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Phytoplankton biomass and community composition in three Texas estuaries differing in freshwater inflow regime

Tiffany Chin^a, Laura Beecraft^{a,*}, Michael S. Wetz^a

^a Harte Research Institute for Gulf of Mexico Studies, 6300 Ocean Drive, Unit 5869, Corpus Christi, Texas, 78412, USA

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Because many estuaries worldwide are experiencing large-scale alterations in freshwater inflows due to climatic and human influences on watersheds, it is critical to understand ecosystem-level responses to freshwater inflow conditions and variability. This study compared environmental conditions and phytoplankton biomass/community composition among three Texas estuaries with differing freshwater inflow regimes to understand the impacts of freshwater inflow magnitude on phytoplankton communities. It was hypothesized that: 1) nutrient concentrations and phytoplankton biomass would be highest in San Antonio Bay (SA), the high inflow estuary and lower in Nueces-Corpus Christi Bay (NC) and Baffin Bay (BB) due to lower average inflows, and 2) the phytoplankton community would be dominated by large and/or fast-growing taxa in SA, with a greater fraction of small and/or slow-growing taxa in NC and BB. Highest inorganic nutrient concentrations were generally observed in SA, while high organic nutrient concentrations were found in BB. Chlorophyll a was relatively high in both SA and BB (mean 16.9–18.5 μ g L⁻¹) while phytoplankton biovolume was highest in BB. Despite distinct freshwater inflow, salinity and nutrient regimes, differences in phytoplankton community composition were less pronounced. Nano- or microplankton were the dominant size class of phytoplankton in each system, and diatoms were the dominant functional group, accounting for 27-49% of total biovolume on average. There were indications that the phytoplankton community was more diverse in SA, especially following inflow events, providing evidence that inflow may act as a disturbance that leads to greater phytoplankton diversity. Results from this study also showed that while freshwater inflow is important for nutrient delivery, low inflow estuaries such as BB are still susceptible to effects of eutrophication due to long residence times and nutrient retention/ recycling. Overall, the differing responses of each of these ecosystems to freshwater inflow highlight the importance of system-specific management plans and consistent monitoring programs in coastal estuaries.

1. Introduction

Freshwater inflows bring new nutrients and sediment loads to estuaries, affecting biogeochemical processes (Sklar and Browder, 1998; Bruesewitz et al., 2013), light availability in the water column (Underwood and Kromkamp, 1999; Azevedo et al., 2014), and primary production (Lancelot and Muylaert, 2011). Additionally, the magnitude of freshwater entering an estuary influences mixing, circulation patterns, and hydraulic flushing regimes (Longley, 1994; Montagna et al., 2018). Freshwater inflows are variable at the scale of individual bays and are dependent on both short-term weather patterns and long-term climatic variation, as well as human influences such as damming and freshwater withdrawals (Kennish, 2002; Montagna et al., 2013).

Phytoplankton are sensitive indicators of environmental change because of their ability to respond rapidly to acute or chronic perturbations (Paerl et al., 2007; Lemley et al., 2016). This, as well as their position at the base of the estuarine food web, highlights the importance of understanding phytoplankton responses to large-scale environmental drivers such as freshwater inflow variability. Freshwater inflow influences estuarine phytoplankton through multiple interacting factors, primarily nutrient regime and flushing time. Nutrient inputs often scale to the level of freshwater inflow and can stimulate phytoplankton

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Abbreviations: BB, Baffin Bay; DIN, dissolved inorganic nitrogen; DNRA, dissimilatory nitrate reduction; DO, dissolved oxygen; DOC, dissolved organic carbon; DON, dissolved organic nitrogen; HAB, harmful algal bloom; N, nitrogen; NC, Nueces-Corpus Christi Bay; SA, San Antonio Bay; TDN, total dissolved nitrogen; TOC, total organic carbon.

^{*} Corresponding author.

E-mail addresses: Tiffany.Chin@uvm.edu (T. Chin), Laura.beecraft@tamucc.edu (L. Beecraft), Michael.Wetz@tamucc.edu (M.S. Wetz).

growth (Mallin et al., 1993), but high magnitude inflows may limit biomass accumulation when flushing times exceed phytoplankton growth rates (Roelke et al., 2013; Azevedo et al., 2014). Higher inflows may also increase sediment loading, which could result in decreased light availability in the water column, introducing the potential for light limitation (Lancelot and Muylaert, 2011). Alternatively, estuarine phytoplankton growth can become nutrient limited under prolonged low-flow conditions in some estuaries such as North Carolina's (USA) Neuse River Estuary (e.g. Wetz et al., 2011), although other studies have shown that phytoplankton growth can continue by utilizing regenerated nutrients, especially in shallow lagoonal systems (Glibert et al., 2010). In addition to influencing phytoplankton growth, freshwater inflow variability can affect phytoplankton community composition. Under high inflow regimes, large and/or fast-growing taxa such as diatoms or chlorophytes are expected to dominate, as they can rapidly uptake (and even store) new nutrients (Paerl et al., 2014; Carstensen et al., 2015; Cloern, 2017). Under low inflow regimes, low "new" nutrient concentrations and greater availability of recycled or organic nutrients may be advantageous for picocyanobacteria due to high surface area to volume ratios, and to mixotrophic dinoflagellates that are also advantaged by longer residence times due to their slower growth rates (Glibert et al., 2010; Longphuirt et al., 2019). There are exceptions, however. For example, blooms of some dinoflagellate taxa have been linked to high inflow and high nutrient conditions (e.g., Litaker et al., 2002; Carstensen et al., 2015).

Along the Texas coast, there is a precipitation gradient that results from a humid, subtropical climate in the north to an arid climate in the south (Texas Water Development Board, 2019). This gradient results in diminishing freshwater inflows along the coast, shifting from river-dominated estuaries in the north to low-inflow hypersaline systems in the south (Montagna et al., 2018). Freshwater inflow to many Texas estuaries has been decreasing over the past century due to damming, drought, and water withdrawals (Montagna et al., 2013), while climate change projections suggest that precipitation (and subsequent inflows) will decrease further by the end of the 21st century along the central and south Texas coast (Nielsen-Gammon et al., 2020). Increasing freshwater demands from population growth in coastal areas are likely to exacerbate the effects of this freshwater inflow reduction (Montagna et al., 2013). These changes could impose stress on estuarine ecosystems by starving estuarine primary producers of limiting nutrients, and thereby negatively affecting food available to higher trophic levels (e.g., Nixon, 2003). This oligotrophication has also been shown to cause a shift in phytoplankton community composition favoring harmful algal bloom (HAB) species in other estuaries (Collos et al., 2009). In Texas, resource managers need to understand the relationship between freshwater inflows and ecosystem structure and function to fulfill state regulatory requirements. Aside from this localized need, the natural inflow gradient that is present on the Texas coast affords an opportunity to quantify large-scale relationships between freshwater inflow and phytoplankton biomass/community composition, and by comparing estuaries varying in inflows, may also offer a glimpse into the future condition of estuaries that are currently experiencing declining inflows.

Here we compared environmental and phytoplankton indicators among three estuaries differing in freshwater inflow regime: San Antonio Bay (SA), which is river-influenced, Nueces-Corpus Christi Bay (NC), considered a neutral estuary based on inflow balance, and Baffin Bay (BB), which has no major river inflows and is frequently hypersaline. Our objectives were to assess if the different freshwater inflow regimes led to differences in environmental conditions and phytoplankton communities among the three bays, and if so, how. We hypothesized that 1) nutrient concentrations and phytoplankton biomass would be highest in the high inflow estuary (SA) and lower in NC and BB due to lower average inflows, and 2) the phytoplankton community would be distinct among bays and freshwater inflow conditions, dominated by large and/or fast-growing taxa in SA due to higher nutrient availability and flushing, with the fraction of small and/or slow-growing taxa increasing from NC to BB due to hypothesized lower nutrient concentrations and less flushing.

2. Methods

2.1. Site characteristics

Each of the estuaries examined in this study can be considered lagoonal systems that are separated from the adjacent Gulf of Mexico by barrier islands, limiting tidal influence and exchange of water (Fig. 1). The diurnal tidal signature for each bay is generally <20-30 cm. SA is the northernmost of the three estuaries and is fed by the San Antonio and Guadalupe rivers. It receives the highest rates of freshwater inflow of the three estuaries and has a positive inflow balance (Montagna et al., 2018). The average depth of SA is 2 m (USEPA, 1999), and the average residence time is 38 days (Montagna et al., 2011). The nearest inlet to the Gulf of Mexico is Pass Cavallo, located approximately 30 km to the north of the mouth of SA. The SA watershed is dominated by agricultural lands and scrub (NOAA C-CAP, https://coast.noaa.gov/digitalcoast/too ls/lca.html). NC receives freshwater inflow from the Nueces River, as well as return flows from wastewater facilities. Because of damming and reservoir construction on the Nueces River, freshwater inflow magnitude has decreased considerably over time and only has a limited influence on the estuary. At present, inflow balance is often neutral or slightly negative due to high evaporation rates and the low inflow rates (Montagna et al., 2018). The average depth of NC is 3 m, but an \sim 14 m deep ship channel facilitates exchange with the adjacent Gulf of Mexico (USEPA, 1999). The average residence time of NC is 356 days (Montagna et al., 2013). Land use in the watershed is dominated by agriculture and developed areas (NOAA C-CAP). BB is the southernmost of the three estuaries. It has an average depth of 2 m and a negative inflow balance on average, resulting in frequent hypersalinity in the upper reaches of the bay (Wetz et al., 2017). Inflows in BB are from ephemeral streams, and the bay often experiences little to no inflow, punctuated by high inflow during El Niño years. The nearest inlets to the Gulf of Mexico are Packery Channel (~41 km north of Baffin Bay) and Port Mansfield (~80 km south of Baffin Bay). Cira et al. (2021) estimated that residence times range from \sim 3 weeks during high rainfall periods to many years during droughts, with an average residence time of >1 year. Land use coverage in the BB watershed is dominated by agriculture, scrub/shrub, and grassland (NOAA C-CAP), and nutrient inputs are from these sources as well as failing sewage treatment infrastructure (Wetz et al., 2017; unpubl. data).

2.2. Field sampling

Monthly sampling was conducted in each bay from March 2018 to July 2019, except for April 2019 when BB was not sampled due to inclement weather. Six sites in BB and four sites each in SA and NC (Fig. 1) were selected to capture the gradient from river influence to ocean exchange. The two additional sites in BB were included because BB has three tributaries with distinct environmental conditions. At each site, surface water (0.1 m) was collected in brown HDPE bottles and stored (i) on ice for nutrient, carbon, and chlorophyll *a* (Chl *a*) analysis and (ii) at ambient water temperature for phytoplankton enumeration. Sites in each bay are shallow and rarely stratified such that a nearsurface sample is representative of the water column. Secchi depth and depth profiles (every 0.5 m) of dissolved oxygen (DO), pH, conductivity, salinity, and temperature were collected using a Professional Plus YSI multiparameter sonde (YSI, Yellow Springs, OH).

Daily inflow data were obtained from USGS river gauges (http://wa terdata.usgs.gov): San Antonio River (#08188500) and Guadalupe River (#08176500) for SA, Nueces River (#08211000) for NC, and Los Olmos Creek (#08212400), San Fernando (#08211900), and Petronila Creek (#08212820) for BB. Inflow averages were calculated for the seven days preceding each sampling date. This timeframe was chosen



Fig. 1. Map of sampling sites within the 3 bays located along the Texas coast of the Gulf of Mexico: Baffin Bay (6 sites), Nucces-Corpus Christi Bay (4 sites), and San Antonio Bay (4 sites).

based on best methods reported by Roelke et al. (2013).

2.3. Water chemistry analyses

Inorganic nutrient (nitrate + nitrite (NO_x), ammonium, orthophosphate, and silicate) and total dissolved nitrogen (TDN) concentrations were determined from the filtrate of water samples that were passed through pre-combusted 25 mm GF/F filters and stored frozen (-20 °C) until analysis. After thawing to room temperature, inorganic nutrient samples were analyzed on a Seal QuAAtro autoanalyzer. TDN samples were analyzed using the High Temperature Catalytic Oxidation method on a Shimadzu TOC-Vs analyzer with nitrogen module. Dissolved organic nitrogen (DON) was determined by subtracting dissolved inorganic nitrogen (DIN; ammonium, NO_x) from TDN. Full details on analytical methods can be found in Wetz et al. (2017).

2.4. Phytoplankton quantification

Chl *a* was analyzed for total, <20 μ m, and <3 μ m size fractions. The <20 and < 3 μ m size fractions were pre-filtered through 20 μ m mesh or Whatman GF/D filters (nominal pore size 2.7 μ m, referred to here as 3

µm), respectively. Samples were collected on 25 mm Whatman GF/F filters at low vacuum pressure (<5 mm Hg) and stored frozen (-20 °C) until analysis. Chl *a* was quantified fluorometrically following passive extraction in 90% acetone for 16–24 h, without acidification, using a Turner Trilogy fluorometer (Welschmeyer, 1994).

Phytoplankton were quantified using a combination of flow cytometry (picophytoplankton and *Aureoumbra lagunensis*) and microscopic identification. Samples for flow cytometric analysis were fixed with glutaraldehyde (ca. 0.002%) and stored at -20 °C until analysis. Samples were thawed in the dark at room temperature, filtered through 20 µm Nytex mesh, and processed on an Accuri C6 Plus flow cytometer (BD BioSciences, San Jose CA) for picophytoplankton quantification (Marie et al., 1999). Additionally, samples for *A. lagunensis* enumeration were stained using a species-specific polyclonal antibody and run in parallel with unstained controls. The detection limit for *A. lagunensis* enumeration was 80,000 cells•ml⁻¹ (Cira and Wetz, 2019), and values below detection limit were treated as zeros. *A. lagunensis* has been known to form persistent, near mono-specific blooms in BB since 1990 (Wetz et al., 2017; Cira and Wetz, 2019), and hence special attention was paid to it. Nano- and microplankton were enumerated using the Utermöhl

method with samples preserved with acid Lugol's (ca. 2%). Samples

(5–10 mL) were settled for 24 h and counted using an Olympus 1X-71 inverted microscope at $200 \times$ magnification. Biovolume was estimated from formulas of geometric shape of cells as described by Hillebrand et al. (1999) and Sun and Liu (2003). When there were conflicts between the formulas in these two sources, formulas from Sun and Liu (2003) were used. Taxa were grouped into nine categories: diatoms, dinoflagellates, euglenoids, unidentified flagellates, cyanobacteria, chlorophytes, *Mesodinium*, *A. lagunensis*, and other unidentified taxa. *Mesodinium* (syn. *Myrionecta*) is included because it is a distinctive mixotrophic ciliate containing chloroplasts and contributes to observed Chl *a* concentrations.

2.5. Statistical analyses

A ln(x+1) transformation was applied prior to some analysis to improve normality, except for relative contributions (i.e. percentages) of phytoplankton size classes and groups. Statistical analyses were performed using PC-ORD Version 7.08 (McCune and Mefford, 2018) and R version 4.1.0 (R Core Team, 2020), including tidyverse (Wickham et al., 2019), skimr (Waring et al., 2021), rstatix (Kassambara, 2020) and broom (Robinson and Hayes, 2020) packages.

Regression analyses and property-property plot visualization of salinity compared to select nutrient and phytoplankton parameters were used to assess the effect of inflow. One-way analysis of variance (ANOVA) and Tukey's HSD was used to assess differences in individual environmental and phytoplankton variables among bays.

Principal Components Analysis (PCA) of the correlation crossproducts matrix was used to visualize patterns of environmental responses among bays, and Non-metric Multidimensional Scaling (NMS) analysis using the Bray-Curtis distance matrix was used to visualize patterns in community composition based on phytoplankton group biovolume. Single factor permutation-based significance tests (multipleresponse permutation procedures, MRPP) was also used to compare environmental (Euclidean distance matrix) and biovolume composition (Bray Curtis distance matrix) responses among bays.

3. Results

3.1. Comparison among bays

The anticipated gradient of freshwater inflow among bays was observed, with average freshwater inflows of 76.4 m³ s⁻¹ to SA, 24.3 m³ s⁻¹ to NC, and 0.2 m³ s⁻¹ to BB (Fig. 2, Table 1). This corresponded to an inverse pattern in salinity, with average salinity of 10.1 in SA, 25.5 in NC and 35.7 in BB (Fig. 2, Table 1). The study encompassed a relatively dry period from March–September 2018, when ~97% of the central Texas coastal region was in mild to moderate drought conditions (unpubl. data obtained from U.S. Drought Monitor). Thereafter, wet conditions generally persisted.

Multivariate analyses indicated that environmental and water chemistry parameters were distinct among the three bays (MRPP: test statistic = -92.66, p-value < 0.001, Association = 0.305), visualized by spatial separation among bays in the PCA ordination (Fig. 3). The first and second axes of the PCA ordination cumulatively explain 55% of the observed variation in the cross products matrix of transformed environmental response data (31.8 and 23.2%, respectively). SA samples were positively associated with freshwater inflow (average 7-day inflow prior to sampling dates) and inorganic nutrients, in particular NO_x and



Fig. 2. Mean daily inflow (a) calculated from USGS daily river gauge data and boxplots of salinity (b) measured monthly at multiple sites within each bay, color coded by bay. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Table 1

Summary of environmental and phytoplankton community variables in Baffin Bay, Nueces-Corpus Christi Bay and San Antonio Bay. Values are mean and range measured across all sampling dates and sites within each bay. Superscript letters indicate significant differences between bays based on 1-way ANOVA and Tukey's HSD pairwise comparisons. Refer to Supplementary Materials for complete ANOVA results (Table S1). ANOVA comparisons for relative group contribution to total biovolume were performed for groups with at least 50% of observations >0 for each site.

	Baffin Bay			Nueces-Corpus Christi Bay			San Antonio Bay		
	Mea	an	Min - Max	Mea	n	Min - Max	Mea	n	Min - Max
Inflow (7 d avg) $(m^3 \cdot s^{-1})$	a	0.2	0–1	b	24.3	2.5–185.7	с	76.4	18.4-223.6
Salinity	а	35.7	6.3–59.5	b	25.5	0.7-37.6	с	10.1	0.3-28.1
Secchi Depth (m)	a	0.5	0.2-1.2	b	0.7	0.2-2.2	с	0.4	0.1-1.2
Ammonium (µM)	a	3.7	0–15.9	b	1	0-11.2	а	4.3	0.2-25.8
NOx (µM)	a	1.5	0.1-18.1	b	0.6	0.1–5.5	с	22.2	0.1-118.8
Orthophosphate (µM)	a	0.8	0-8.2	b	1.5	0–10.6	с	3.2	0.1-8.9
Silicate (µM)	а	100.6	4.5-280	а	103.9	9.5-462.9	b	149.5	26.6-301.3
DON (µM)	а	69.1	45.9–111.2	b	35.3	17.9–64.5	b	38.6	10.1–78.3
DIN:DIP	а	41.5	0.1-886.3	b	2.7	0–29.3	а	12.1	0.2-108.6
Total Chlorophyll a (µg·L ⁻¹)	a	18.6	3.6-62.8	b	9.6	4–17.3	а	17.2	2–59.2
Percent microplankton Chl a	a	29.5	0.9-87.9	ab	24.2	2.6-81.6	b	17.9	0.1–74.5
Percent nanoplankton Chl a	a	61.7	11.5–90	ab	67.2	14.2–91	b	72.4	22.6–94.7
Percent picoplankton Chl a	а	8.8	0.3-26.4	а	8.6	0.7–54	а	9.8	0.4–39.7
Total Biovolume (µm ³ · mL ^{−1})	а	$1.24 \cdot 10^7$	$(1.63 \cdot 10^5) - (7.78 \cdot 10^8)$	b	$8.81 \cdot 10^5$	$(1.67 \cdot 10^5) - (4.86 \cdot 10^7)$	b	$1.02\cdot 10^6$	$(3.56 \cdot 10^4) - (6.81 \cdot 10^6)$
Percent diatoms	а	42.8	0–100	а	49.4	0-99.1	b	26.7	0–93.6
Percent dinoflagellates	а	16.5	0-91.8	ab	22.8	0-91.2	b	24.8	0–94.8
Percent picocyanobacteria	a	26.4	0-86.9	b	15.9	0.1-83.3	ab	19.6	0-85.6
Percent flagellates	a	4.8	0-87.3	а	5.7	0–62	b	13.1	0–73.6
Percent euglenophytes		3	0–99.9		0.7	0–14.3		1.8	0-25.2
Percent Mesodinium		1.6	0–65.6		1.1	0–11		7.4	0–94
Percent A. lagunensis		4	0-85.1		0	0–0		0	0–0
Percent chlorophytes		0	0–1.9		0	0-0.2		0.5	0–15.1
Percent unidentified		0.9	0–17.1		4.5	0–70.3		6.1	0–76.4



Axis 1 (31.8%)

Fig. 3. Principal Components Analysis (PCA) of select environmental and water chemistry response parameters measured at multiple sites in San Antonio (SA), Nueces-Corpus Christi (NC), and Baffin (BB) Bays over the 17-month sample period.

orthophosphate, BB samples were associated with higher salinity and often with increased DON, while NC samples were intermediate between SA and BB with respect to the inflow-salinity gradient.

When examined individually, all environmental and water chemistry parameters except water temperature were significantly different among bays (ANOVA, $\alpha = 0.05$) (Table 1, Table S1). Secchi depth was shallowest in SA (mean = 0.4 m), intermediate in BB (0.5 m), and deepest in NC (0.7 m; Table 1). DON concentrations were much higher in BB (mean = 69.1 μ M) compared to NC (35.3 μ M) and SA (38.6 μ M). NO_x concentrations were highest in SA (mean = 22.2 μ M), intermediate in BB (1.5 μ M), and lowest in NC (0.6 μ M), while ammonium concentrations were higher in BB (3.7 μ M) and SA (4.3 μ M) compared to NC (1.0 μ M). Orthophosphate concentrations were highest in SA (3.2 μ M), intermediate in NC (1.5 μ M) and lowest in BB (0.8 μ M), while silicate concentrations were higher in SA (149.5 μ M) compared to NC (103.9 μ M) and BB (100.6 μ M; Table 1).

Total Chl *a* was lower in NC compared to BB and SA (Table 1, Fig. 4). The nanoplankton size class (3–20 μ m) comprised most of the Chl *a* measured in all three systems, averaging 2–3 times higher concentrations compared to micro (>20 μ m) and picoplankton (<3 μ m) Chl *a* (Table 1). In BB, microplankton had higher relative contribution to total Chl *a* than in SA (Table 1), while the contribution of nanoplankton was lower in BB than SA. The micro- and nanoplankton size classes were not different between NC and the other two bays. The contribution of picoplankton was similar among all three bays (Table 1). Community composition based on group biovolume was statistically different among bays (MRPP: test statistic = -10.36, p-value < 0.001, association = 0.027). However, the within-group association was very low, indicating heterogeneity within the bays, consistent with the lack of visual separation of samples grouped by bay in the NMS ordination of biovolume community composition (Fig. S1). Total phytoplankton biovolume was

significantly higher in BB compared to NC and SA (Table 1, Fig. 4). The ratio of Chl *a*:biovolume was higher for SA compared to NC and BB (Fig. S2).

SA exhibited a relatively heterogeneous phytoplankton community on average, with contributions from diatoms (26.7% of total biovolume), dinoflagellates (24.8%), picocyanobacteria (19.6%) and unidentified flagellates (13.1%) (Table 1). In contrast, the contribution of diatoms was significantly higher in BB (42.8%) and NC (49.4%) than in SA. The contribution of dinoflagellates was highest in SA and NC (22.8%), and lower in BB (16.5%). The contribution of picocyanobacteria was highest in BB (26.4%), lowest in NC (15.9%) and intermediate in SA (19.6%). No other groups contributed \geq 10% to total biovolume on average in any of the bays.

3.2. Influence of inflow events

Silicate and orthophosphate displayed significant inverse correlations with salinity across the three systems (Table 2, Table S2, Fig. S3), indicating increasing concentrations with inflow. NO_x also correlated inversely with salinity, though not significantly for BB, and with a higher magnitude in SA. Ammonium showed no apparent correlation with salinity. Salinity did not have a strong influence on phytoplankton biomass – a significant inverse correlation was only observed between total Chl *a* and salinity for NC. Interestingly, there was a significant positive correlation between salinity and total biovolume in SA, suggesting a flushing effect of inflow that limited biomass accumulation (Table 2).

During the study period, distinct freshwater inflow events and/or prolonged periods of rainfall affected each estuary. Although the study was not specifically designed to test for the ecosystem response to specific inflow events as noted by the relatively low sampling frequency



Fig. 4. Total Chl *a* (a) and biovolume (b) over time, color-coded by bay (BB – Baffin Bay, NC – Nueces-Corpus Christi Bay, SA – San Antonio Bay). Note: an outlier point in December 2018 for site BB4 had a total biovolume of $7.78 \cdot 10^8 \,\mu\text{m}^3$ mL is not shown within the y-range of this figure. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Table 2

Slope parameters of linear regression analysis of salinity vs. nutrient and phytoplankton parameters for all observations combined and each bay individually (SA – San Antonio Bay, NC – Nueces-Corpus Christi Bay, BB – Baffin Bay). Bolded values are statistically significant at $\alpha = 0.05$. Please refer to Table S2 for full details.

	All bays	SA	NC	BB
Ammonium (μM)	-0.02	0.10	0.01	-0.04
NO _x (μM)	- 0.62	- 2.18	- 0.05	-0.04
Orthophosphate (μM)	- 0.09	- 0.19	- 0.20	- 0.04
Silicate (μ M)	-2.30	-4.14	-9.33	- 0.34
Total Biovolume	-0.03	-0.14	-0.13	-0.21
$(\mu m^3 \cdot mL^{-1})$	6.41 · 10 ⁴	5.48 · 10 ⁴	$1.54 \cdot 10^4$	$-7.17 \cdot 10^5$

(monthly), some additional insight can be drawn through examination of these periods. For example, changes in nutrient concentrations observed during the inflow events are broadly reflective of the differences observed between bays. NO_x increased sharply from $15 \pm 9 \,\mu$ M to

 $37\pm21~\mu\text{M}$ in SA during a brief high rainfall, high inflow period in April 2018 and again from $7\pm6~\mu\text{M}$ to $41\pm33~\mu\text{M}$ during a prolonged high rainfall, high inflow period that occurred in September 2018–February 2019 (Figs. 2 and 5), while NO_x either did not vary or decreased during inflow events in BB occurring in June and September 2018 and in NC from September–November 2018. Orthophosphate and silicate concentrations were generally higher in SA during the wet period, with both peaking in October 2018 at 6.6 \pm 1.7 μM and 224 \pm 38 μM respectively (Fig. 5). A similar pattern was observed in NC and BB during high inflow periods.

Chl *a* initially decreased in SA coinciding with an April 2018 inflow event (from 16.2 \pm 8.6 μ g L $^{-1}$ to 7.9 \pm 5 μ g L $^{-1}$) and then subsequently increased to 19.5 \pm 12.4 μ g L $^{-1}$ in May 2018 (Figs. 2 and 4). During the late 2018-early 2019 wet period, Chl *a* was variable and averaged 12.1 \pm 7.2 μ g L $^{-1}$, but as in May 2018, it increased considerably to 36.1 \pm 21.4 μ g L $^{-1}$ as inflow, and presumably flushing, decreased. In August 2018 just prior to the start of the prolonged wet period, the phytoplankton community in SA had >90% biovolume of diatoms or



Fig. 5. Boxplots of nutrient concentrations of (a) silicate, (b) orthophosphate, (c) NO_x and (d) DON summarized for all sampling sites on each sampling date over time, color-coded by bay (BB – Baffin Bay, NC – Nueces-Corpus Christi Bay, SA – San Antonio Bay). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

dinoflagellates. During the wet period, the community became more diverse, with several groups contributing $\geq 10\%$ of biovolume, including diatoms (21%), dinoflagellates (25%), flagellates (21%), picocyanobacteria (10%) and Mesodinium (16%) (Fig. 6). As inflow subsided and salinity began to increase, however, a diatom bloom was eventually observed in March 2019. In NC, the response of Chl a to freshwater inflow was equivocal at best, with responses varying by time and date. In June 2018 just prior to the start of the wet period, diatoms were the dominant functional group in NC, representing 33-86% of total biovolume depending on site (Fig. 7). There was also a large contribution of unidentified phytoplankton at the upper estuary site, NC1. Sites in the lower estuary had a nominal contribution from dinoflagellates (8-26%) and picocyanobacteria (11-32%). During the freshwater inflow events of summer-fall 2018, diatom relative abundance decreased, while there was increased representation from dinoflagellates and picocyanobacteria, and occasionally euglenoids and flagellates. In BB, Chl a changed little in response to a June 2018 inflow event but increased noticeably as inflow decreased following an inflow event in September 2018 (Figs. 2 and 4). After the June 2018 event, the community became less diverse as fewer functional groups contributed to the overall biovolume, particularly dinoflagellates and picocyanobacteria (Fig. 8). After the September 2018 event, there was no obvious immediate shift in community composition, although by November 2018 when inflow had decreased and salinity was increasing again, diatoms accounted for >95% of biovolume at all but one station (Fig. 8).

4. Discussion

Freshwater inflow is an important driver of nutrient loading, flushing rates, and phytoplankton dynamics in estuaries, and in many coastal regions worldwide freshwater inflow rates are changing due to climatic and anthropogenic influences. Aside from freshwater inflow, there are other environmental factors that are also relevant to phytoplankton dynamics, necessitating studies such as this to determine the role of inflow in the hierarchy of possible influencing factors. This study quantified patterns in nutrients and phytoplankton among three estuaries lying along a naturally occurring freshwater inflow gradient to better understand the role that freshwater inflow plays in phytoplankton dynamics of the region and in similar estuaries elsewhere. It was hypothesized that 1) nutrient concentrations and phytoplankton biomass would be highest in the high inflow estuary (SA) and lower in NC and BB due to lower average inflows, and 2) the phytoplankton community would be distinct among bays and freshwater inflow conditions, dominated by large and/or fast-growing taxa in SA, with the fraction of small and/or slow-growing taxa increasing from NC to BB. As discussed below, results from this study are relevant to these and other estuaries worldwide given changes in freshwater inflow regimes that are being observed.

Over the course of the study, base inflow rates were highest in SA, followed by NC and BB. There were at least seven inflow events to SA where river discharge exceeded $100 \text{ m}^3 \text{ s}^{-1}$, compared to two in NC and



Fig. 6. Phytoplankton biovolume color-coded by functional groups on each monthly sampling date, March 2018–July 2019, for each site (panels SA1 – SA4) in San Antonio Bay. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)



Fig. 7. Phytoplankton biovolume color-coded by functional groups on each monthly sampling date, March 2018–July 2019, for each site (panels NC1 – NC4) in Nueces-Corpus Christi Bay. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

one in BB. These observations are consistent with historical inflow conditions that exist because of a gradient of decreasing precipitation from the northern estuary (SA) to the southern estuary (BB) (Longley, 1994; Montagna et al., 2018). As a result of this inflow gradient as well as high evaporation rates to the south, salinities were lowest on average in SA, intermediate in NC, and highest in BB. NO_x concentrations were significantly different among each of the three bays (SA > BB > NC), with NO_x concentrations ten to fifteen times higher in SA than the other two bays, likely due to both higher average inflows and a watershed that has a high percentage of agricultural land use (Montagna et al., 2018). Property-property plots showed a strong inverse correlation between NO_x and salinity for SA, that was less pronounced in the other two. Ammonium concentrations were typically higher in SA and BB compared to NC. For all three systems, property-property plots showed no correlation between ammonium and salinity, suggestive of internal sources such as regeneration (Morin and Morse, 1999; Gardner et al., 2006). BB and SA are also shallower than NC and given the high average wind speed in this region as well as frequency of resuspension events (Carlin et al., 2016; Reisinger et al., 2017; see also: https://windexchang e.energy.gov/maps-data/325), injection of ammonium into the water column from sediments is a strong possibility (Lawrence et al., 2004). Overall, the low inorganic nitrogen concentrations observed in NC are consistent with observations of Turner et al. (2015), who also demonstrated low inorganic nitrogen concentrations over the course of a year at several sites in Corpus Christi Bay. Even though the flood conditions observed during late 2018 caused a noticeable drop in salinities of upper NC, there was little to no discernible effect on inorganic nitrogen concentrations in either Nueces or Corpus Christi Bay. This suggests that external nitrogen loads to the system were quickly removed from the water column. Because phytoplankton biomass actually decreased at the Nueces Bay sites during the wet/low salinity period, this leads us to speculate that any riverine inorganic nitrogen loads to NC are rapidly denitrified. Prior work by Gardner et al. (2006) showed that the relative importance of denitrification (a nitrogen removal pathway) compared to DNRA (a nitrogen retention pathway) increased at lower salinities in Texas estuaries. Likewise, Bruesewitz et al. (2013) showed that in nearby Copano Bay, denitrification rates increased following storm events and indicated that the estuary was a net sink for nitrogen during high inflow conditions.

Phosphate concentrations were different among all three bays (SA >



Fig. 8. Phytoplankton biovolume color-coded by functional groups on each monthly sampling date, March 2018–July 2019, for each site (panels BB1 – BB6) in Baffin Bay. *Note: differences in y-axis scale among site panels, e.g. a large diatom bloom was quantified at site BB4 in December 2018 that was an order of magnitude higher than any other sample, and presence of other groups is difficult to see. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

NC > BB). Property-property plots and regression analysis showed an inverse correlation between phosphate and salinity in each, suggesting that the watersheds are an important source and pointing to the freshwater inflow gradient as a cause of the differences between bays. Furthermore, previous work has shown that BB can be strongly phosphorus-deficient at times, perhaps due to sorption of phosphorus to sediments (Cotner et al., 2004). Silicate concentrations were greater in SA compared to the other two systems, and property-property plots showed an inverse relationship between silicate and salinity for all three bays, supporting a role for freshwater inflow in leading to the higher silicate in SA (see also Paudel et al., 2015). However, silicate concentrations were similar between BB and NC despite differences in inflow. One possibility is that the shallowness of BB promoted enhanced exchange of remineralized silicate from the sediments compared to in the deeper NC, as previous work has suggested that wind-induced resuspension of estuarine sediments can contribute to silicate in the overlying water column (Paudel et al., 2015).

The hypothesis that phytoplankton biomass would be highest in SA and decrease along with decreasing inflow from NC to BB was not substantiated. Biovolume was notably higher in BB, in particular during specific high-density events, but lower and roughly equivalent between SA and NC, whereas Chl a was high and equivalent in SA and BB, but lower in NC. Secchi depths were generally shallower in SA, indicating reduced light availability compared to the other two bays. It is wellestablished that the amount of Chl a per cell increases under lightlimited conditions (Lewitus et al., 2005; Reynolds, 2006). The observed ratio of Chl a: biovolume was highest in SA and lowest in BB, supporting the notion that light limitation may have been more pronounced in SA. Light limitation can be a common feature in some estuaries, particularly those such as SA that experience both relatively high freshwater inflow and high turbidity due to mixing (Pennock and Sharp, 1994). Taxon-specific differences in pigment content:biovolume ratio may also play a role. For example, one of the most abundant diatoms observed during bloom periods in BB, Rhizosolenia, contains relatively small chloroplasts compared to total cell volume, and in general diatoms often contain a large vacuole, potentially contributing to the lower Chl: biovolume ratios of BB samples compared to SA. More-detailed observations in future studies are needed to fully explain these patterns and discrepancies between Chl a and biovolume.

To further explain differences among bays in terms of phytoplankton biomass indicators, we can also look at nutrients. Previous field and experimental studies have shown that N is the main nutrient limiting to

phytoplankton growth in many Texas estuaries (Örnólfsdóttir et al., 2004; Dorado et al. 2015), even in BB that occasionally displays very high DIN:DIP ratios (i.e., >16:1; Wetz et al., 2017). As noted above, SA had relatively high inorganic N concentrations throughout the study. Thus, phytoplankton growth in SA would appear less likely to be nutrient limited than in the other two bays, whereas light may be the factor that limits phytoplankton growth potential in it, as previously discussed. Interestingly, despite receiving relatively low inflows on average, BB has undergone eutrophication over the past \sim 4 decades and has seen long-term increases in both N and Chl a concentrations in both the bay and watershed streams (Wetz et al., 2017). This is consistent with work showing that low inflow estuaries such as BB can be particularly susceptible to eutrophication (Bricker et al., 2008; Scavia and Liu, 2009). Although it had low inorganic N concentrations, BB had relatively high DON concentrations, some of which is accessible to mixotrophic phytoplankton (Wetz et al., 2017). New work has also indicated the potential for high rates of photoammonification in BB, which would further increase bioavailability of the DON (Liu and Shank, 2015, H. Abdulla, unpubl. data). In addition, internal ammonium regeneration rates can be quite high in BB (Morin and Morse, 1999; Gardner et al., 2006), providing a continuous N source for phytoplankton. Thus, the eutrophication of BB is the likely cause of its deviation from the expected inflow-phytoplankton relationship, i.e., phytoplankton biomass is higher than expected from freshwater inflow magnitude alone because of nutrient loading and retention. In contrast, persistent N-limitation is likely in NC, as noted by very low DIN:DIP (mean 2.7 \pm 4.6) ratios and the previously discussed low inorganic N concentrations.

Despite observing distinct environmental and water chemistry conditions between bays, differences in phytoplankton composition were not pronounced. We hypothesized that larger and/fast growing taxa would be favored in SA, while smaller and/or slower growing taxa would be favored in BB, with a community of intermediate composition in NC. In terms of size fractions, the nanoplankton and microplankton were the overall largest contributor to Chl a among all three bays, whereas the contribution of picoplankton was low (<10%) and similar among bays. Thus, the hypothesis was not fully supported. Likewise, diatoms were the dominant phytoplankton group by biovolume in all three bays, consistent with findings from other estuaries worldwide (Carstensen et al., 2015). One common feature of all three estuaries is that they experience high average wind conditions for much of the year (Carlin et al., 2016; Reisinger et al., 2017; see also: https://windexchang e.energy.gov/maps-data/325). Wind-driven turbulence may competitively favor diatoms by maintaining them in the water column, resuspending benthic taxa, and/or by increasing turbidity (Jäger et al., 2008), resulting in reduced light availability and rapidly changing light exposure as cells are transported through the water column - conditions to which many diatoms are specifically well-adapted (Litchman, 1998; Depauw et al., 2012). Nonetheless, there were a few noticeable patterns that are worth discussing. First, it appears that the phytoplankton community was generally more diverse in SA than in NC or BB, which we suspect to be due to the influence of freshwater inflow events that act as a disturbance on the phytoplankton community. For example, there were four functional groups that contributed at least 10% of total biovolume in SA on average; diatoms, dinoflagellates, picocyanobacteria and flagellates. In contrast, only diatoms, dinoflagellates and picocyanobacteria contributed at least 10% of total biovolume on average in NC and BB. Furthermore, since 1990, there have been multiple time periods, especially during drought conditions, when prolonged, near monospecific blooms A. lagunensis have been observed in BB (Buskey et al., 2001; Cira et al., 2021). As observed here, the communities of both SA and NC tended to see a greater contribution from a larger number of functional groups during inflow events, primarily from flagellates, cvanobacteria and Mesodinium in addition to the already numerically significant diatoms and dinoflagellates, adding further evidence for the role of inflow as a disturbance (Buyukates and Roelke, 2005). In contrast, the relative contribution of different functional groups of phytoplankton either did not change or decreased in BB during and after inflow events. It is unclear why this was the case, as a previous study showed increased diversity of functional groups during a prolonged wet period in BB (Cira et al., 2021). One possibility is that the inflow events observed during this study were too short in duration to cause noticeable shifts in community composition, or the preceding dry periods were too short to have established a low diversity community. Another pattern that was observed in both SA and BB was that diatom blooms tended to occur following a lag period after freshwater inflow events, primarily as the inflow was decreasing and presumably flushing was as well. Although additional data is needed to explore this phenomenon in these systems, it is possible that the diatoms may have been outcompeted by e. g., flagellates and dinoflagellates during the ephemeral stratification that occurs immediately following and during freshwater inflow events but are poised to rapidly outcompete those taxa once stratification subsides, taking advantage of the still prevalent nutrients and the diatom's ability to avoid grazing mortality (e.g., Cloern, 2017).

Phytoplankton biomass and composition are highly variable in space and time and are influenced by a variety of environmental factors (see e. g., Cloern, 2017). Results presented here highlight the importance of freshwater inflow in estuarine phytoplankton dynamics, but also point to other factors (e.g., light availability) that may be important to understand if we are to get a holistic view of phytoplankton community dynamics in estuaries of the study region. In addition, the role of freshwater inflow in shaping estuarine phytoplankton community diversity requires additional attention considering: 1) the general pattern observed here of increased relative importance to overall biovolume from more functional groups in the high inflow SA compared to the other estuaries, 2) the diversification of functional group contributions following inflow events to SA and NC, and 3) the persistence of monospecific harmful blooms of *A. lagunensis* that have been observed in the low inflow BB over the past three decades.

Finally, some conclusions can be reached based on study results in terms of potential impacts of future reductions in freshwater inflow that are expected for the central Texas coast. In the case of NC, long-term decreases in inflow due to damming have already led to increases in salinity and localized decreases in Chl a (Kim et al., 2014; Palmer and Montagna, 2015; Bugica et al., 2020). Relatively low phytoplankton biovolume and Chl a were also observed here. The consequences are unclear, although studies in other systems have shown that this oligotrophication can lead to reductions in upper trophic level production (Nixon, 2003). As observed in our study, it appears that riverine N inputs to NC are rapidly removed prior to having an impact on the bay itself. This oligotrophication may be exacerbated if lower inflows continue in the future. However, an alternate future is also possible. Specifically, previous work showing that the relative importance of denitrification compared to DNRA decreases with increasing salinity is relevant (Gardner et al., 2006). This increasing importance of DNRA with increasing salinities would conceivably increase ammonium availability and N retention in the system. This then could lead one to speculate that NC may see less effective denitrification/more effective DNRA in the future under decreasing inflow scenarios, causing it to become more sensitive to external loads. This is important given the rapid urbanization and growing influence of stormwater and wastewater-derived nutrients in the system (Rebich et al., 2011). Further work is needed, given that the negative effects of nutrient retention are already manifesting in the adjacent low inflow estuary, BB. In BB, episodic inflow events appear to stimulate high magnitude blooms, but after a lag period. As noted by a long-term increase in Chl a and nutrients (Wetz et al., 2017), the system also appears to be ineffective at removing these nutrients over longer timescales, consistent with emerging evidence of the susceptibility of this and similar low inflow estuaries to the effects of anthropogenic nutrient loadings. Furthermore, dense and/or prolonged blooms of A. lagunensis using organic and/or recycled nutrients during lower rainfall conditions cause harm to the ecosystem overall (see e.g., Buskey et al., 2001; Wetz et al., 2017). Drier conditions in the future may lead to

more estuaries experiencing similar conditions to BB, with periods of hypersalinity and extended blooms resulting from internal recycling of riverine nutrients received during episodic inflows. The differing responses of each of these ecosystems to freshwater inflow highlight the importance of system-specific management plans and consistent monitoring programs in coastal estuaries.

CRediT authorship contribution statement

Tiffany Chin: Writing – original draft, Investigation, Data curation. Laura Beecraft: Writing – original draft, Visualization, Formal analysis. Michael S. Wetz: Writing – review & editing, Supervision, Resources, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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