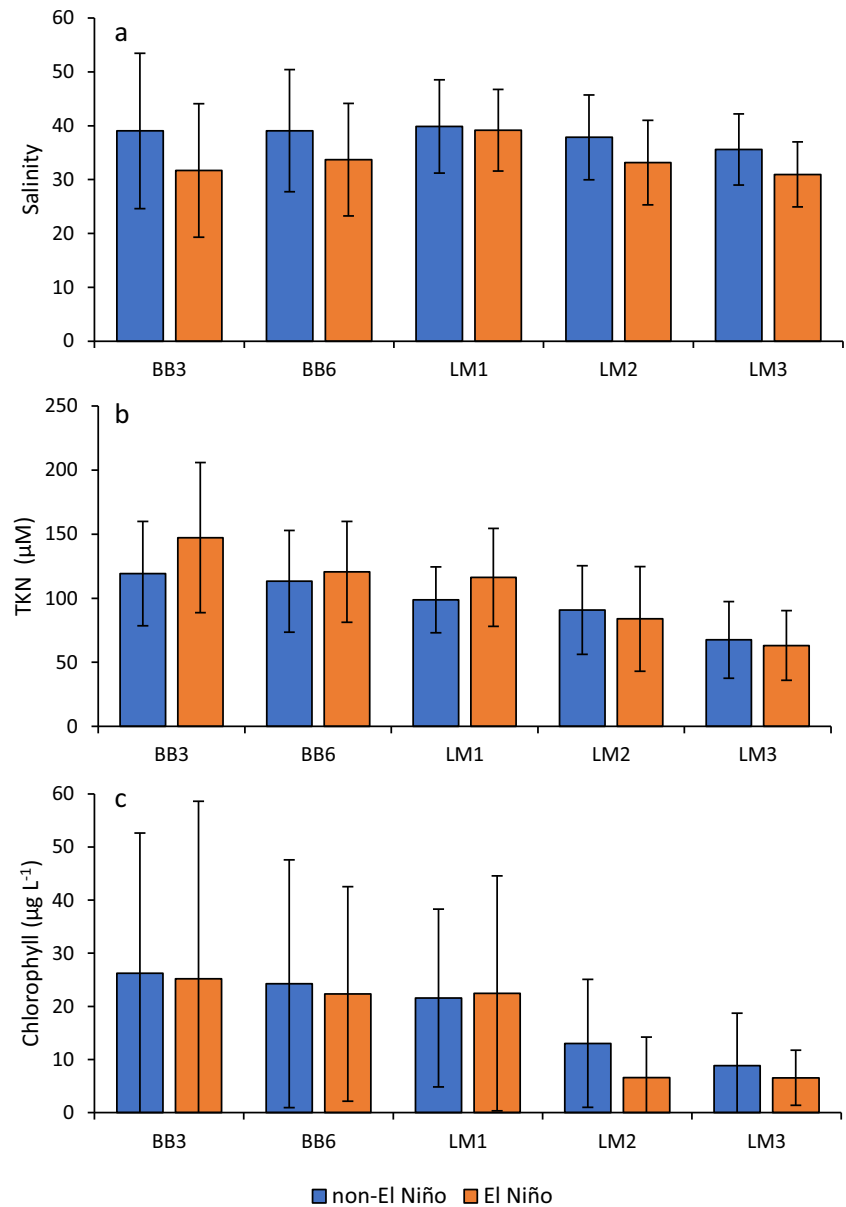
Chlorophyll concentrations ranged from $8.4 \pm 9.1 \mu\text{g L}^{-1}$ at LM3 to a high of $26.1 \pm 27.5 \mu\text{g L}^{-1}$ at BB3 (Fig. 2c), though maximum concentrations reached $139.0 \mu\text{g L}^{-1}$ at BB3 during non-EN conditions. Chlorophyll concentrations were higher within and at the mouth 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, $25.2 \pm 33.4 \mu\text{g L}^{-1}$; BB6, $22.4 \pm 20.2 \mu\text{g L}^{-1}$; LM1, $22.5 \pm 22.1 \mu\text{g L}^{-1}$) were > twofold higher than in Upper Laguna Madre (LM2, $6.6 \pm 7.6 \mu\text{g L}^{-1}$; LM3, $6.6 \pm 5.2 \mu\text{g L}^{-1}$; Fig. 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. 2c). In Upper Laguna Madre, chlorophyll concentrations were higher in non-EN conditions by $2.3 \mu\text{g L}^{-1}$ at LM3, and by $6.5 \mu\text{g L}^{-1}$ at LM2 (which reflect ~30% and ~100% increase compared with EN conditions, respectively; Fig. 2c).

Monthly Environmental Conditions from 2013 to 2016

The first 2 years of sampling were characterized by drought (May 2013–March 2015), with non-EN conditions in place for most of this time (May 2013–November 2014). The last year of sampling occurred during EN conditions and was characterized by high rainfall beginning in March 2015. Non-EN conditions corresponded with higher salinity and DOC concentrations at all sites in the monthly field-sampling program (BB1–BB5; Figs. 3 and 4). Sites BB1 and BB2, at the heads of Cayo del Grullo and Laguna Salada, generally had higher DON and orthophosphate concentrations, and lower DIN to dissolved inorganic phosphorus (DIP) ratios than sites BB3–BB5 (Fig. 4).

From April to June 2015, salinity stratification was observed (ESM 3a) but was generally low on other dates. Temperatures peaked in summer months and were lowest in winter months (ESM 3b). The lowest average winter temperatures progressively increased each year (2013/2014, 9.9 ± 0.4 °C; 2014/2015, 14.0 ± 0.5 °C; 2015/2016, 17.7 ± 0.9 °C; ESM 3b). Average NH_4^+ and N+N concentrations were almost twice as high from April 2015 onward under low salinity conditions (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 (NH_4^+ , $3.0 \pm 3.6 \mu\text{M}$;

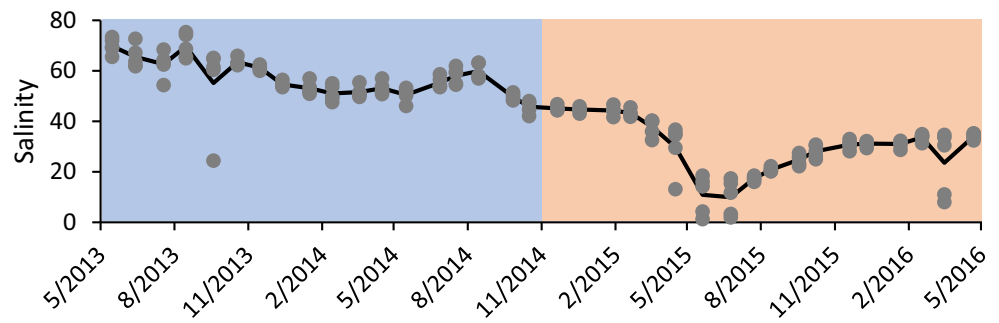
Fig. 2 Average (\pm standard deviation) (a) salinity, (b) TKN (μM), and (c) chlorophyll ($\mu\text{g L}^{-1}$) for five TCEQ sites in Baffin Bay and Upper Laguna Madre during non-El Niño conditions and El Niño conditions from 1993 to 2015



N+N, $1.5 \pm 4.4 \mu\text{M}$; ESM 3c,d). 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 (ESM 3e). Silicate

concentrations were lower under low salinity conditions ($54.5 \pm 48.1 \mu\text{M}$) compared to high salinity conditions ($78.3 \pm 16.3 \mu\text{M}$; ESM 3f), corresponding with increased biovolume of diatoms during low salinities (see the “Phytoplankton

Fig. 3 Average salinity (black line; values at each of five monitoring sites represented by gray points) from May 2013 to April 2016. Shaded area depicts non-El Niño (blue) and El Niño (orange) conditions



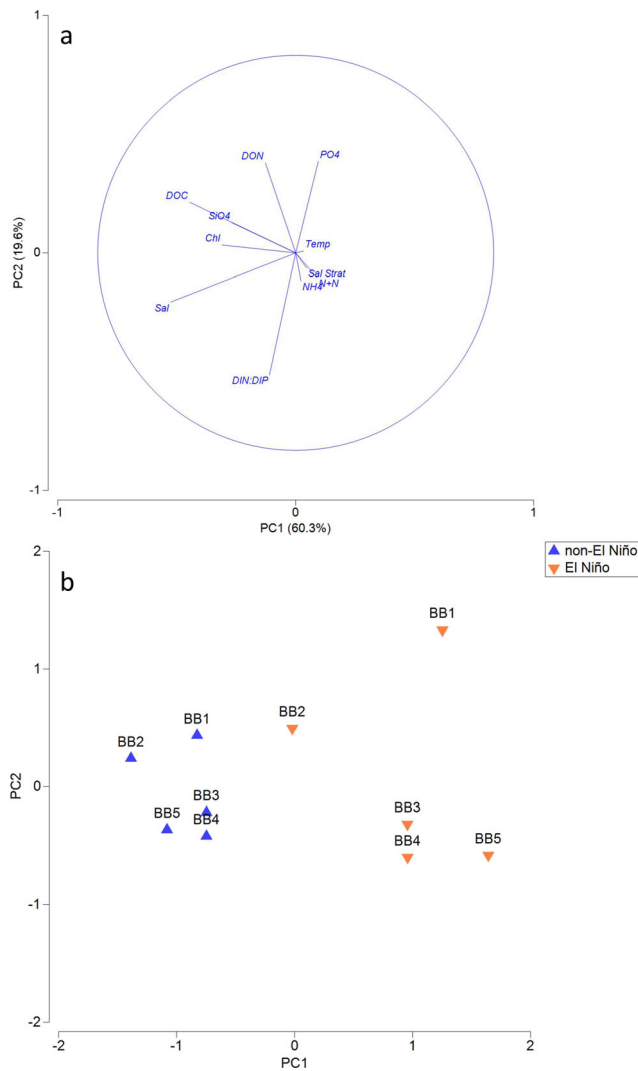


Fig. 4 Plots of the first two principal components (PC) from analysis of monthly water quality data at five sites in Baffin Bay from May 2013 to April 2016. Plots include (a) PC loadings and (b) PC scores for each station during non-EN (blue) and EN (orange) conditions

Dynamics from 2013 to 2016” section). Lowest DON concentrations occurred during the spring of 2015, reaching a minimum average of $41 \mu\text{M}$ in May 2015 (ESM 3g). DON was consistently higher than concurrent DIN concentrations throughout the sampling period (ESM 3c,d,g). Overall, there was no clear temporal trend in DON concentrations (ESM 3g). Variability in ciliate biovolume was not aligned with seasonal cycles or interannual shifts in salinity conditions (ESM 3h). Ciliate biovolume was typically higher in 2015 than the other years (ESM 3h).

From May 2013 to February 2015, residence time was estimated to be > 1 year for all but three months. Residence time was estimated to be < 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 to April 2016 (ESM 2).

Phytoplankton Dynamics from 2013 to 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, $25.7 \pm 11.7 \mu\text{g L}^{-1}$; ESM 4). During high salinity conditions, chlorophyll concentrations peaked in summer months, but the seasonal pattern was less pronounced after the onset of low salinity conditions in 2015 (ESM 4). 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. 5).

nMDS analysis showed that the phytoplankton community was different in EN and non-EN periods (Fig. 6). During high salinity conditions from May 2013 to March 2015, the phytoplankton community was dominated by *A. lagunensis*, which accounted for an average of 87% of community biovolume during this period (Fig. 5). The second and third most prevalent groups were dinoflagellates and diatoms, only accounting for an average of 9% and 3% of community biovolume, respectively (Fig. 5). *A. lagunensis* biovolume peaked in summer months (Fig. 5), as did the proportion of *A. lagunensis* in relation to other groups (Fig. 5). In contrast, dinoflagellate biovolume peaked in winter months, and diatom biovolume peaked in spring months (Fig. 5).

After the onset of low salinity conditions in spring 2015, phytoplankton biovolume decreased by over 40% on average and community composition changed (Fig. 5). *A. lagunensis* biovolume decreased sharply across all sites and remained low at most sites in the bay (Fig. 5). The exception was BB2, where *A. lagunensis* biovolume rebounded by summer 2015, despite the low (< 30) salinity measured during this time (Fig. 5b). Average dinoflagellate biovolume also decreased from the high to low salinity period (Fig. 5). Biovolume of diatoms was higher in low salinity conditions, accounting for an average of 29% of community biovolume (Fig. 5). Most diatom biovolume in the high salinity period consisted of benthic taxa (89%), while during the low salinity period planktonic taxa dominated (64%; ESM 5). Benthic taxa were primarily pennate forms such as naviculoids and *Cylindrotheca* spp. Planktonic diatoms were dominated by *Rhizosolenia* spp., though *Thalassionema* spp. and *Thalassiosira* spp. were also commonly observed. *Mesodinium* sp. 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. 5). Highest *Mesodinium* sp. biovolume tended to occur in winter (Fig. 5). For example, in the 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. 5).

Other phytoplankton groups, including cryptophytes, chlorophytes, picocyanobacteria, and unidentified flagellates,

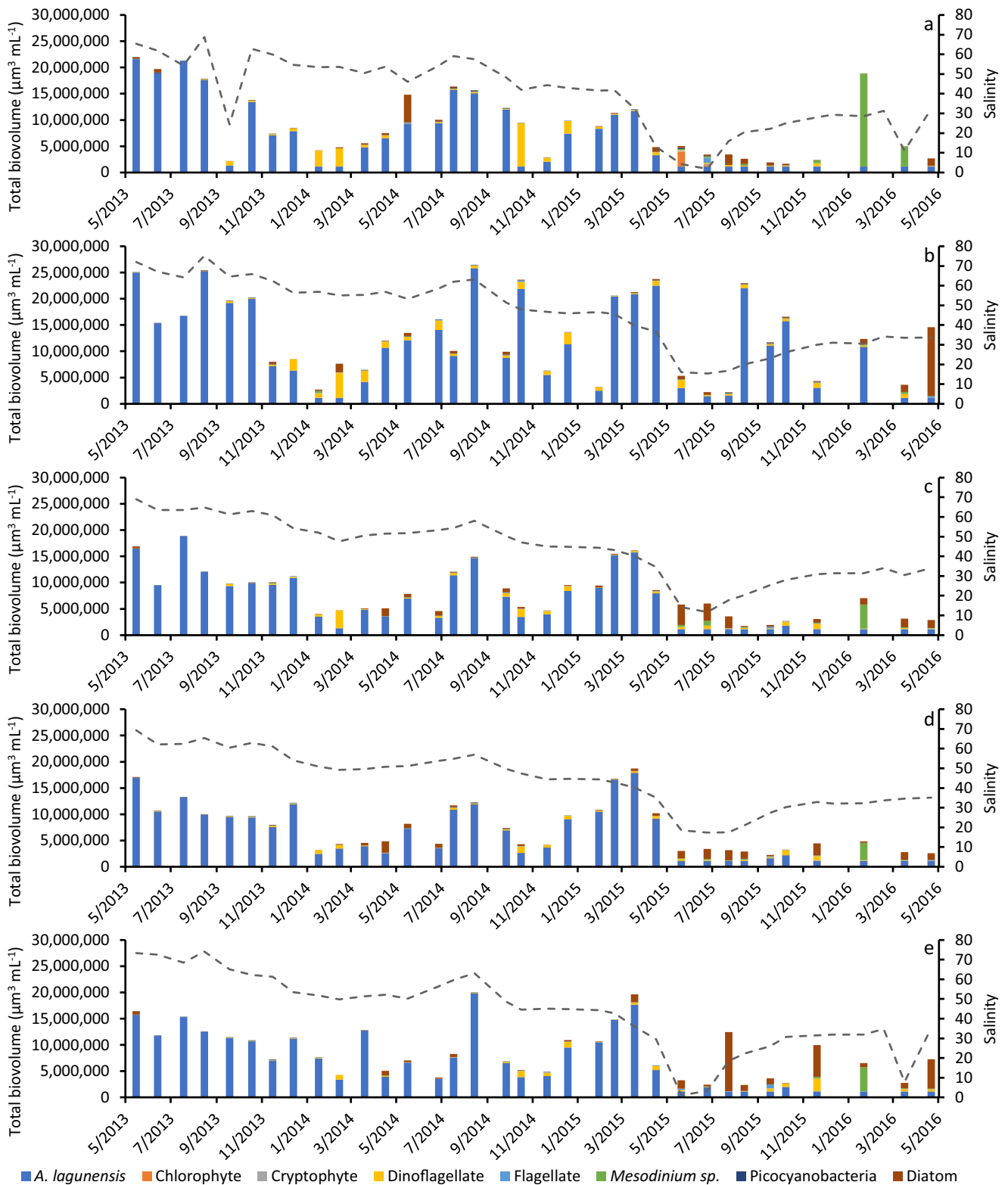


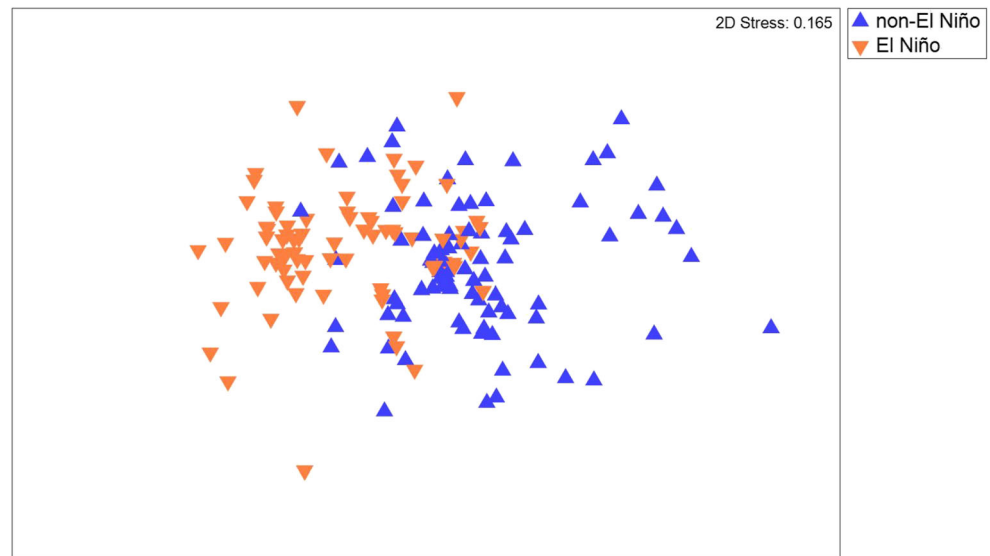
Fig. 5 Biovolume of phytoplankton groups at five monitoring stations in Baffin Bay, (a) BB1, (b) BB2, (c) BB3, (d) BB4, and (e) BB5, from May 2013 to April 2016. When *A. lagunensis* was BDL, biovolume

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

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. 6 Non-metric multi-dimensional scaling (nMDS) plot of the phytoplankton community assemblage at five sites in Baffin Bay from May 2013 to April 2016 during non-EN (blue) and EN (orange) conditions



(ESM 6). 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. 5).

Discussion

In this study, we examined nutrient-phytoplankton dynamics in Baffin Bay-Upper Laguna Madre, TX. 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, we were 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 phytoplankton dynamics in low-inflow estuaries and show that while nutrient concentrations and phytoplankton composition behaved similar to river influenced estuaries in response to rainfall/inflow variability, the phytoplankton biomass response was more complex and requires consideration of multiple environmental drivers. We elaborate below on the spatial and temporal distribution of nutrients and phytoplankton in the system, as well as environmental and ecological factors that contributed to these similarities and differences with river-influenced estuaries.

Texas estuaries have 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). In the long-term dataset, 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 the monthly sampling program, total dissolved nitrogen (TDN) increased by 11 μM from January 2015 (just prior to EN-related salinity decrease) to April 2016 (during EN). The net increase in nitrogen (as TKN or TDN) during EN conditions in both the long-term and 3-year dataset, as well the observed increase in NH_4^+ and $\text{N}+\text{N}$ 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 (Caffrey et al. 2007; Peierls et al. 2012). Based on spatial patterns in the historical data, it appears that watershed-derived TKN is diluted by tidal exchange and mixing as water masses move out of Baffin Bay into Upper Laguna Madre. Further work is needed to understand exchange of nutrients 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).

For phytoplankton, there is typically a trade-off 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; Phlips et al. 2020). However, in shallow lagoonal systems, internal nutrient recycling and sources can often sustain phytoplankton growth for some time 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. A recent study in Baffin Bay found very high 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 that DON was susceptible to high rates of photoammonification 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 DON 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, implying that it is able to grow on some fraction of the DON in this system (Buskey et al. 1998; Agostoni and Erdner 2011). Thus, while external nutrient loadings affect nutrient stocks 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). This is consistent with previous work showing the prevalence of *A. lagunensis* blooms in the system during low rainfall, low inorganic nutrient conditions (e.g., Buskey et al. 2001; Cira and Wetz 2019). A strong temporal coherence between picocyanobacteria and *A. lagunensis* was observed, consistent with prior studies (Kang et al. 2015; Hall et al. 2018). However, picocyanobacteria biovolume was relatively low and inconsequential, which was somewhat surprising given that conditions were conducive to picocyanobacteria (i.e., generally warm waters, low freshwater inflows, low inorganic nutrient concentrations; Murrell and Lores 2004). 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. Dinoflagellates were also not a major component of the phytoplankton community overall, but did occasionally have relatively high biovolume in the winter months during non-EN conditions at select sites. Seasonal peaks of dinoflagellate biovolume in winter months are a common feature in other coastal systems (Rothenberger et al. 2009; Lee 2017) and have been explained in part by mixotrophy, which allows dinoflagellates to thrive under low light conditions (Millette et al. 2017). Unfortunately, we were unable to resolve mixotrophic from non-mixotrophic taxa because of difficulty associated with enumerating Lugol’s-preserved samples (e.g., Rothenberger et al. 2009), so the ecological role and drivers of the winter dinoflagellate peaks remain enigmatic at this point.

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 *Mesodinium* sp.) became more prevalent. This reflects a shift in phytoplankton community composition and an increase in diversity that could be due to several factors, including (1) release of competition for nutrients because of the increased nutrient loads and concentrations associated with inflow (e.g., Dorado et al. 2015), (2) increased flushing that favored fast growing taxa, and/or (3) release from the stress of harsh salinities (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). In laboratory studies, *A. lagunensis* growth rates peak at ~ 0.6 day^{-1} in salinities of 30–50 but decrease at salinities < 30 (Buskey et al. 1998). Although salinity plays an important role in *A. lagunensis* blooms, Hall et al. (2018) pointed to a significant role for residence time in the population dynamics of an *A. lagunensis* bloom in Guantánamo Bay. This is an important distinction because residence time changes concurrently with salinity changes and thus the effects of one can be attributed to changes in the other. 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% (day^{-1}) within Baffin Bay, which could be significant for *A. lagunensis*. However, as seen at BB2 in summer 2015, *A. lagunensis* biovolume rebounded, even with salinities < 30. Interestingly, this occurred during a period of increasing residence times. Cira and Wetz (2019) found that *A. lagunensis* abundances were persistently high at BB2 compared with the rest of Baffin Bay, and proposed BB2 is an

“incubator” for *A. lagunensis* within the bay. BB2 has many conditions favorable to *A. lagunensis* including high DON, shallowness that would facilitate benthic-pelagic coupling of nutrients, and it is thought to be less well flushed than other parts of the bay. Other studies have also shown that similar small, poorly flushed tributaries can serve as incubators for slow growing harmful phytoplankton taxa (e.g., Philips et al. 1999; Qin and Shen 2019). In this case, the unique nature of BB2 from a nutrient standpoint and as a potential incubator for *A. lagunensis* seed stock offers an opportunity to focus watershed restoration efforts to maximize reduction in the future frequency of blooms.

The decrease in *A. lagunensis* biovolume during the high rainfall, low salinity period of spring 2015 corresponded with an increase in biovolume of diatoms and *Mesodinium* sp. Prior to 2015, benthic forms of diatoms (primarily naviculoids) were most prevalent, whereas in 2015, planktonic forms (primarily *Rhizosolenia* spp., *Thalassionema* spp.) 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 Jr. et al. 1993). The dominance of both planktonic diatoms and *Mesodinium* sp. during the low salinity period can be attributed to higher freshwater inflow and accompanying nutrient pulses. Many planktonic diatom taxa are high-nutrient adapted and have high growth rates ($\sim 1\text{--}2\text{ d}^{-1}$; e.g., Shikata et al. 2008; Dorado et al. 2015; 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). The increase in biovolume of *Mesodinium* sp. is consistent with studies on its relationship with freshwater inflow and salinity (e.g., Johnson et al. 2013). Even though *Mesodinium* sp. is a mixotroph, nitrate can be its primary nitrogen source and the organism may require relatively high nutrient concentrations (Smith Jr. and Barber 1979; Lindholm 1985). Highest *Mesodinium* sp. 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 *Mesodinium* sp. (Sanders 1995; Johnson et al. 2013). Taylor et al. (1971) reported that maximum *Mesodinium* sp. abundances occurred at temperatures just above 15 °C, which would limit *Mesodinium* sp. to the cooler months in Baffin Bay. The combination of lower salinities, greater nutrient availability, and optimal temperatures may explain why highest *Mesodinium* sp. biovolume was found in the winter of 2015/2016.

Conclusions

This study highlights the substantial interannual variability in nutrients and phytoplankton biomass/composition that occurs in Baffin Bay-Upper Laguna Madre, a low-inflow South Texas estuary. Results show similarities to river-dominated estuaries in terms of inorganic nutrient concentrations, which tended to be higher under higher inflows, and in terms of phytoplankton composition, which favored slow-growing taxa during lower inflows and faster growing taxa during higher inflows (Olli et al. 2019). Interestingly during low inflow, long residence time 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*. These findings are consistent with emerging evidence showing that in some estuaries, decreases in freshwater inflows and associated increases in residence times and salinities can still facilitate high 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 hypersalinity and presumably less diverse phytoplankton 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, high organic nutrient levels, and low inflows has pushed the system to dominance by harmful taxa (Wetz et al. 2017). 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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Declarations

Conflict of Interest The authors declare no competing interests.

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