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FINAL REPORT

Influence of Freshwater Inflow Gradients on Estuarine Nutrient-Phytoplankton Dynamics

by
Michael S. Wetz, Ph.D.
and
Tiffany Chin, M.S. candidate
Harte Research Institute for Gulf of Mexico Studies
Texas A&M University - Corpus Christi
6300 Ocean Drive, Unit 5869
Corpus Christi, Texas 78412
Phone: 361-825-2132
Fax: 361-825-2025
Email: Michael.Wetz@tamucc.edu

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I. Executive Summary

Freshwater inflow is a critical driver of estuarine ecosystem structure and function. A major challenge for resource managers is the need to plan for ecological changes resulting from future changes in freshwater inflows. To do this, one must first understand the mechanistic linkages between freshwater inflow and components of the estuarine ecosystem. Here we report results from a 17-month study of nutrients and phytoplankton in three Texas estuaries with contrasting levels of freshwater inflow; San Antonio Bay (SA; high inflow), Nueces-Corpus Christi Bay (NC; intermediate inflow), and Baffin Bay (BB; low inflow). The goal of this study was to test the effects of freshwater inflow volume and variability on estuarine biogeochemistry and phytoplankton biomass/community composition in support of the Senate Bill 3 (2007) adaptive management environmental flows process. This is important because phytoplankton are often the main primary producers in estuaries, and the community composition of the phytoplankton community will dictate the efficiency of energy flow to higher trophic levels. Furthermore, some phytoplankton taxa are harmful to marine life and overall ecosystem health.

The hypothesis that nutrient concentrations would be highest in SA, intermediate in NC, and lowest in BB was only partially supported. Phosphate concentrations were highest in SA and decreased from NC to BB, consistent with it being derived from riverine sources. Likewise, silicate concentrations were highest in SA, also consistent with a riverine source. Silicate concentrations were lower in NC and BB, but still not at limiting levels (to phytoplankton growth) and equivalent on average between NC and BB. N+N concentrations were highest in SA, but low and roughly equivalent in NC and BB. Ammonium concentrations were approximately 4-fold higher in SA and BB than NC. DON concentrations in BB were approximately 2-fold higher than in SA or NC, where they were roughly equivalent. As with nutrients, the hypothesis that chlorophyll concentrations or phytoplankton biomass would be highest in SA, intermediate in NC, and lowest in BB was only partially supported. Total chlorophyll was comparable between SA and BB, and approximately 2-fold lower in NC, whereas total biovolume was highest in BB, and lower but equivalent in SA and NC. Nano- and microplankton represented the dominant size fraction of phytoplankton in all three bays, while they had similarly low relative contribution (~9-10% of total) from pico-sized chlorophyll (i.e., < 3 µm). BB had the greatest contribution from > 20 µm cells, primarily the diatom *Rhizosolenia sp.* that bloomed in late 2018 through early 2019. This study represents the first to take a comparative approach of Texas estuaries to quantify the effects of large-scale differences in freshwater inflow magnitude on nutrients and phytoplankton. Using modern techniques to quantify the full size spectrum of phytoplankton, findings show that the relationship between freshwater inflow magnitude and the biomass/composition of the phytoplankton community is not straightforward. First and foremost, the relationship is confounded by factors affecting availability of limiting nutrients (in this case, N). This was noted in Baffin Bay where, despite the lowest overall inflow magnitude, phytoplankton biomass was quite high as a result of the cultural eutrophication that has taken place as well as apparent high regeneration rates in the system. In this cursory analysis, we found evidence of other factors also influencing both phytoplankton biomass and community composition, namely light conditions, flushing and potentially even degree of mixing. Additional quantitative modeling and statistical analyses will be undertaken to more rigorously evaluate the effects of these different factors.

II. **Introduction**

Estuaries are among the most productive and diverse aquatic ecosystems on Earth, providing food resources and habitat for many ecologically and economically important fish and shellfish species (Hobbie 2000). Nutrients and organic matter delivered via freshwater inflow fuel the rich primary and secondary productivity of estuaries that ultimately provide food resources for numerous fish and shellfish species (Sklar and Browder 1998; Nixon and Buckley 2002). Furthermore, the salinity gradient created by freshwater inflow mixing with seawater creates important habitat for nekton and benthic organisms (Nixon and Buckley 2002). A major challenge for resource managers is the need to plan for future changes in freshwater inflows. For example, global climate projections suggest the possibility of more frequent and/or intense precipitation events, drought and heat waves in the near future (Christensen et al. 2007; Meehl et al. 2007), which may act synergistically with burgeoning human freshwater needs to dramatically alter the nature of freshwater inflow to estuaries (Flemer and Champ 2006; Christensen et al. 2007).

Nutrient/organic matter loading to estuaries, and subsequent growth of bacteria and primary producers that utilize these substrates, is often positively correlated with the degree of freshwater inflow (Jassby et al. 1993; Mallin et al. 1993; Harding et al. 1994; Wetz et al. 2011). Growth of intermediate trophic levels such as zooplankton and benthic fauna has also been shown to be linked to freshwater inflows via effects on food availability (i.e., phytoplankton, detritus) and/or habitat (i.e., salinity) (Montagna and Kalke 1992; Montague and Ley 1993; Kimmel and Roman 2004; Rutger and Wing 2006). Examples of the higher trophic level importance of freshwater inflow come from studies that: 1) link fisheries production or landings to nutrient loads, or 2) document declines in estuarine fisheries as a result of sharp reductions in freshwater inflow.

Despite the conceptual framework linking freshwater inflow to overall estuarine productivity, it has become clear that the mechanistic linkages between inflow rates and organisms occupying various trophic levels are quite complex. For example, at the level of primary producers (phytoplankton), while inflow can be important for providing otherwise limiting nutrients, flows that are too high can actually decrease flushing times and limit phytoplankton productivity/biomass (Murrell et al. 2007; Peierls et al. 2012; Azevedo et al. 2014). In addition, evidence is emerging that in some systems, low flows do not necessarily preclude high productivity/biomass because of the availability of internal (to the ecosystem) nutrient pools (Pinckney et al. 2001; Glibert et al. 2010; Hemraj et al. 2017; Geyer et al. 2018). Freshwater inflow variability can also strongly influence the underwater light environment in estuaries through its effects on water column organic matter loading (Livingston et al. 1997; Wetz et al. 2011), which in turn may alter the balance between benthic and pelagic primary producers. During prolonged low freshwater inflow conditions, light penetration tends to increase (Wetz et al. 2011), possibly favoring benthic microalgal growth (Stutes et al. 2006; Murrell et al. 2009). The implication is that despite the reduction in allochthonous organic matter/nutrient inputs and pelagic (phytoplankton) production during low freshwater inflow conditions, perhaps benthic productivity can compensate for the lack of pelagic productivity. Aside from effects on phytoplankton productivity/biomass, it is now well known that different freshwater inflow levels often select for different phytoplankton functional groups (Roelke et al. 2013; Paerl et al. 2014; Harding et al. 2016). The response by these different functional groups is dependent on system-specific attributes, such as nutrient regime, flushing dynamics and light environment, among other factors (Cloern 2005; Cloern 2018).

Here we report results from a 17-month study of nutrients and phytoplankton in three Texas estuaries with contrasting levels of freshwater inflow; San Antonio Bay, Nueces-Corpus Christi Bay, and Baffin Bay. The goal of this study was to test the effects of freshwater inflow volume and variability on estuarine biogeochemistry and phytoplankton abundance/community composition in support of the Senate Bill 3 (2007) adaptive management environmental flows process. This study was centered around two specific hypotheses:

H1 - Nutrient concentrations and chlorophyll/phytoplankton biomass are highest in the high inflow estuary, San Antonio Bay, intermediate in Nueces-Corpus Christi Bay, and lowest in Baffin Bay as a result of decreasing inflow magnitude.

H2 – Owing to hypothesized higher nutrient levels, the phytoplankton community will be dominated by large and/or fast-growing taxa in San Antonio Bay, with the fraction of small and/or slow growing taxa increasing from Nueces-Corpus Christi Bay to Baffin Bay.

III. Methods

Site descriptions

Three estuaries were chosen to represent the freshwater inflow gradient on the Texas Gulf Coast: San Antonio Bay, Nueces-Corpus Christi Bay, and Baffin Bay. San Antonio Bay (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 (Montagna et al. 2018) and has a positive inflow balance. The average depth of SA is 2 m, and the average residence time is ~1 mo (Bianchi et al. 1999). The Nueces-Corpus Christi Bay system (NC) receives freshwater inflow from the Nueces River, which is dammed, as well as return flows from wastewater facilities. Salinity in NC is influenced by exchange with coastal ocean water via the Corpus Christi Ship Channel, as model outputs suggest its presence affects salinity by ~±3 and greatly increases tidal fluxes (Powell et al. 1997). Inflow balance in NC is often neutral or slightly negative due to high evaporation rates and low inflow rates (Montagna et al. 2018). The average depth of NC is 2.3 m, with average residence times of ~1 year (Bianchi et al. 1999). Baffin Bay (BB) is the southernmost of the three estuaries. It is a lagoonal estuary with an average negative inflow rate and 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 inflows punctuated by periods of flooding during El Niño years. Residence times are on the order of ~1 mo during high rainfall periods to >1 year during drought (Cira and Wetz, unpubl. data).

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 in each

SA and NC (Fig. 1) were selected to capture the gradient from river mouth to ocean endmember. At each site, surface water was collected in brown HDPE bottles and stored on ice for nutrient, carbon, and chlorophyll *a* (Chl *a*) analysis. Additional water samples were collected and stored at ambient temperature for phytoplankton enumeration. Secchi depth as well as hydrographic depth profiles (0.5 m) of DO, pH, conductivity, salinity, and temperature were collected using a YSI multiparameter sonde.

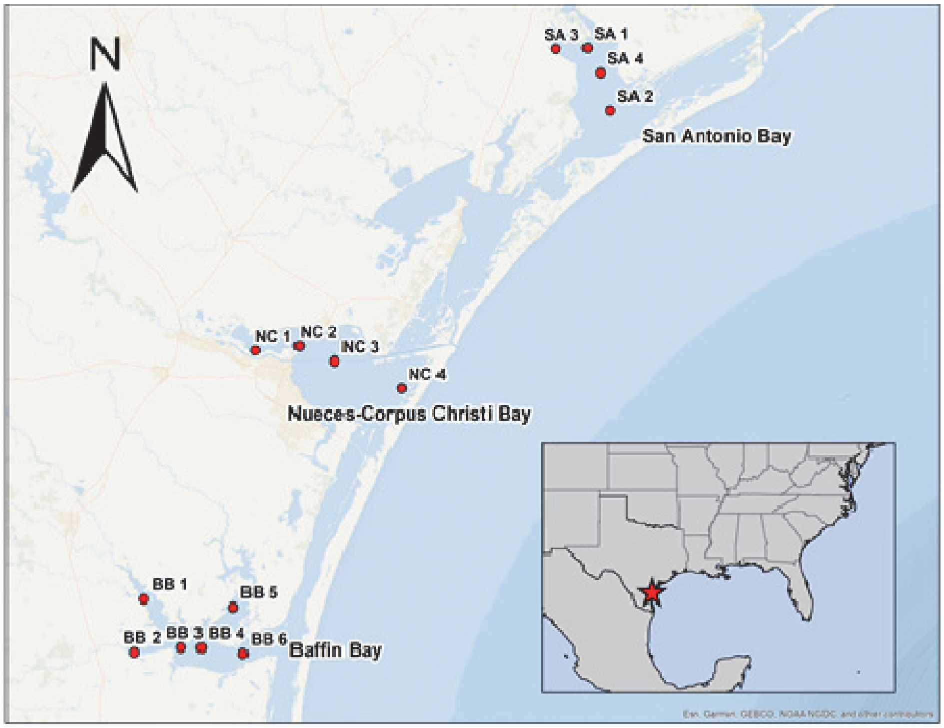

Figure 1 – Map showing sampling locations in the three bay systems.

Biogeochemical analyses

Inorganic nutrient concentrations (nitrate + nitrite, hereafter N+N; ammonium; phosphate; silicate) were determined from the filtrate of water samples that were passed through 25 mm GF/F filters and stored frozen (-20ºC) until analysis. After thawing to room temperature, samples were analyzed on a Seal QuAAtro autoanalyzer. Standard curves with five different concentrations were run daily at the beginning of each run. A standard curve allows for determination of analyte concentration in a sample from a determined relationship between known concentration and instrument response. Fresh standards were made prior to each run by diluting a primary standard with low nutrient surface seawater. Deionized water (DIW) was used as a blank, and DIW blanks were run at the beginning and end of each run, as well as after every 8-10 samples to correct for baseline shifts.

Dissolved organic carbon (DOC) and total dissolved nitrogen (TDN) were determined using the filtrate of water samples that were passed through precombusted 25 mm GF/F filters and stored frozen (-20ºC) until analysis. Samples were analyzed using the High Temperature Catalytic Oxidation method on a Shimadzu TOC-Vs analyzer with nitrogen module (SM 5310-

B, ASTM D5176-08). Standard curves were run twice daily using a DIW blank and five concentrations of either acid potassium phthalate solution or potassium nitrate for DOC and TDN, respectively. Three to five subsamples were taken from each standard and water sample and injected in sequence. Reagent grade glucosamine was used as a laboratory check standard and inserted throughout each run, as were Consensus Reference Water (Hansell 2005) deep-water standards of known DOC/TDN concentration. Dissolved organic nitrogen (DON) was determined by subtracting dissolved inorganic nitrogen (ammonium, nitrate + nitrite (N+N)) from TDN.

Phytoplankton analyses

Chl *a* was obtained by filtering (< 5 mm Hg) a known volume of sample water through Whatman 25 mm GF/F filters that were then stored frozen (<-20°C) for future analysis. Three size classes were analyzed: > 20 µm, 3-20 µm, and < 3 µm. Size-fractions were estimated as follows:

< 3 µm = GF/D filtrate

< 20 µm = 20 µm mesh filtrate

3-20 µm = < 20 µm - < 3 µm

> 20 µm = Whole - < 20 µm

Chl *a* was extracted from the filters by soaking in 90% HPLC grade acetone for 16-24 hours. Fluorometric determination of chl *a* was performed with a Turner Trilogy fluorometer without acidification.

Samples for flow cytometric analysis were fixed with 80 µl glutaraldehyde to 4 mL sample water and stored at -20°C until analysis. Picoplankton and *Aureoumbra lagunensis* (brown tide) were enumerated on an Accuri C6 Plus flow cytometer. Samples were thawed in the dark at room temperature then filtered through 20 µm Nytex mesh. Samples for *A. lagunensis* enumeration then underwent a multistep polyclonal antibody staining process that is specific to *A. lagunensis*. Stained samples were analyzed on the flow cytometer along with unstained controls for *A. lagunensis* enumeration. Filtered unstained subsamples were used to enumerate picoplankton.

Nano- and microplankton were enumerated using the Utermohl method with samples that were preserved with 1 mL acid Lugol's solution to 60 mL sample water. Sample volumes of 5 to 25 ml were settled for 24 hours and subsequently counted at 200x magnification using an Olympus BX-51 inverted microscope. Transects of settled chambers were counted until a minimum of 100 cells of the most abundant genera were identified. The volume of sample settled and area of chamber counted were used to calculate number of cells per milliliter for each taxa present. Cell measurements were used to calculate biovolume using formulas determined by the geometric shape of cells (Hillebrand et al. 1999; Sun and Liu 2003).

IV. <u>Results</u>

Environmental conditions

On average, salinities were lowest in SA (10.1 ± 6.3), intermediate in NC (25.5 ± 7.8), and highest in BB (35.7 ± 11.3) (Table 1). All three bays experienced a shift from dry conditions to wet conditions, characterized by increased inflow and lower salinity. In SA and NC, this shift occurred in September 2018, while BB experienced increased inflow earlier, beginning in July 2018 (Fig. 2). Inflows to BB were episodic in nature and frequently at or near zero. During dry conditions when inflow was lower, all bays experienced higher salinities (Fig. 3). Under dry conditions, maximum salinity in SA was observed at SA2 (28.1 in June 2018), which is closest to ocean exchange. In contrast, maximum salinity during dry conditions in NC and BB occurred at upper estuary sites (37.6 in June 2018 at NC1 and 59.5 in June 2018 at BB5). Salinity minimums in each bay were concurrent with higher inflows and occurred at upper estuary sites. Secchi depth in each bay was shallow during lower inflow, higher salinity conditions and deeper throughout the rest of the study period (Fig. 4). Water temperature was highest in the summer and lowest in the winter in all three bays (Fig. 5).

Table 1 – Mean ± SD for salinity and nutrients (µM) in the three bay systems.

Bay	Salinity	Ammonium	N+N	DON	Phosphate	Silicate
SA	10.1 ± 6.3	4.3 ± 4.9	22.2 ± 27.5	34.4 ± 9.6	3.2 ± 2.4	149.5 ± 60.5
NC	25.5 ± 7.8	1.1 ± 1.5	0.6 ± 1.0	34.3 ± 8.9	1.5 ± 2.0	101.6 ± 95.5
BB	35.7 ± 11.3	3.9 ± 3.8	1.5 ± 2.3	65.7 ± 9.8	0.8 ± 1.1	99.4 ± 55.6

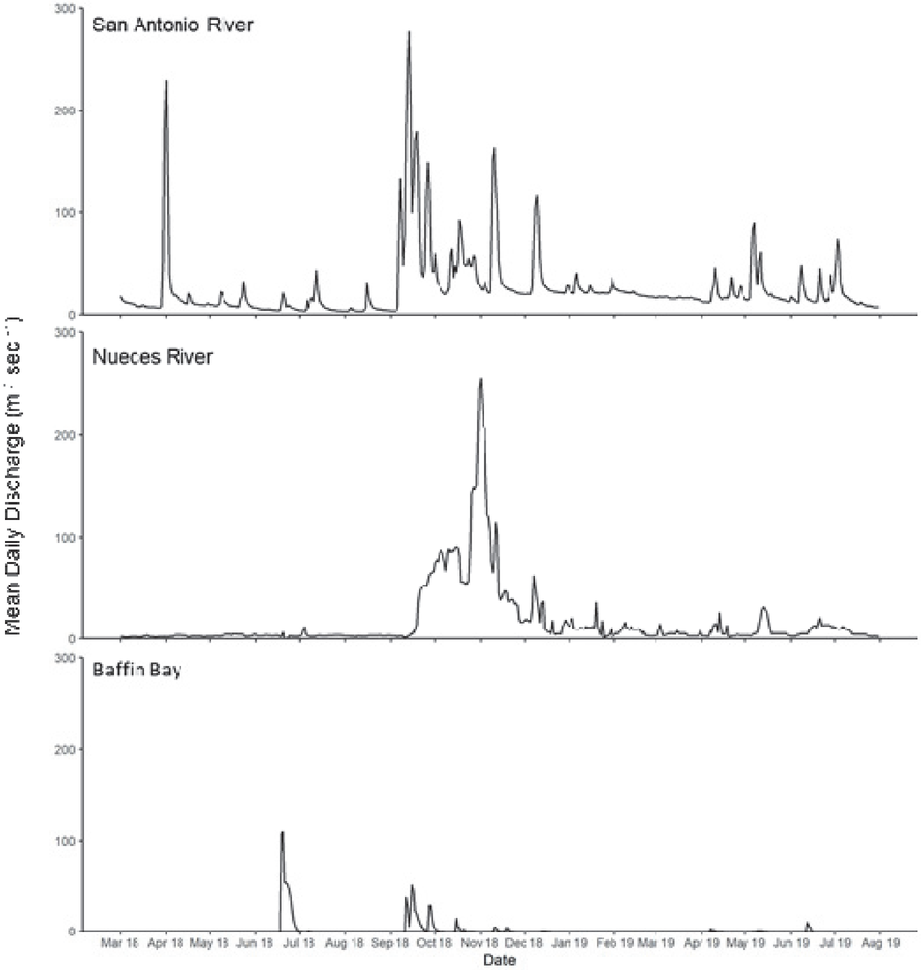

Figure 2 – Mean daily freshwater discharge to each of three bay systems during the study.

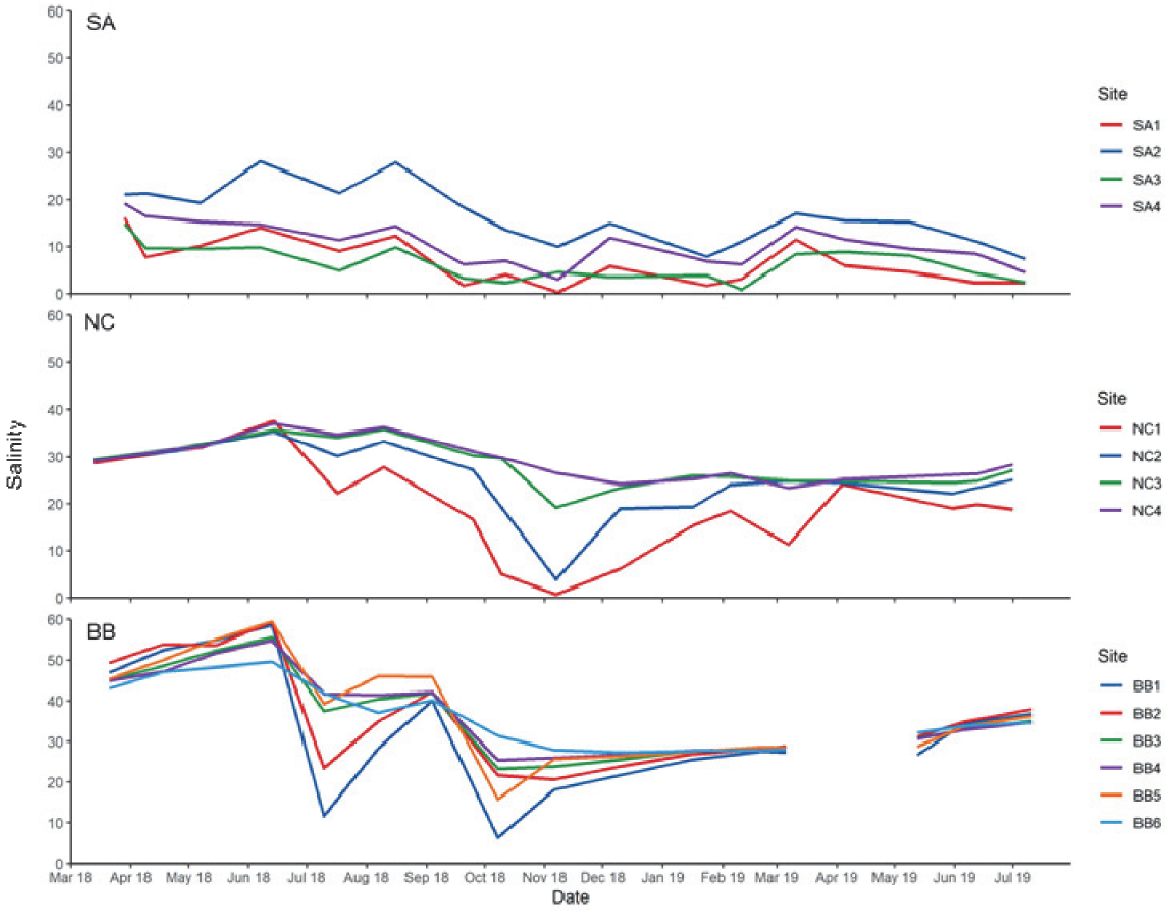

Figure 3 – Salinity in the three bay systems during the study.

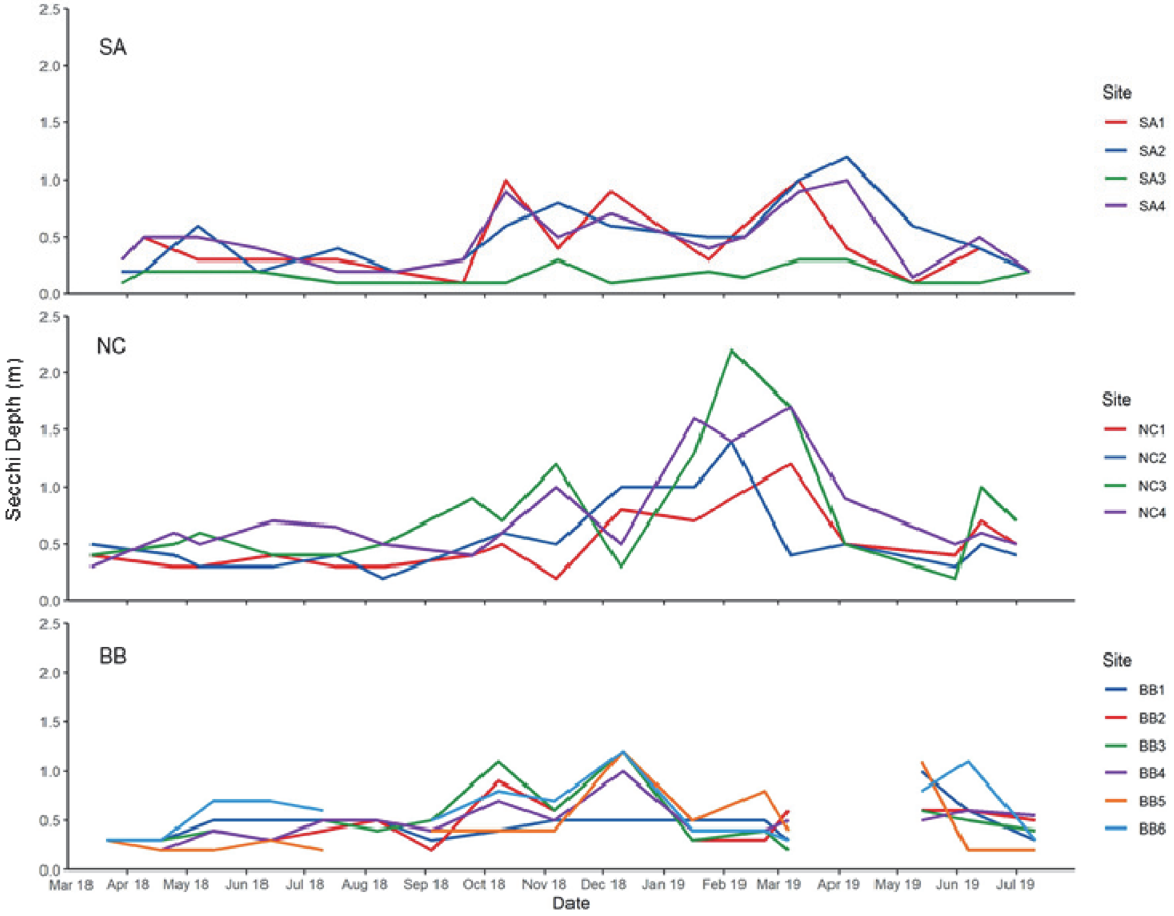

Figure 4 – Secchi depth in the three bay systems during the study.

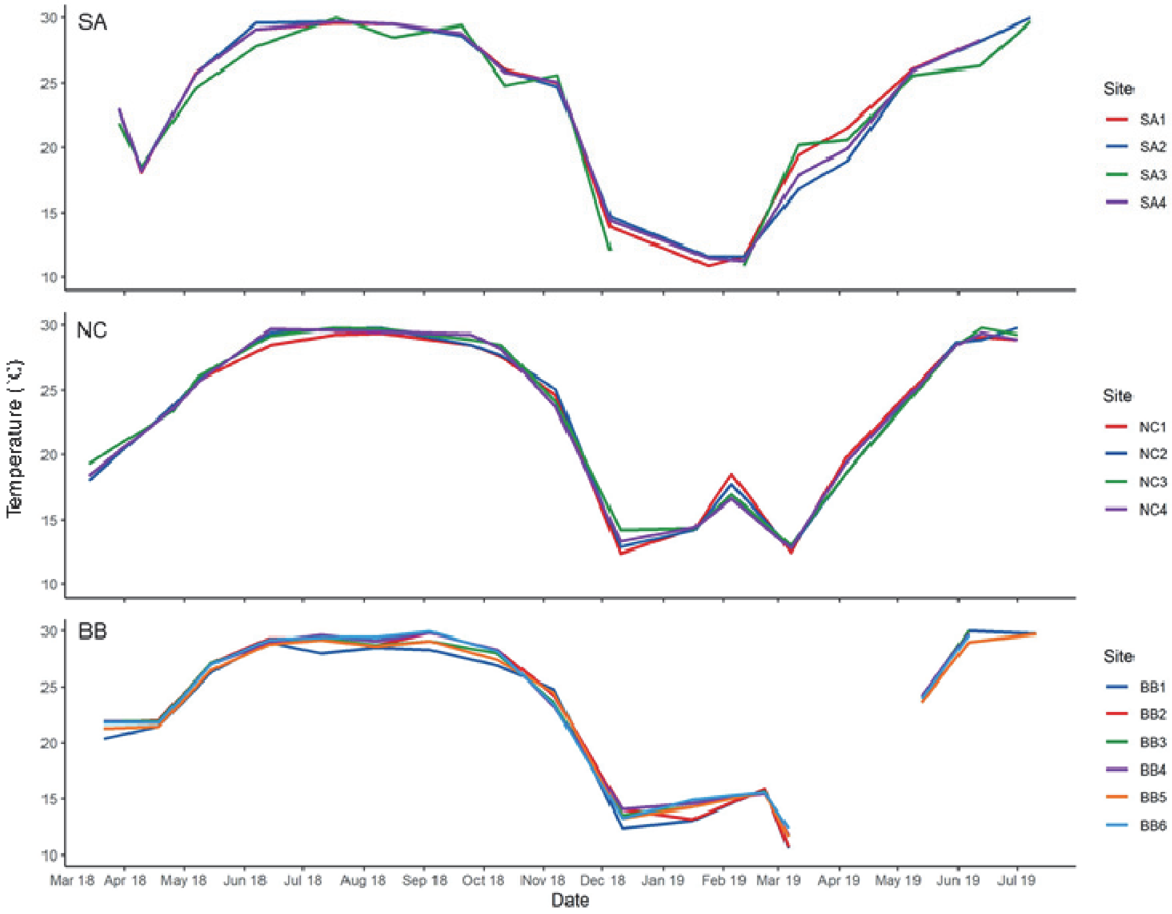

Figure 5 – Water temperature in the three bay systems during the study.

Nutrients

Ammonium concentrations were approximately 4-fold higher in SA (4.3 ± 4.9 μM) and BB (3.9 ± 3.8 μM) than in NC (1.1 ± 1.5 μM)(Table 1). N+N concentrations were highest in SA (22.2 ± 27.5 μM), but low and roughly equivalent in NC (0.6 ± 1.0 μM) and BB (1.5 ± 2.3 μM). DON concentrations in BB (65.7 ± 9.8 μM) were approximately 2-fold higher than in SA (34.4 ± 9.6 μM) or NC (34.3 ± 8.9 μM), where they were roughly equivalent. Phosphate concentrations were highest in SA (3.2 ± 2.4 μM) and decreased from NC (1.5 ± 2.0 μM) to BB (0.8 ± 1.1 μM). Likewise, silicate concentrations were highest in SA (149.5 ± 60.5 μM), and lower in NC (101.6 ± 95.5 μM) and BB (99.4 ± 55.6 μM).

In SA, ammonium was highest during March and April 2018 (max: 25.8 μM in March 2018) and then decreased in the following months (Fig. 6). Ammonium concentrations in SA peaked at intermediate salinity levels (Fig. 7). N+N was lowest from June 2018-September 2018, then increased at all sites from October 2018-February 2019, with a maximum of 118.8 μM occurring at SA1 in January 2019 (Fig. 8). The bay-wide average N+N for the entire study period was 22.2 ± 27.5 μM. N+N was highest at low salinities and decreased with increasing salinity (Fig. 9). DON was higher at SA3 than at other sites on most dates (Fig. 10). The maximum DON concentration was observed at SA3 in August 2018 (53.6 μM), and the minimum concentration was observed at SA1 in June 2019 (8.7 μM). Variability in DON was greater at low salinity than at higher salinity, and DON appeared to decrease at salinity <5 (Fig. 11). Phosphate was lower at SA2 or SA4 on all dates except in March 2019, when phosphate was lowest at SA3 (Fig. 12). Phosphate was highest at low salinities and decreased as salinity increased (Fig. 13). Silicate concentrations varied considerably (from 26.6 to 301.3 μM), but followed consistent patterns across all sites, with concentrations rising to a maximum during fall 2018 and falling to minimum in spring 2019 (Fig. 14). Silicate concentrations decreased with increasing salinity (Fig. 15).

In NC, bay-wide averages of ammonium and N+N were all very low throughout the study period (1.1 ± 1.5 μM and 0.6 ± 1.0 μM, respectively) (Figs. 6,8). NC1, located in Nueces Bay and closest to the river mouth, experienced higher concentrations and greater variability in all nitrogen species than the other sites. However, the range of variability was still small, from 0.1 to 11.2 μM for ammonium and 0.1 to 5.5 μM for N+N. DON was consistently highest at NC1 throughout the study (Fig. 10). DON was generally highest from May 2018 to October 2018, then decreased from November 2018 to February 2019, and finally increased thereafter. Phosphate and silicate increased at all sites concurrent with increased inflows from September 2018 to December 2018 (Figs. 12,14). The highest concentrations of phosphate and silicate occurred at sites NC1 and NC2, which are closer to riverine inflow than the other two sites. NC3 experienced a slight increase in phosphate and silicate in November 2018, but little change was observed at NC4, indicating that riverine nutrient inputs were assimilated prior to reaching the ocean endmember.

In BB, ammonium concentrations were generally < 1-2 μM, but episodic increases were observed (Fig. 6). For example, a brief increase was observed in June 2018 at all sites. An apparent prolonged increase began in February 2019 at most sites and concentrations remained elevated through summer 2019. Ephemeral increases were also observed at BB1 and BB6. Ammonium generally peaked at intermediate to high salinity levels (Fig. 7). N+N concentrations were consistently low among all sites from March 2018 to November 2018 (Fig. 8). An ephemeral spike in N+N (18.1 µM) were observed at BB1 in December 2018. In May 2019, higher N+N concentrations were observed at all sites, but these were all < 10 µM. There was no clear spatial pattern in DON (Fig. 10). Temporally, DON concentrations were slightly lower from late 2018 to early 2019 compared to other periods. Bay-wide average DON was 65.7 ± 9.8 µM. DON increased with decreasing salinities from March to September 2018, but appeared to decrease with decreasing salinities throughout the rest of the study period (Fig. 11). Phosphate was higher at BB1 than other sites except during November 2018 when it reached a maximum of 8.2 µM at BB5 (Fig. 12). In general, phosphate appeared to increase with decreasing salinities, especially at BB1 (Fig. 13). Silicate increased from March to October 2018, then declined sharply at all sites until reaching a minimum in December 2018 (Fig. 14). Silicate increased again until February 2019 when concentrations dropped and remained relatively low throughout the rest of the study. Silicate tended to increase with decreasing salinities (Fig. 15).

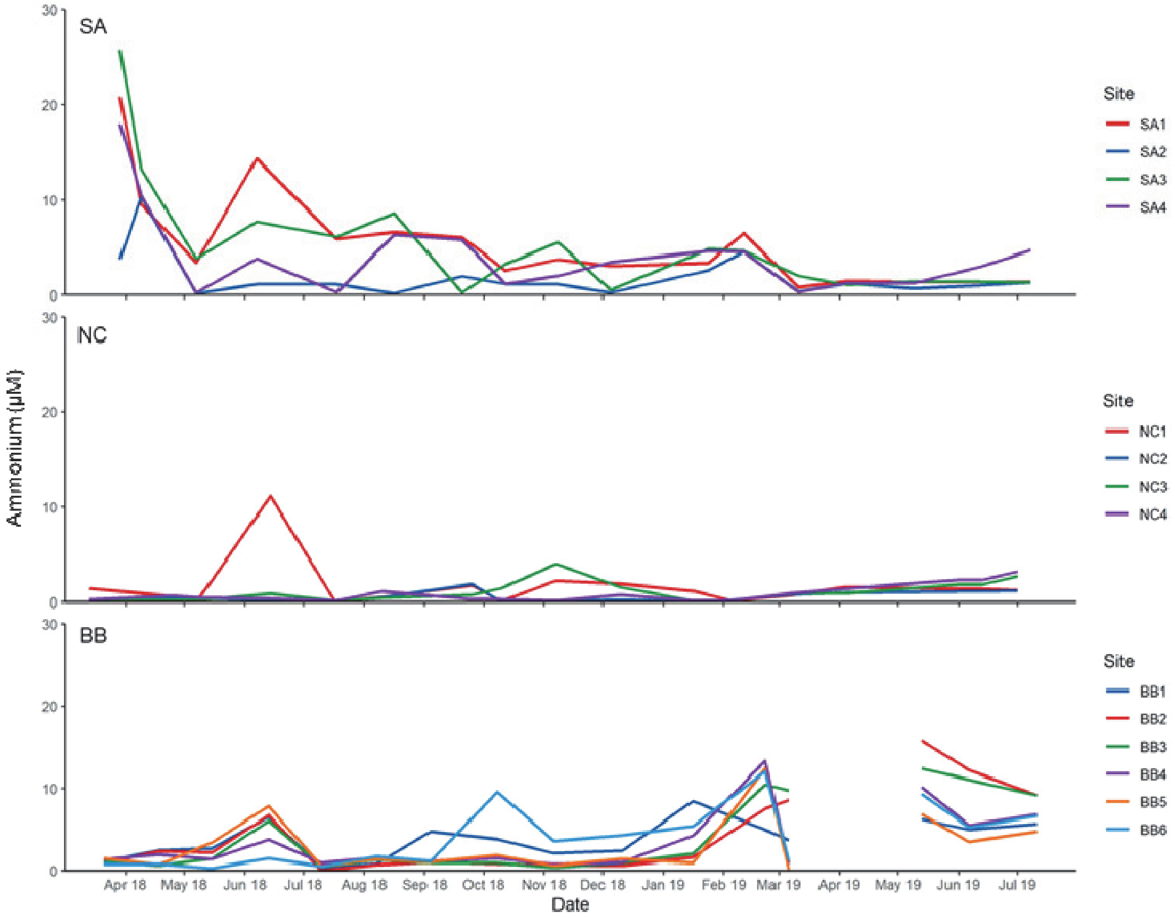

Figure 6 – Ammonium in the three bay systems during the study.

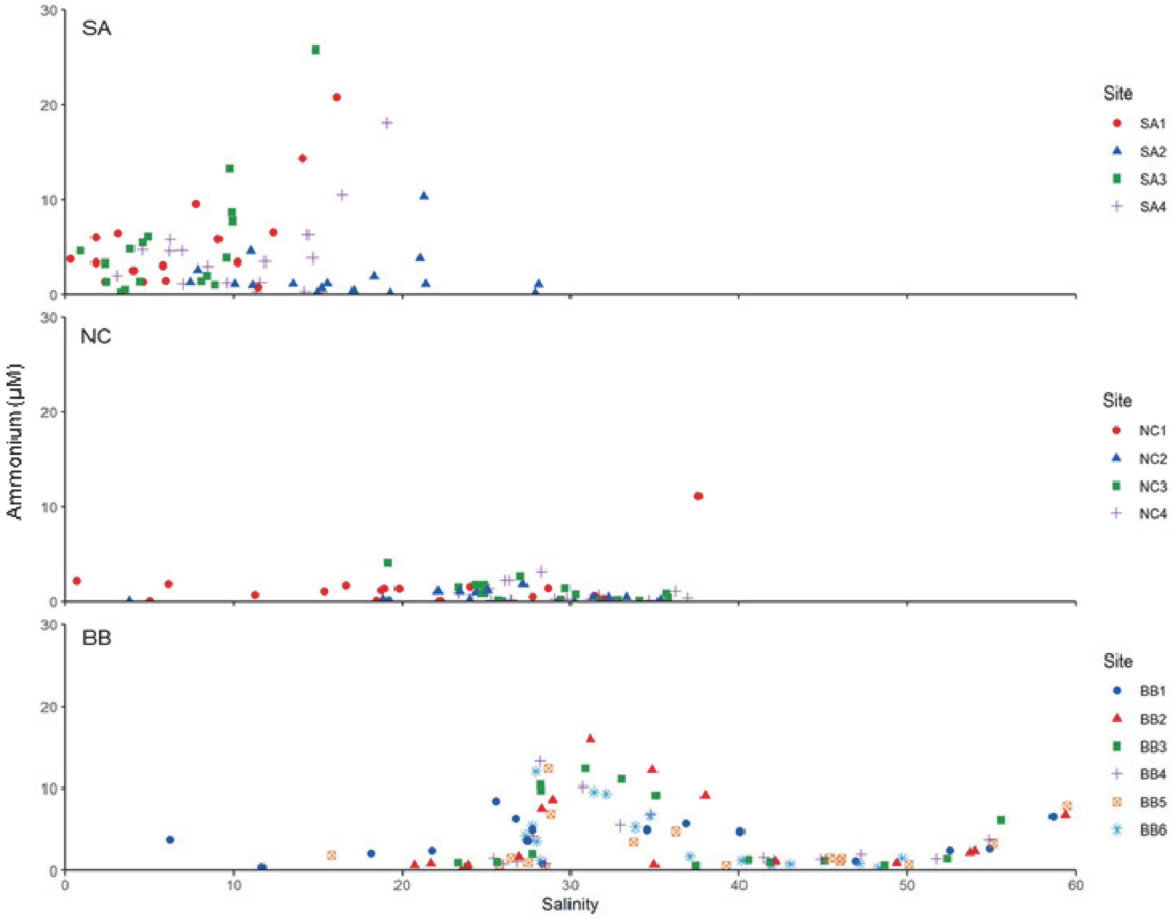

Figure 7 – Ammonium-salinity relationship in the three bay systems during the study.

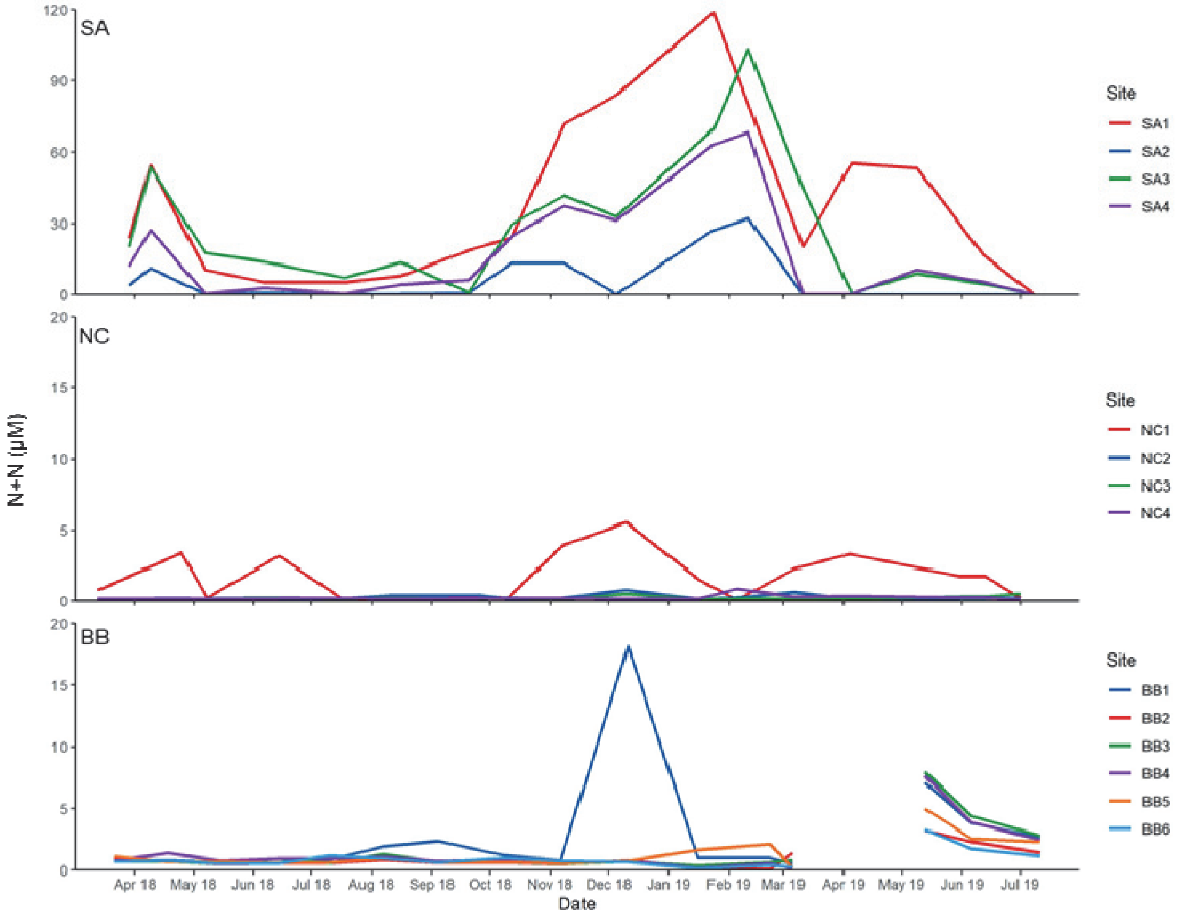

Figure 8 – N+N in the three bay systems during the study.

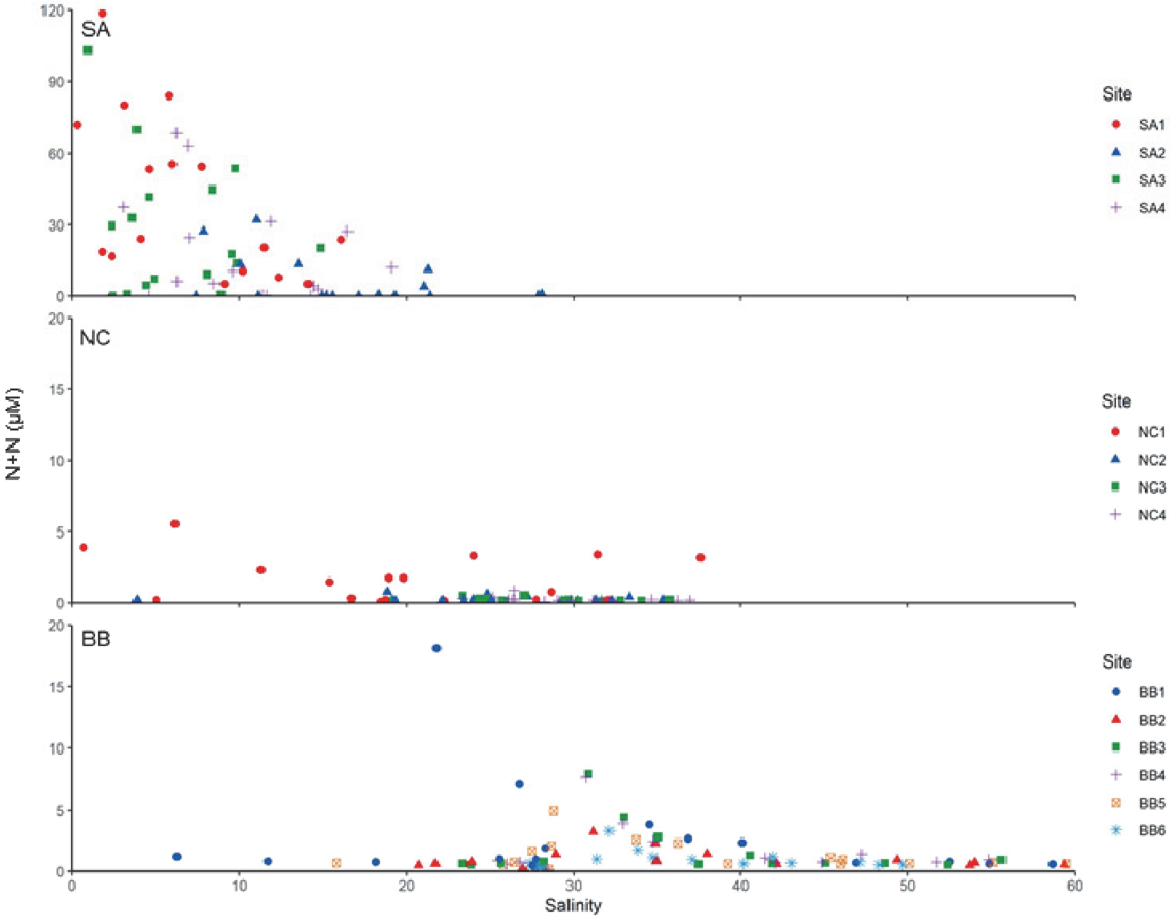

Figure 9 – N+N-salinity relationship in the three bay systems during the study.

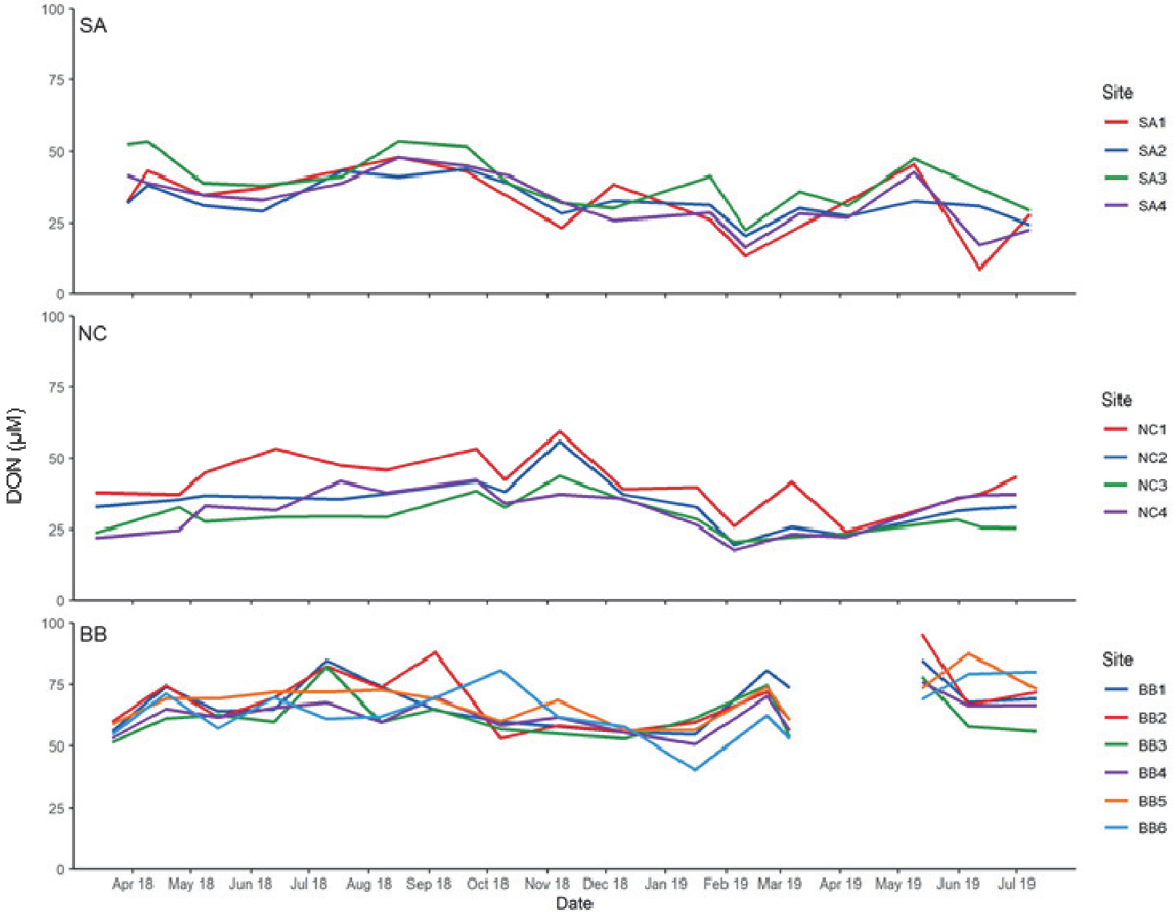

Figure 10 – DON in the three bay systems during the study.

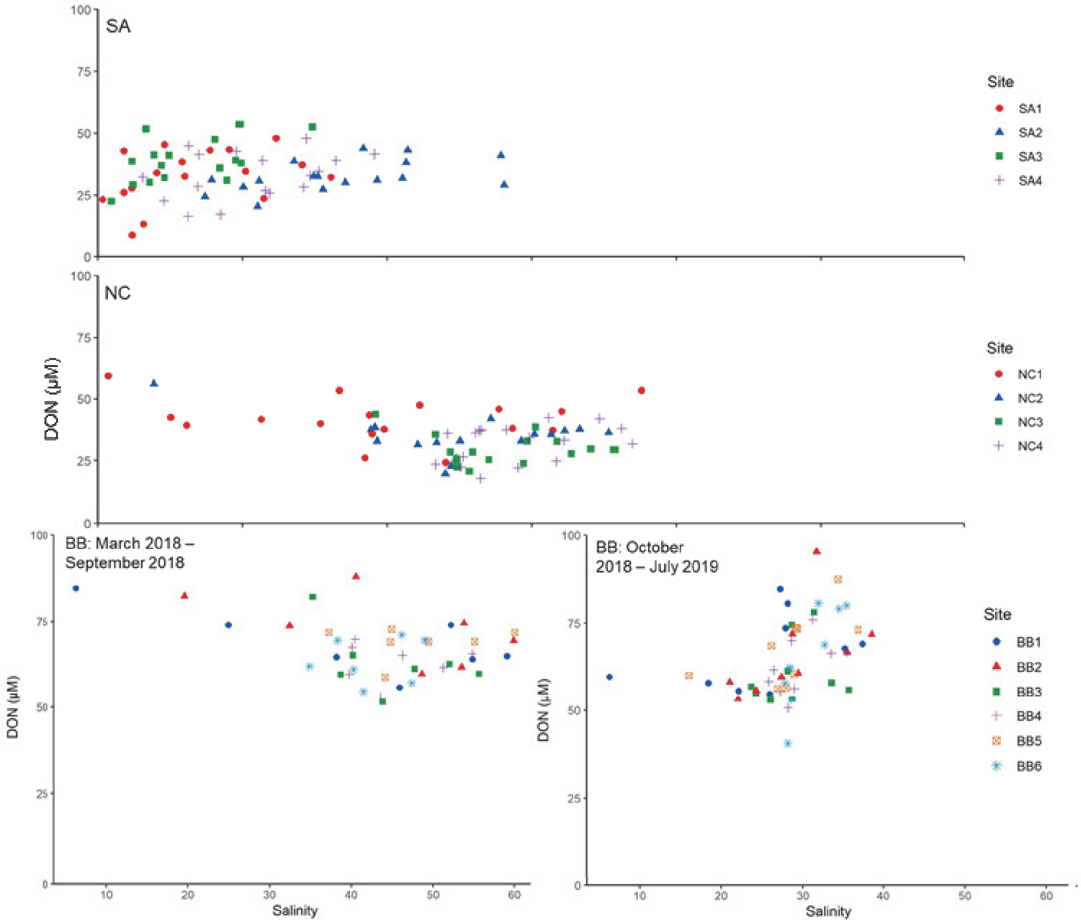

Figure 11 – DON-salinity relationship in the three bay systems during the study.

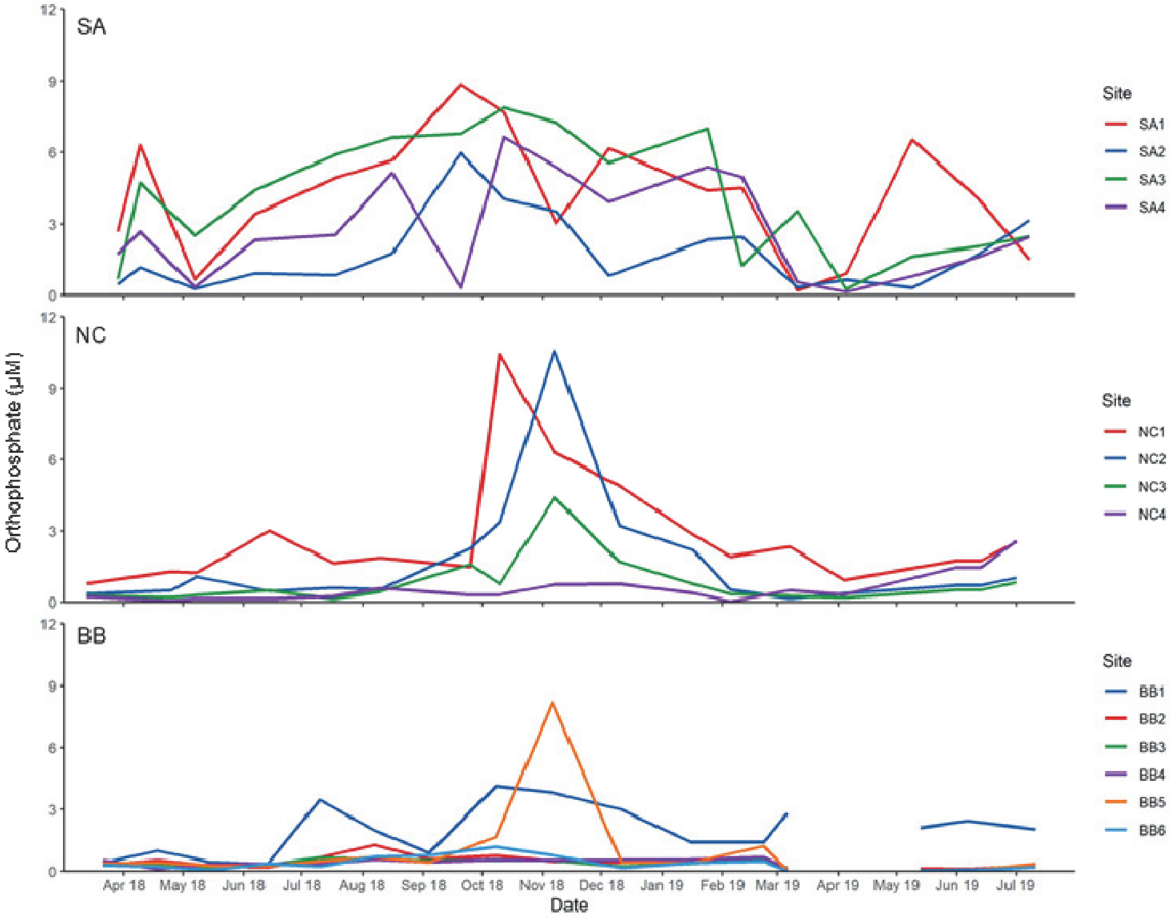

Figure 12 – Phosphate in the three bay systems during the study.

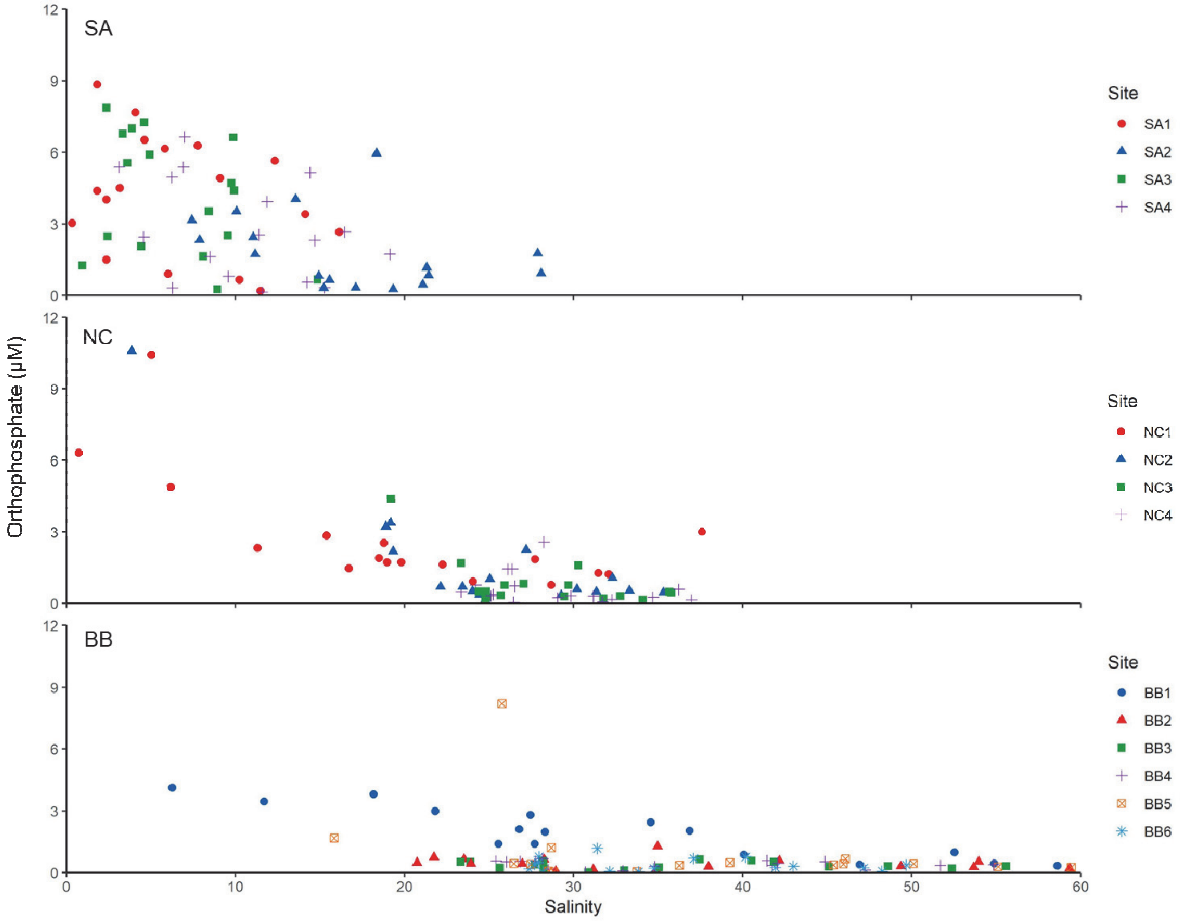

Figure 13 – Phosphate-salinity relationship in the three bay systems during the study.

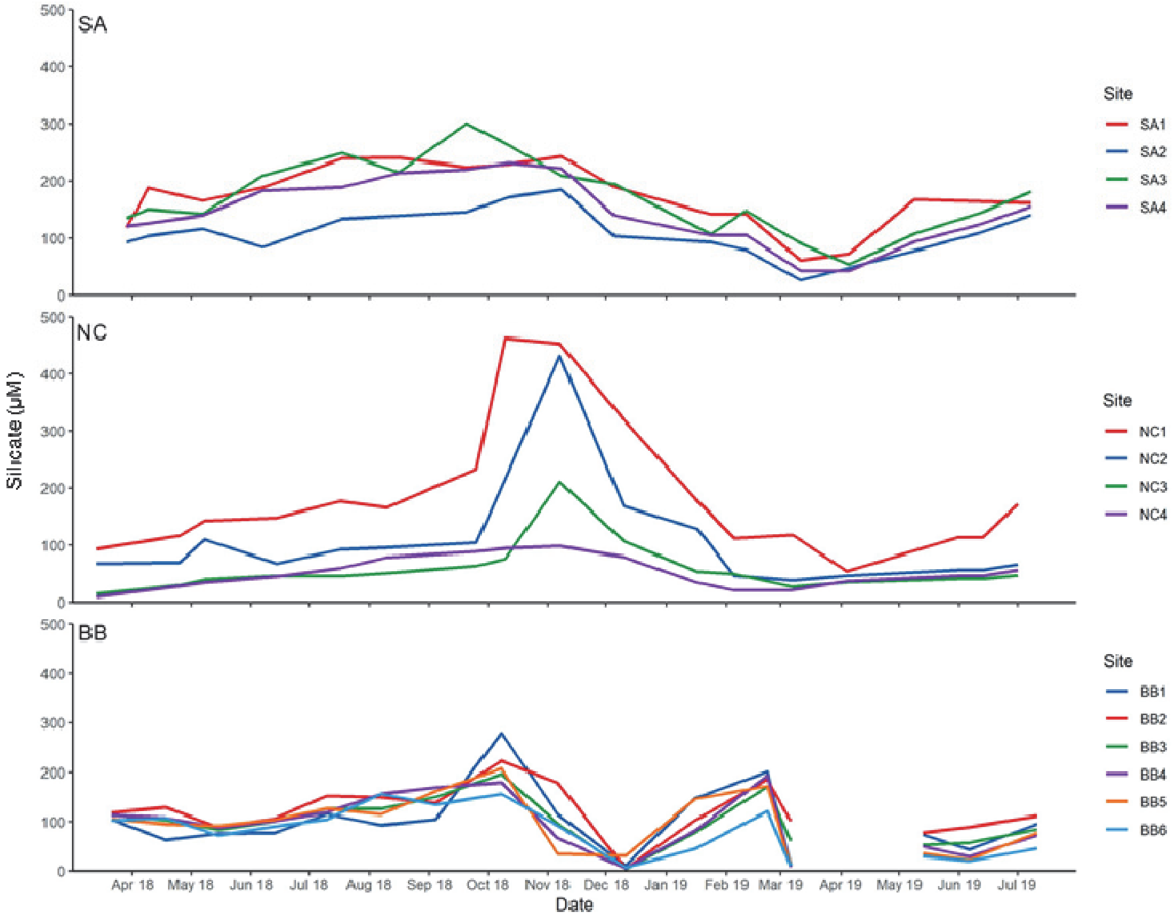

Figure 14 – Silicate in the three bay systems during the study.

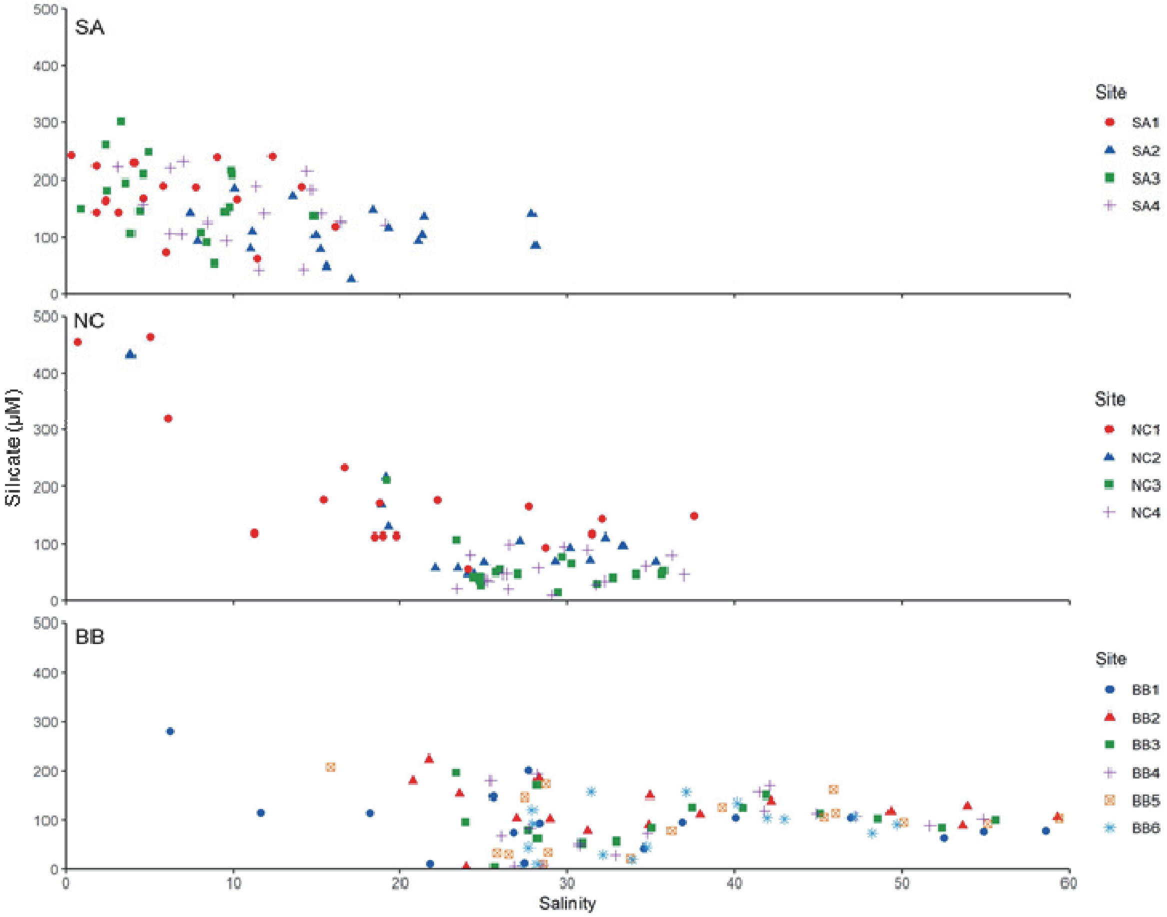

Figure 15 – Silicate-salinity relationship in the three bay systems during the study.

In SA, nutrient limitation was variable across sites and time (Fig. 16). Phosphorus (P) limitation occurred at SA1 in winter 2018/2019 and spring 2019 and at SA3 in March 2018 and January 2019. A switch from nitrogen (N) to phosphorus (P) limitation at SA4 in September 2018 resulted from a drop in phosphate. NC was strongly N-limited throughout the study period (Fig. 16). The dissolved inorganic nitrogen (DIN) to dissolved inorganic phosphorus (DIP) ratio (DIN:DIP) was above the Redfield ratio of 16:1 at only two time points at site NC4 (April 2018 and February 2019). All other sites consistently had DIN:DIP ratios below 10:1. Most sites in BB were N-limited until May 2019 when all sites except BB1 became strongly P-limited (Fig. 16). This P-limitation regime persisted through July 2019, the end of the study period. Neither SA nor NC experienced silicate limitation during the study period (Fig. 17). DIN:silicate ratios in BB were generally low, indicating N limitation, with the exception of December 2018. At this time, all sites experienced an increase in DIN:silicate ratios, although only BB1 was >1 (Fig. 17).

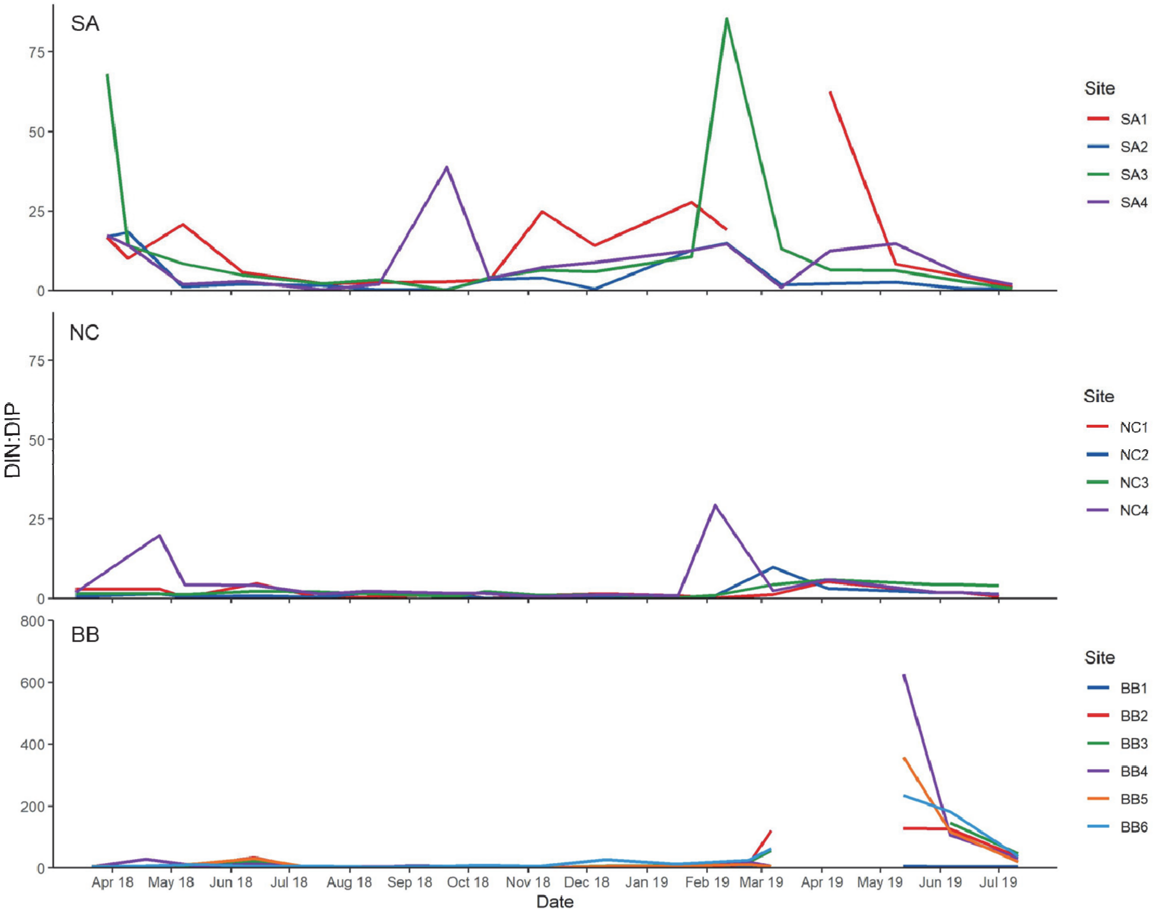

Figure 16 – Ratio of DIN to phosphate in the three bay systems during the study. Ratios >16 indicate potential for P limitation of phytoplankton growth, while ratios <16 indicate potential for N limitation.

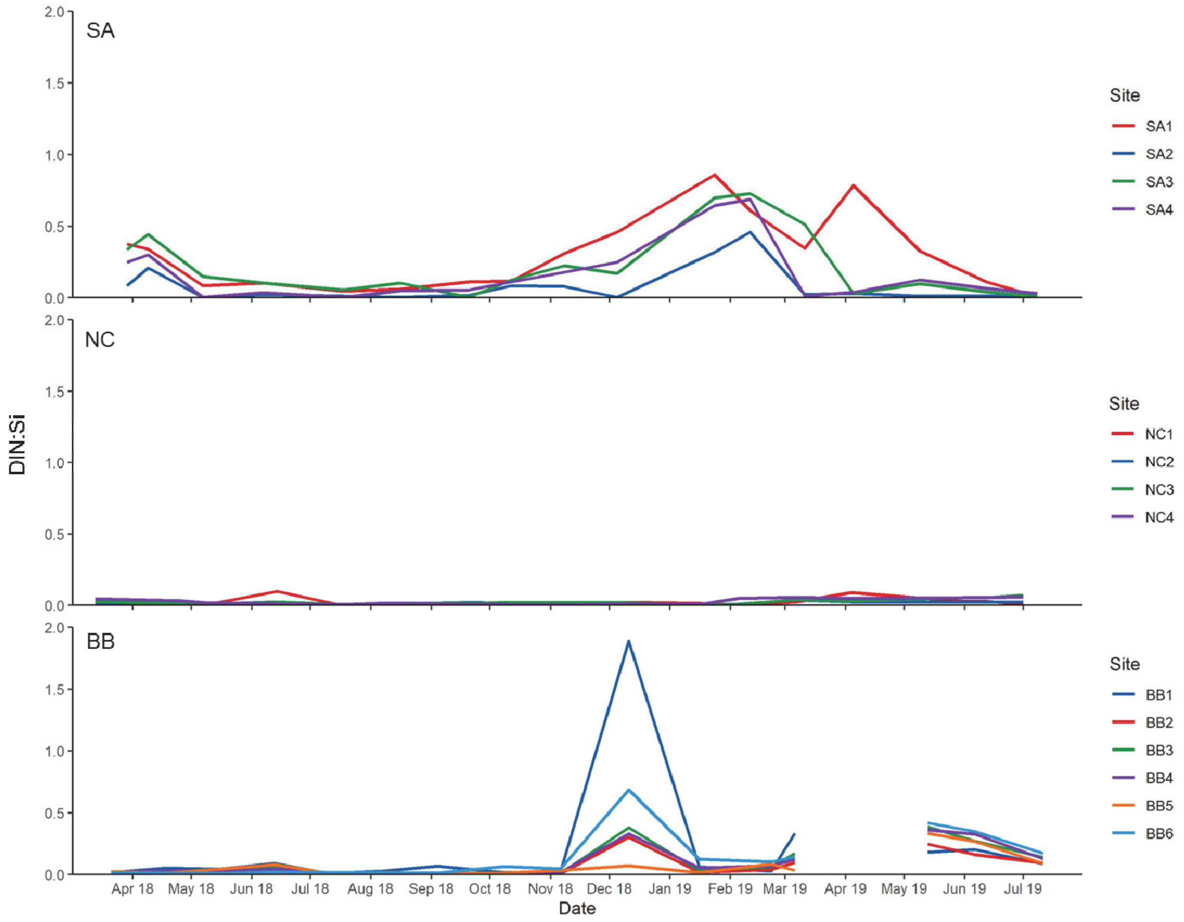

Figure 17 – Ratio of DIN to silicate in the three bay systems during the study. Ratios >1 indicate potential for Si limitation of phytoplankton growth, while ratios <1 indicate that Si is likely not limiting.

Size Fractionated Chlorophyll a

On average, chlorophyll *a* was highest in BB (18.5 ± 13.4 µg/l), followed by SA (16.9 ± 11.7 µg/l) and NC (9.5 ± 3.5 µg/l) (Table 2). The percentage of chlorophyll in the >20 µm fraction was highest in BB (29.2 ± 23.2 %), intermediate in NC (23.9 ± 18.3 %) and lowest in SA (17.4 ± 16.9 %). The percentage of chlorophyll in the 3-20 µm fraction was highest in SA (73.1 ± 16.3 %), intermediate in NC (67.8 ± 18.5 %), and lowest in BB (62.3 ± 21.1 %). The percentage of chlorophyll in the < 3 µm fraction was nearly equivalent between bays, ranging from 8.6 to 9.8%.

Table 2 - Mean ± SD for chlorophyll (µg/l) and size-fractions (% total) in the three bay systems.

Bay	Chl	% >20 µm	% 3-20 µm	% <3 µm
SA	16.9 ± 11.7	17.4 ± 16.9	73.1 ± 16.3	9.8 ± 6.5
NC	9.5 ± 3.5	23.9 ± 18.3	67.8 ± 18.5	8.6 ± 7.9
BB	18.5 ± 13.4	29.2 ± 23.2	62.3 ± 21.1	8.9 ± 6.0

In SA, chlorophyll *a* was dominated by the nanoplankton size class with occasional large contribution from the microplankton size class (Fig. 18; Table 2). Picoplankton (< 3 µm size class) were not a dominant contributor to chlorophyll at any site throughout the study period. Overall, chlorophyll was higher in spring/summer 2019 than during the same time period in 2018. In NC, all sites were dominated by nanoplankton for most of the study period, with a higher contribution of > 20 µm size class to total chlorophyll during late 2018-early 2019 (Fig. 19; Table 2). No clear seasonal or interannual patterns were observed in chlorophyll. In BB, spring and summer were characterized by the dominance of the 3-20 µm size class, whereas the contribution of > 20 µm size class to chlorophyll was greatest between October 2018 and March 2019 (Fig. 20; Table 2). Overall, chlorophyll was higher in the tributaries (BB1, BB2, and BB5) than in the other sites located in the bay proper.

Phytoplankton community composition

In SA, the proportion of dinoflagellates to total biomass was highest compared to the other two bays (Fig. 21). This was most pronounced at sites SA2 and SA4, where dinoflagellates composed a large portion of biovolume in summer and fall 2018. High diatom biovolume was observed at SA1, SA2, and SA4 in March 2019 (3.1 x 10^6 µm^3/mL, 5.9 x 10^6 µm^3/mL, and 6.0 x 10^6 µm^3/mL, respectively), and all sites had an increase in picocyanobacteria in summer 2019 (May 2019 to July 2019).

Overall phytoplankton biovolume in NC was similar to SA. In spring and summer 2018, biovolume was higher in Nueces Bay (NC1 and NC2) than in Corpus Christi Bay (NC3 and NC4) (Fig. 22). Community composition was dominated by diatoms at all sites from March 2018 to August 2018. A shift from diatom or mixed communities to dinoflagellate-dominated communities began in August 2018. In December 2018, NC2, NC3, and NC4 shifted from dinoflagellate-dominated to diatom-dominated. This shift occurred later at NC1, in January and

February 2019. Summer 2019 (May to July 2019) was characterized by low total biovolume and higher abundances of picocyanobacteria.

Maximum biovolume in BB was much higher than those in SA and NC (Fig. 23). *A. lagunensis* was present at all sites except BB3 in March 2018 and persisted through June 2018 at BB2. Picocyanobacteria biovolume was most pronounced in summer-fall 2018 and summer 2019 but was still relatively low when compared to other taxa. Lowest community biovolume occurred at all BB sites during summer and early fall (May 2018-October 2018 and May 2019-July 2019). Much higher biovolume was observed during late fall 2018-winter 2019. Diatoms dominated the phytoplankton community at all sites during December 2018 and at all sites except BB2 during November 2018. Diatom blooms reached a maximum biovolume of 7.8 x10^8 μm^3/mL at BB4 in December 2018. In January 2019, diatom and total biovolume decreased at all sites except BB5 where a bloom of *Euglena* occurred. *Euglena* biovolume was 3.4 x10^7 μm^3/mL which was 99.9% of total biovolume at this site in January 2019. *Euglena* were not a dominant contributor to phytoplankton biovolume at this or any site during the study. Diatom abundance rebounded at all sites in March 2019 but declined by May 2019.

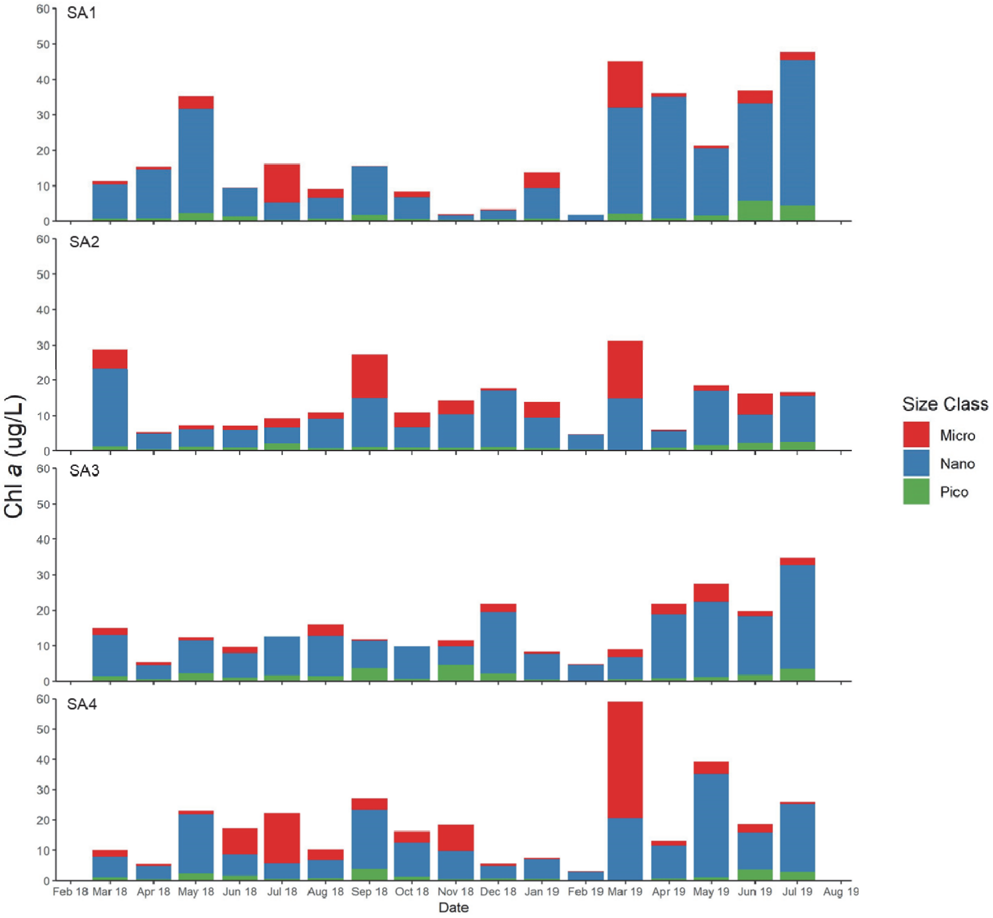

Figure 18 – Size fractionated chlorophyll in SA during the study.

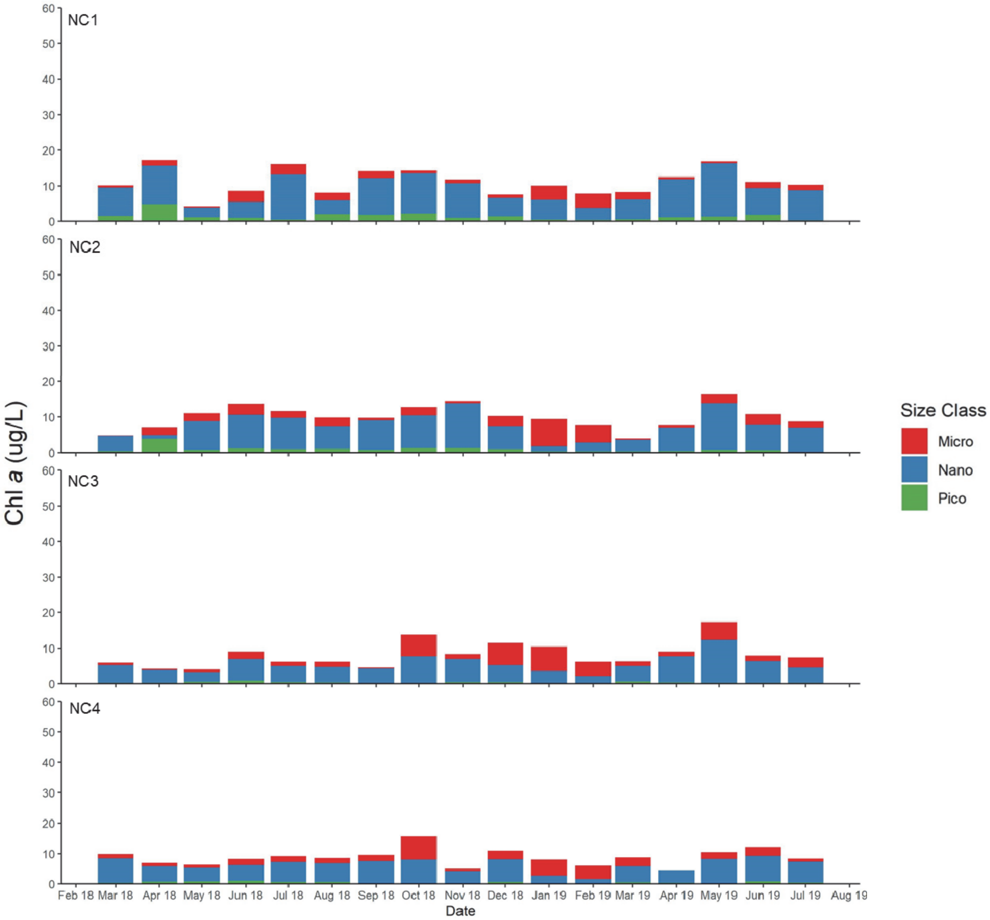

Figure 19 – Size fractionated chlorophyll in NC during the study.

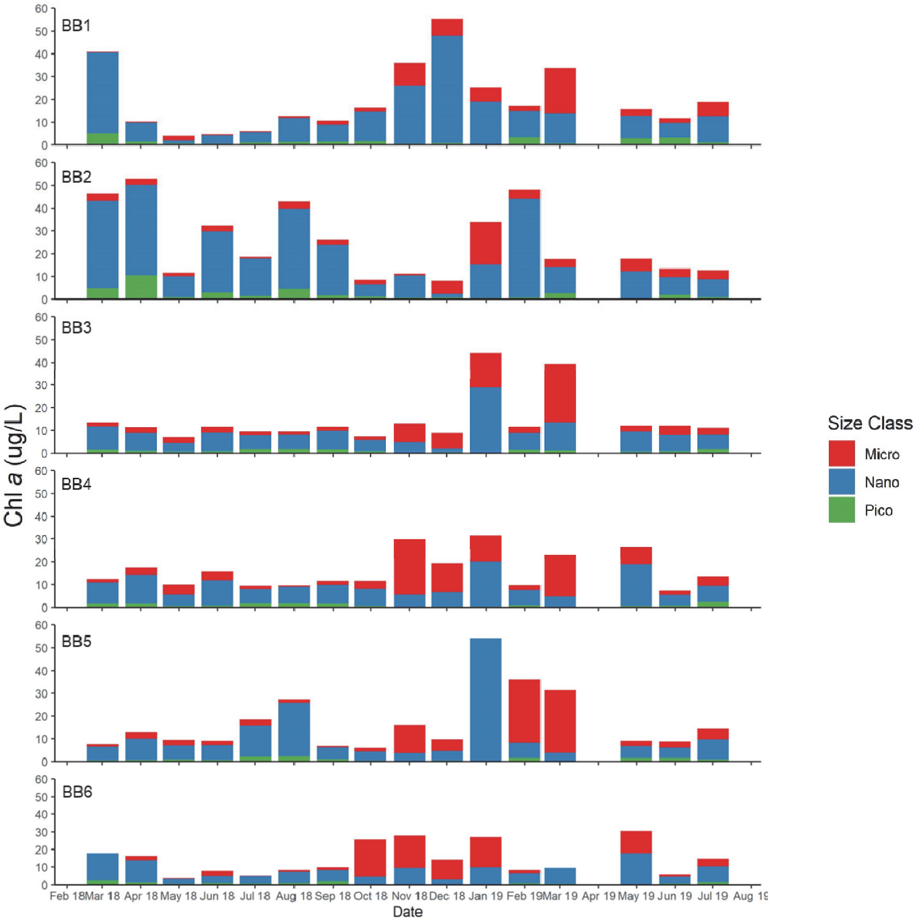

Figure 20 – Size fractionated chlorophyll in BB during the study.

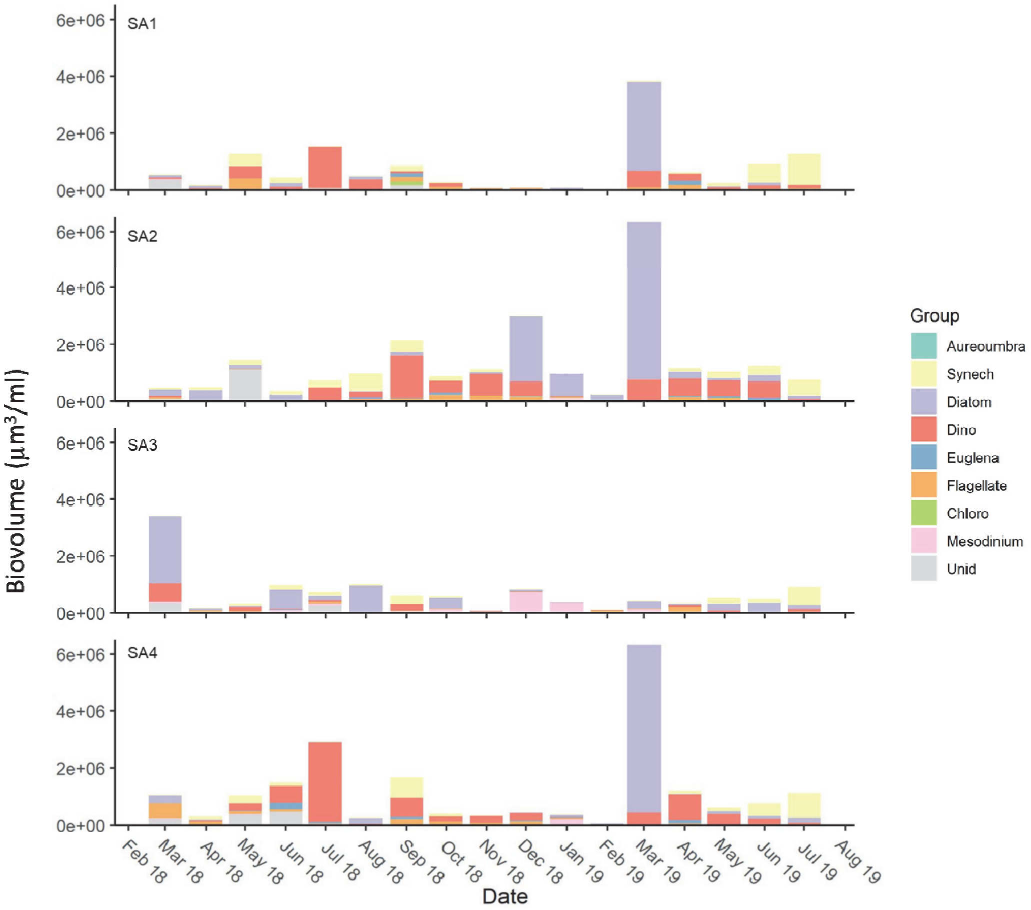

Figure 21 – Phytoplankton biovolume in SA during the study.

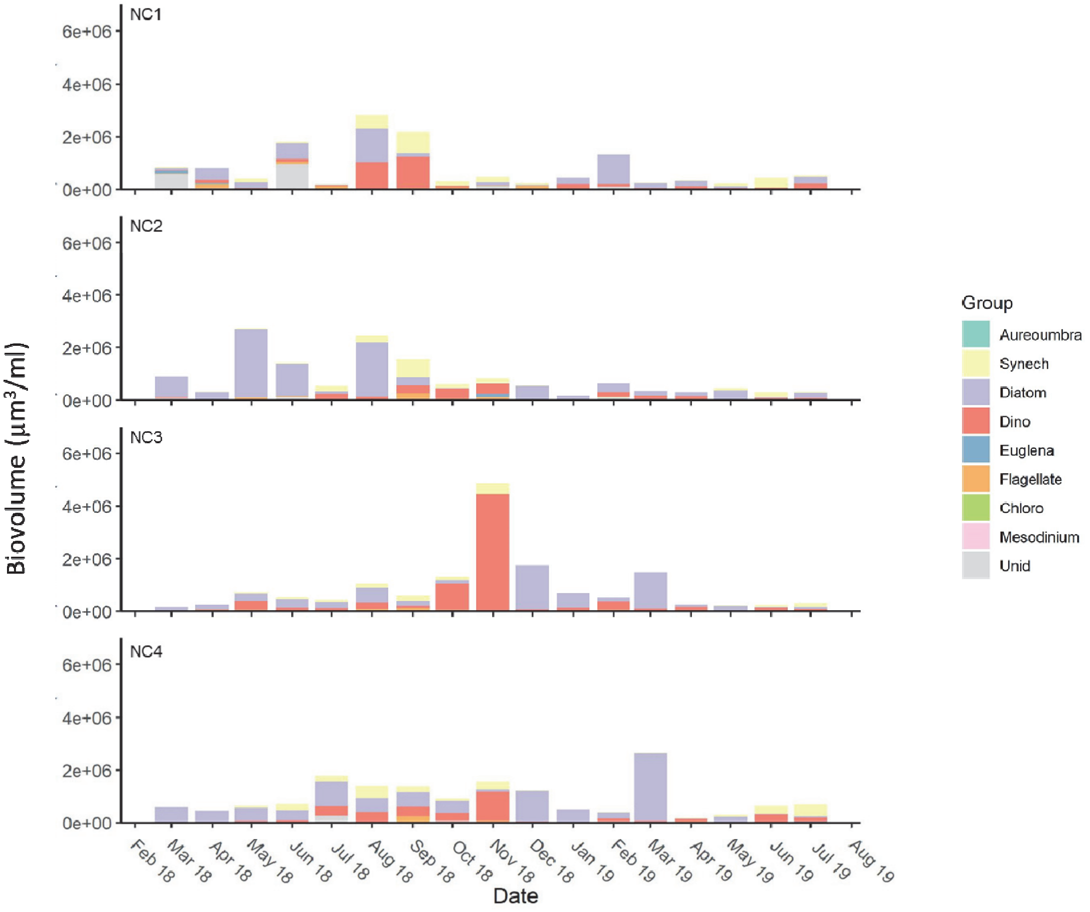

Figure 22 – Phytoplankton biovolume in NC during the study.

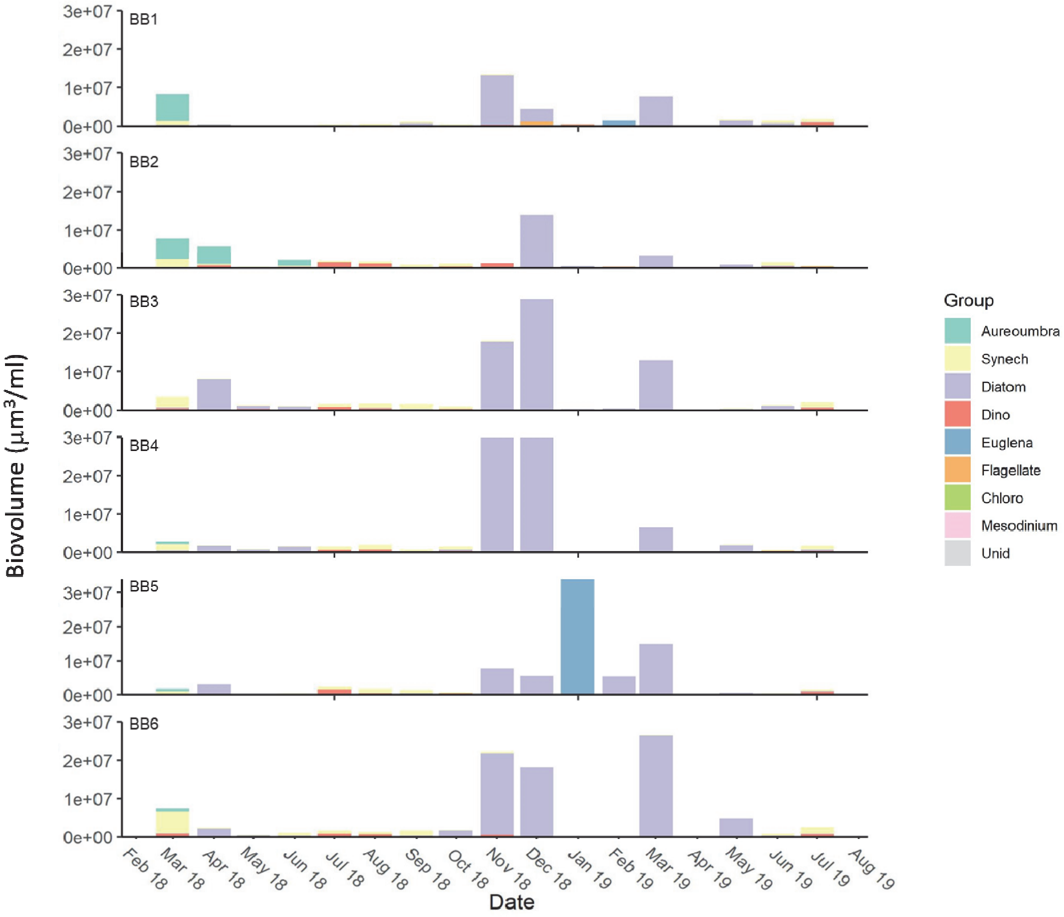

Figure 23 – Phytoplankton biovolume in BB during the study.

V. Discussion

Freshwater inflow is a critical driver of estuarine ecosystem structure and function (Palmer et al. 2011). In Texas, legislation exists calling for the water permitting process to consider the ecological soundness of rivers, bays and estuaries, and riparian lands in relation to freshwater inflow. As a result, the Texas Commission on Environmental Quality (TCEQ) set environmental flow standards for bays and estuaries using recommendations provided by teams of scientific experts and stakeholder committees. These flow standards are evaluated periodically through an adaptive management process. Findings from this study advance our understanding of the relationship between inflow, nutrients and the biomass/composition of the phytoplankton community, which is critical from a trophic transfer standpoint and for understanding potential conditions that are favorable to the growth of harmful taxa. This is important given that these estuaries lie along a precipitation/inflow gradient that should in theory lead to differences in nutrient-plankton dynamics (e.g., Montagna et al. 2018). Furthermore, there has not been a comprehensive assessment to date of the phytoplankton communities in these systems using modern techniques for classifying the full size spectrum of phytoplankton. Findings from this study are placed in the context of the two hypotheses that guided development of this work.

Hypothesis 1 - Nutrient concentrations and chlorophyll/phytoplankton biomass are highest in the high inflow estuary, San Antonio Bay, intermediate in Nueces-Corpus Christi Bay, and lowest in Baffin Bay as a result of decreasing inflow magnitude and subsequent nutrient loadings.

Over the course of the study, base inflow rates were highest to SA, followed by NC and BB. There were at least seven inflow events to SA where river discharge exceeded 100 m^3s^{-1}, compared to two in NC and one in BB. These observations are consistent with historical inflow conditions that exist in part because of a gradient of decreasing precipitation from the northern estuary (SA) to the southern estuary (BB). 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.

The hypothesis that nutrient concentrations would be highest in SA, intermediate in NC, and lowest in BB was only partially supported. Phosphate concentrations were highest in SA and decreased from NC to BB, consistent with it being derived from riverine sources. Likewise, silicate concentrations were highest in SA, also consistent with a riverine source. Silicate concentrations were lower in NC and BB, but still fairly high and equivalent on average between NC and BB.

N+N concentrations were highest in SA, but low and roughly equivalent in NC and BB. Ammonium concentrations were approximately 4-fold higher in SA and BB than NC. Ammonium vs. salinity plots for both SA and BB indicate that the ammonium is likely derived from internal regeneration at intermediate salinities, consistent with previous work in these systems demonstrating the importance of regenerated N (Longley 1994). In addition, previous work has shown that dissimilatory nitrate reduction to ammonium (DNRA) rates can be quite high under higher salinity conditions, such as those found in Baffin Bay at times (An and Gardner 2002; Gardner et al. 2006). This would aid in the retention and availability of ammonium. Overall, inorganic nitrogen (N) concentrations were lowest in NC, consistent with findings from Turner et al. (2015) who also demonstrated low inorganic N concentrations over the course of a year at several sites in Corpus Christi Bay. Even though the flood conditions that were observed during late 2018 caused a noticeable drop in salinities of NC, implying a clear riverine influence on the water column, there was little to no discernible effect on inorganic N concentrations in those bays. This suggests that external N loads to the system were quickly utilized by microbes. Indeed, there was a sharp increase in phytoplankton biomass at the upper Corpus Christi Bay site (NC3) in October to December 2018. Nonetheless, we would have also expected higher phytoplankton biomass further upstream (in Nueces Bay) if phytoplankton uptake was a factor in the lack of apparent increase in inorganic N concentrations downstream. Instead, phytoplankton biomass decreased at the Nueces Bay sites during the wet/low salinity period, leaving us to speculate that any riverine inorganic N loads to NC are rapidly denitrified. Prior work by Gardner et al. (2006) showed that the relative importance of dentrification (an N removal pathway) compared to DNRA (an N 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 N during high inflow conditions.

DON concentrations in BB were approximately 2-fold higher than in SA or NC, where they were roughly equivalent. Previous work has also demonstrated this phenomenon and attributed it to excessive nutrient loading in the watershed (Wetz et al. 2017; Montagna et al. 2018). DON vs. salinity plots for BB show an increasing DON trend at lower salinities for dates up to and including the first significant rainfall event in summer 2018 (March to September 2018), but show a decreasing DON trend at lower salinities using dates after October 2018. We attribute this to a classic “first flush” effect, where the initial rainfall washed in N that had accumulated in the watershed, whereas the next significant rainfall led to a dilution effect. Similar to what occurred during the secondary high rainfall period in BB, DON appears to decrease at lower salinities in SA, suggesting that a fraction of the DON in the bay is internally produced and may be diluted at high flows/low salinities. In NC, DON increased briefly during the wet fall of 2018, but the DON rapidly decreased thereafter, likely due to remineralization.

To summarize the effects of freshwater inflow on nutrient conditions, SA appears to display high inorganic N concentrations because of its relatively high inflows as well as an apparent internal source of ammonium such as sediment pore waters or even N fixation. At the lower end of freshwater inflow magnitudes, BB displays very high N concentrations, but it is difficult to disentangle the effects of inflow magnitude from the excessive nutrient concentrations that have developed in its watershed creeks, thus BB is probably not a good example of how a pristine low inflow system would behave. A better example of a low inflow estuary to compare with SA would be NC, which experiences relatively low inflows but not excessive nutrient loads. As noted above, it appears that riverine N inputs are rapidly removed prior to having an impact on the bay itself, including nutrient concentrations. Why that is remains unclear. Yet it may be worth speculating on potential future impacts of lower inflows/higher salinities in NC. Specifically, previous work showing that the relative importance of denitrification to DNRA decreases with increasing salinity may have some bearing. 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. Further work is clearly needed, given that the negative effects of nutrient retention are already manifesting in BB as eutrophication symptoms (Wetz et al. 2017).

As with nutrients, the hypothesis that chlorophyll concentrations or phytoplankton biomass would be highest in SA, intermediate in NC, and lowest in BB was only partially supported. Total chlorophyll was comparable between SA and BB, and approximately 2-fold lower in NC. We attribute this to factors affecting the availability of N, which has been argued to be the main phytoplankton growth limiting nutrient in many Texas estuaries (Wetz et al. 2017). As noted above, SA had relatively high inorganic N concentrations throughout the study due to consistently higher inflow levels as well as internal regeneration. Likewise, BB had relatively high DON concentrations, some of which is accessible to mixotrophic phytoplankton (Wetz et al. 2017). New work has also indicated potential for high rates of photoammonification, which would further increase bioavailability of the organic N (D. Felix, unpubl. data). In addition, previous work has shown that internal ammonium regeneration rates can be quite high in BB (Gardner et al. 2006), providing a continuous N source for blooms. To summarize, the findings from BB suggest that the effects of low freshwater inflows on nutrient availability to phytoplankton may be countered by other factors, namely increasing nutrient loads due to cultural eutrophication and likely also to factors that increase N retention.

It is worth mentioning that temporal patterns in chlorophyll did not always mirror patterns in phytoplankton biomass. For example, in SA there were a number of instances of relatively high chlorophyll but low biomass. Previous work has shown that the chlorophyll per cell in phytoplankton can vary considerably depending on a variety of factors, including light availability, nutrient availability, and even community composition (Falkowski and Kiefer 1985; Lawrenz and Richardson 2011). In the SA example, the higher chlorophyll and lower biomass may be indicative of a lower light environment in which phytoplankton would be expected to increase their light harvesting pigments. This pattern was less common in NC or BB. Given the higher volume of inflows and shallower Secchi depth in SA, it is possible that the system is much more turbid and hence, light may be influencing the chlorophyll levels. Another indicator in support of this was the high proportion of biomass that was from dinoflagellates in SA, many of which are capable of tolerating low light conditions by employing mixotrophic energy acquisition strategies. Overall these findings suggest that some caution must be exercised when using chlorophyll as an indicator of phytoplankton biomass, especially for studies aimed at quantifying the effects of inflow on phytoplankton communities.

Hypothesis 2 - Owing to hypothesized higher nutrient levels, the phytoplankton community will be dominated by large and/or fast growing taxa in San Antonio Bay, with the fraction of small and/or slow growing taxa increasing from Nueces-Corpus Christi Bay to Baffin Bay.

Previous studies have shown that large, fast growing phytoplankton taxa such as diatoms tend to dominate under high nutrient, high inflow regimes (Roelke et al. 2013; Paerl et al. 2014; Dorado et al. 2015; Harding et al. 2016). In contrast, low nutrient estuarine conditions with limited flushing and stratified conditions tend to promote growth of small, slow growing taxa such as picocyanobacteria (Malone et al. 1991; Agawin et al. 2000). However, as noted by Cloern (2018), there are exceptions to these rules. We hypothesized that SA would have a greater fraction of its phytoplankton biomass in the form of large and/or fast growing taxa, whereas NC and BB phytoplankton biomass would consist of a larger fraction of small cells. This hypothesis proved false, with all three bays having similarly small relative contribution (~9-10% of total) from pico-sized chlorophyll (i.e., < 3 µm). This may be due to the higher nutrient conditions observed in BB and SA, as well as the overall high winds and lack of stratification in these bays. BB had the greatest contribution from > 20 µm cells, primarily the diatom *Rhizosolenia sp.* that bloomed in late 2018 through early 2019. Previous work in the Chesapeake Bay indicates that *Rhizosolenia sp.* may be an indicator of nutrient enriched conditions (see Harding et al. 2016), which we suspect to be the case in BB. It was surprising that even in NC, despite having relatively low nutrient concentrations as well as receiving low inflows, nano- and microplankton were still the greatest contributors to chlorophyll and biomass. The prevalence of diatoms was particularly surprising, given that we tend to think of them being associated with high inflow or nutrient conditions. One possibility is that diatom biomass in NC is tied not necessarily to an active pelagic population, but instead is linked to diatoms that are resuspended from the benthos. This is a common phenomenon in shallow estuarine waters such as NC (Shaffer and Sullivan 1988; Underwood and Kromkamp 1999). Additional work is planned to examine the relationship between wind and diatom prevalence in each bay system to determine if this is likely.

Conclusions

This study represents the first to take a comparative approach of Texas estuaries to quantify the effects of large-scale differences in freshwater inflow magnitude on nutrients and phytoplankton. Using modern techniques to quantify the full size spectrum of phytoplankton, we found that the relationship between freshwater inflow magnitude and the biomass/composition of the phytoplankton community was not straightforward. First and foremost, the relationship is confounded by factors affecting availability of limiting nutrients (in this case, N). This was noted in Baffin Bay where, despite the lowest overall inflow magnitude, phytoplankton biomass was quite high as a result of the cultural eutrophication that has taken place as well as apparent high regeneration rates in the system. In this cursory analysis, we found evidence of other factors also influencing both phytoplankton biomass and community composition, namely light conditions, flushing and even degree of mixing. Additional quantitative modeling and statistical analyses will be undertaken to more rigorously evaluate the effects of these different factors.

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VII. References

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