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The University of Vermont
College of Arts and Sciences
Honors College

UNDERGRADUATE HONORS THESIS

**SEASONAL VARIABILITY OF THE ELEMENTAL STOICHIOMETRY OF
PHYTOPLANKTON IN TWO EUTROPHIC BAYS OF LAKE CHAMPLAIN**

by

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Abstract

Lake Champlain, located between the Adirondack Mountains of New York and the Green Mountains of Vermont, has had increased algal and cyanobacteria blooms during the summer months in recent years. In part due to climate change and increased nutrient loading into the lake due to anthropogenic activities, cyanobacteria blooms are of special concern, as cyanobacteria can produce cyanotoxins that are harmful to animal and human health. This research aims to assess the extent of synchrony between resource and primary producer nutrient stoichiometry (carbon: nitrogen: phosphorus; C:N:P) to determine trends relating to bloom initiation, growth, and senescence. We collected samples once per week in two eutrophic bays of Lake Champlain (Missisquoi Bay and Saint Albans Bay) from June-November 2021, and determined dissolved C:N:P in the water column and particulate C:N:P in seston. We found that seston stoichiometry diverged from the predicted optimal Redfield ratio (106:16:1, C:N:P) and from ambient resource stoichiometry the most during bloom events. Specifically, during a late August bloom in Missisquoi Bay, C:N decreased and C:P increased relative to ambient concentrations. In St. Albans Bay, C:N also decreased during the bloom period in August, but C:P remained stable relative to ambient nutrient stoichiometry. This was also reflected in nutrient concentrations, where seston N increased and ambient N remained stable. These trends suggest phytoplankton are experiencing fluctuating nutrient limitation with bloom development, where P limitation may initially trigger blooms, but N-limitation is induced during growth which may be compensated by nitrogen fixation. These results have important implications for bloom toxicity, as increased seston N may facilitate the production of N-rich neurotoxins such as anatoxin-a, produced by N-fixing genera.

Introduction and Literature Review

2.1: Background on Phytoplankton and Cyanobacteria

Harmful phytoplankton blooms are a local and global threat to water resources (Van de Waal et al., 2009). Cyanobacteria, among the most common bloom-forming phytoplankton in lakes, are photoautotrophic bacteria that fix carbon which, like other phytoplankton, functions as an energy source for aquatic food webs (Van de Waal et al., 2014). Cyanobacteria are approximately 3.5 billion years old and are present in almost all aquatic and terrestrial ecosystems (Whitton & Potts, 2012). The growth and survival of cyanobacteria are determined by several factors, including temperature, light, stress tolerance, and available nutrients (Whitton & Potts, 2012). Cyanobacteria are a large and diverse taxonomic group whose long evolutionary history allows them to persist across a wide range of environmental conditions. These adaptations include accessory pigments that allow them to tolerate low light, gas vesicles that facilitate buoyancy and vertical movement in the water column, the ability to fix atmospheric nitrogen, and the ability to actively take up bicarbonate when carbon dioxide is depleted (Whitton & Potts, 2012). Additionally, they produce secondary metabolites, several of which are toxic.

2.2 Cyanotoxins

It is known that cyanobacteria can produce many different secondary metabolites that are toxic, but the timing and magnitude of toxin production remains difficult to predict. Cyanotoxins fall into a variety of toxin categories, including hepatotoxins (damages liver), neurotoxins (damage nerve tissue), cytotoxins (damages specific cells, like those in the liver, nervous system, and brain), and toxins with the potential to cause other more mild irritations (Funari & Testai, 2008). Ingestion of cyanotoxins is the route of exposure that can be the most acute (i.e. drinking contaminated

water), but chronic exposure to low levels via activities like bathing or swimming in such waters also pose a human health risk (Funari & Testai, 2008). In addition, there have also been studies on cyanotoxins bioaccumulating in liver tissue of fish, which can in turn have negative impacts on other consumers in the food web (Bownik, 2010; Ferrão-Filho, Kozlowsky-Suzuki, 2011). Cyanotoxins are most commonly released into the environment as a bloom decays, the cyanobacteria cell wall degrades, and the toxins are released from the cell into the aquatic environment (Bownik, 2010).

2.3 Anthropogenic Impacts on Bloom Frequency and Severity

Despite cyanobacteria's long presence on Earth, anthropogenic activities and climate change have amplified lake nutrient inputs and cycles, resulting in increased frequency and severity of toxic cyanobacteria blooms in many lakes worldwide. Severe cyanobacteria blooms are expected to increase globally with climate change due to warming surface waters and increased nutrient delivery resulting from more frequent and intense storm events (Ho et al., 2019; Stockwell et al., 2020).

Anthropogenic activities such as large-scale agriculture have amplified nutrient cycling in the biosphere and increased nutrient loading to lakes. Anthropogenic activities that contribute to climate change can also cause increased bloom severity/frequency. As lakes are getting warmer, there is increased vertical stratification in the summer months, which creates stable conditions and a stronger nutrient concentration gradient (Paerl et al., 2011). A stronger concentration of nutrients available where the phytoplankton grow (due to light availability) will ultimately result in the utilization of those nutrients for such growth. In addition, cyanobacteria tend to favor warmer temperatures, so as lakes warm, and the cyanobacteria density in lakes increase. Additionally, toxic

species have the greatest tolerance to high light intensity and reactive oxygen, so increased stratification and warming may favor toxic over non-toxic strains. Increased bloom biomass represents increased organic carbon, which fuels greater rates of degradation and microbial respiration as blooms decay, amplifying nutrient cycles and creating a positive feedback loop that favors cyanobacteria growth (Paerl et al., 2011). Understanding these patterns can provide insight on how phytoplankton communities in Lake Champlain will respond to future anthropogenic disturbances and can be used to predict how similar lakes will respond under similar conditions.

2.4 Nutrient Stoichiometry, Limits to Phytoplankton Growth, and Homeostasis

Cyanobacteria, and all phytoplankton, utilize nutrients in specific elemental ratios for growth (Wagner et al., 2019). Average optimal growth in aquatic ecosystems is often measured relative to the Redfield ratio (106:16:1; molar ratio of C:N:P), where divergence from this ratio is often interpreted as growth limitation by one or more nutrients (Redfield, 1934). The Redfield ratio is an average value, and different species have different nutrient requirements and thus variable responses to the nutrients in their environment (Sterner & Elser, 2002). They can range from being plastic and having the same nutrient stoichiometry as their environment, to homeostatic and maintaining their elemental composition during nutrient assimilation and growth, resisting environmental change (Sterner & Elser, 2002). Because of this, studying both the elemental composition of phytoplankton and ambient water column stoichiometry can provide insight into how phytoplankton function under fluctuating nutrient inputs. It was previously thought that most cyanobacteria were phosphorus limited, and that they could easily obtain nitrogen via nitrogen fixation when it was limited, but that idea has come to change over time (Scott & McCarthy 2010; Scott et al. 2013). Now both phosphorus limitation, nitrogen limitation, and co-limitation by these

two nutrients are considered significant and critical in understanding how cyanobacteria are limited by the nutrients in their environments (Paerl et al., 2011).

Various studies have been performed to look at nutrient limitation of phytoplankton and cyanobacteria, via C:N:P. In an experimental lake in Ontario, S.N. Levine and D. Schindler tested nutrient limitation by supplying the lake with a roughly consistent level of phosphorus, but then varied the nitrogen added, having N:P ratios from about 8:1 to 50:1 (1999). What they found was that the N:P that saw some cyanobacteria species thrive was not the same ratio for other cyanobacteria species (Levine & Schindler, 1999). Different cyanobacteria species having different preferred N:P ratios means that blooms may occur under varying conditions, and that solutions for lakes with cyanobacteria blooms will not have a singular approach. Levine and Schindler added that low nitrogen levels in the water column are not necessarily indicative of a low supply of nitrogen for phytoplankton, as nitrogen from sediments and nitrogen from nitrogen fixation in lakes may be recycled back into the water column (and is recycled easier than phosphorus is) (1999), though we now know that much of this could be lost to the atmosphere, particularly in eutrophic lakes (Scott et al. 2019; Loeks-Johnson & Cotner, 2021).

While useful, the Redfield ratio is no longer considered fixed for optimal growth across many phytoplankton species (Oliver, et al., 2012). For example, more is known now about how phytoplankton perform luxury consumption, which refers to the storage of nutrients when they are in excess, changing the phytoplankton elemental ratio even when certain nutrients are not immediately being utilized for growth. In addition, we now know that phytoplankton can vary substantially in their responses to nutrient limitation, for example, in carbohydrate accumulation when nitrogen or phosphorus are limited (Oliver, et al., 2012).

2.5 Effects of Nutrient Availability on Toxins Present

Previous research indicates that there is often a decrease in nitrogen rich toxins when nitrogen is limiting (Van de Waal et al., 2009). When phosphorus is limiting, however, nitrogen-rich toxins may increase, but not always (Van de Waal et al., 2009). The experiments by Van de Waal et al. studied *Microcystis* variants specifically, by analyzing cultures given varying amounts of nitrate and CO₂. Their results suggest that with rising CO₂ levels and nutrient loading in lakes, cyanotoxin production will continue to increase (2009). Other work indicates that when there is this excess of nitrogen, cyanobacteria will store it rather than using it to produce toxins (Wagner et al., 2019). Wagner et al. also studied *Microcystis* and found organisms with “optimal” stoichiometry produced more toxins than their counterparts (2019). This means that understanding the optimal stoichiometry can be critical to predicting toxin production.

2.6: Lake Champlain: Missisquoi Bay, and Saint Albans Bay

Research is currently being conducted in Lake Champlain to better understand and identify the drivers of toxic cyanobacteria blooms and how they have changed over time. First, it is important to note that shallow bays of Lake Champlain have had more frequent and intense cyanobacteria blooms in the past few decades (Isles et al., 2015). In the Northeast arm of Lake Champlain, eutrophication near the St. Albans Bay began around the same time as sewer installation/expansion in the early 1900’s and intensified around 1960-1970 corresponding with urban development (Levine et al., 2012). In the Missisquoi Bay, eutrophication corresponded with increased agricultural activity in the 1970’s (Levine, et al., 2012).

These shallow bays, and shallow lakes in general, often have more intense blooms due to large catchment areas compared to the lake’s total volume, warmer surface temperatures, and

greater benthic nutrient access (sediment at the bottom of the lake), meaning more nutrient-rich sediment can interact with the water column (Isles et al., 2015). Ultimately, input of nutrients into the lake is an important long-term influencer of the quantity and severity of blooms, but which nutrient or nutrients limit phytoplankton growth at any given time varies both seasonally and spatially (Levine et al., 1997).

2.7: Research Questions, Goals

This research will address two primary questions. First, how does cellular and ambient water column C:N:P change during initiation, exponential growth, and senescence of cyanobacteria blooms? Second, how does this stoichiometry differ between the two sites, Missisquoi Bay and Saint Albans Bay? The goal of this research is to attempt to identify potential trends between the elemental stoichiometry of phytoplankton between the two bays that could then be applicable across the whole lake, and other similar lake systems.

Methods

Site Descriptions

Lake Champlain lies between New York's Adirondack Mountains, and Vermont's Green Mountains, and drains north into Canada. It is 194km long, 19km wide (at its widest point), 122m deep, and holds a volume of approximately 264km³ (Levine et al., 2012). The Northeast Arm, which includes Saint Albans, is entirely in Vermont/the United States, whereas Missisquoi Bay is split by the border between Vermont/US and Canada (Levine et al., 2012). Both Missisquoi Bay and Saint Albans Bay are shallower than the main lake (Missisquoi Bay being the shallower of the

two). Lake Champlain flows south to north (so in the direction from Saint Albans Bay to Missisquoi Bay.)

Field methods

Samples were collected weekly between June and November 2021 at EPSCoR BREE high-frequency monitoring buoy sites in Missisquoi and St. Albans Bay, Lake Champlain. Water samples for chemical analysis were collected in the upper 2 meters of the euphotic zone (sample depth determined as 2x Secchi depth, or to just above the bottom of the lake if Secchi was visible at bottom) with an integrated hose sampler. For this project, samples for dissolved organic carbon (DOC), total dissolved nitrogen (TDN), and total dissolved phosphorus (TDP) were filtered in the field using 0.45 μm polycarbonate syringe filters. Samples for DOC and TDN were stored in combusted amber glass vials and TDP in HDPE (Nalgene) bottles. All were kept on ice until returning to the lab, then refrigerated at 4°C until analysis. Water samples for particulate seston nutrient analysis were passed through a mesh sieve in the field to remove large grazers, stored in opaque amber HDPE bottles, and stored on ice until returning to the lab for processing, described below. Additional samples were collected by the Morales-Williams lab for cyanotoxins, phytoplankton community composition, and metagenomic analyses.

Laboratory methods

Seston samples were vacuum filtered immediately upon returning to the lab, onto pre-combusted, rinsed, and weighed glass fiber filters (Millipore GF/F, 0.7 μm). One-liter samples were filtered in duplicate for P analysis (approximately 250 mL each) and separately for C and N analysis (approximately 250 mL each). The filters were then dried at 60 degrees Celsius for

approximately 24 hours, and pre-and post-filter weights recorded. Particulate seston samples were analyzed for C:N by collaborators Nicole Wagner and Thad Scott at Baylor University.

Water column phosphorus was analyzed colorimetrically using a persulfate digestion and molybdate blue spectrophotometer method (APHA). Seston phosphorus was analyzed following the same method, but filters were folded and placed in vials with reagents, and then these samples were measured for absorbance. DOC and TDN were analyzed using a total carbon analyzer with external TDN module (Shimadzu).

Data Analysis/Statistical methods

Data was organized and descriptive statistics were calculated in excel. All nutrient, stoichiometry, and high-frequency data time series visualizations were created using R software.

Results

Elemental composition of water and seston

We found higher average water column and seston C, N, and P concentrations in Missisquoi Bay compared to St. Albans Bay over the study period, with greater differences between seston values than water values (Table 1). Similarly, elemental C:P, N:P, and C:N ratios were, on average, greater in Missisquoi Bay than St. Albans (Table 1). Seston elemental composition at both sites diverged from the Redfield threshold (106:16:1 C:N:P) with C:P above Redfield and N:P below Redfield (Missisquoi 112:14:1; St. Albans 120:11:1).

Table 1. Mean \pm standard error of carbon, nitrogen, and phosphorus concentrations and molar ratios in surface water and seston over the sampling period in St. Albans and Missisquoi Bay.

Site	Sample	C (mg L ⁻¹)	N (mg L ⁻¹)	P (μg L ⁻¹)	C:P	N:P	C:N
St. Albans	seston	2.03 \pm 0.23	0.28 \pm 0.04	47.60 \pm 6.28	120.37 \pm 10.54	11.42 \pm 1.07	9.76 \pm 0.58
St. Albans	water	3.50 \pm 0.27	0.43 \pm 0.14	25.80 \pm 4.12	572.70 \pm 125.29	44.81 \pm 10.12	13.11 \pm 0.80
Missisquoi	seston	2.94 \pm 0.46	0.48 \pm 0.10	66.60 \pm 9.00	111.567 \pm 10.37	14.240 \pm 1.87	8.394 \pm 0.43
Missisquoi	water	3.93 \pm 0.09	0.46 \pm 0.07	39.10 \pm 5.96	423.13 \pm 10.37	43.73 \pm 1.87	11.77 \pm 0.43

Timing of bloom events

In Missisquoi Bay, peak phycocyanin was measured by the data buoy during the last two weeks of August, 2021 indicating a cyanobacteria bloom event at this time (Figure 1). St. Albans had elevated phycocyanin values through August 2021, indicating a persistent bloom over the entire month (Figure 1).

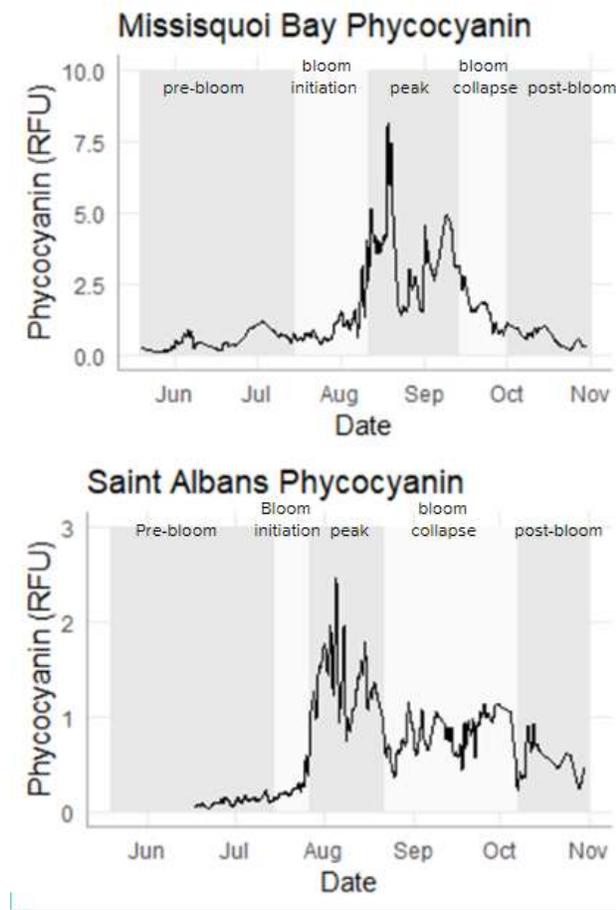


Figure 1: Time series of phycocyanin in Missisquoi Bay and Saint Albans. Bloom period dates were selected qualitatively, by trends in the graphs.

Temporal variability in nutrient concentrations and ratios

Over the study period in Missisquoi Bay, water column dissolved organic carbon and seston carbon spiked during the bloom event and decreased immediately following the bloom (Figure 2a, 2d). Total dissolved nitrogen was stable during the bloom in Missisquoi Bay but increased from an approximate average seasonal value of 0.50 mg N L⁻¹ to 1.50 mg N L⁻¹ in November (Figure 2b). In contrast, seston

N increased significantly during the late August bloom event in Missisquoi Bay (Figure 2e).

Phosphorus increased in surface water and in seston during the bloom, then spiked in hypolimnetic samples when the bloom senesced (Figure 2c and 2f).

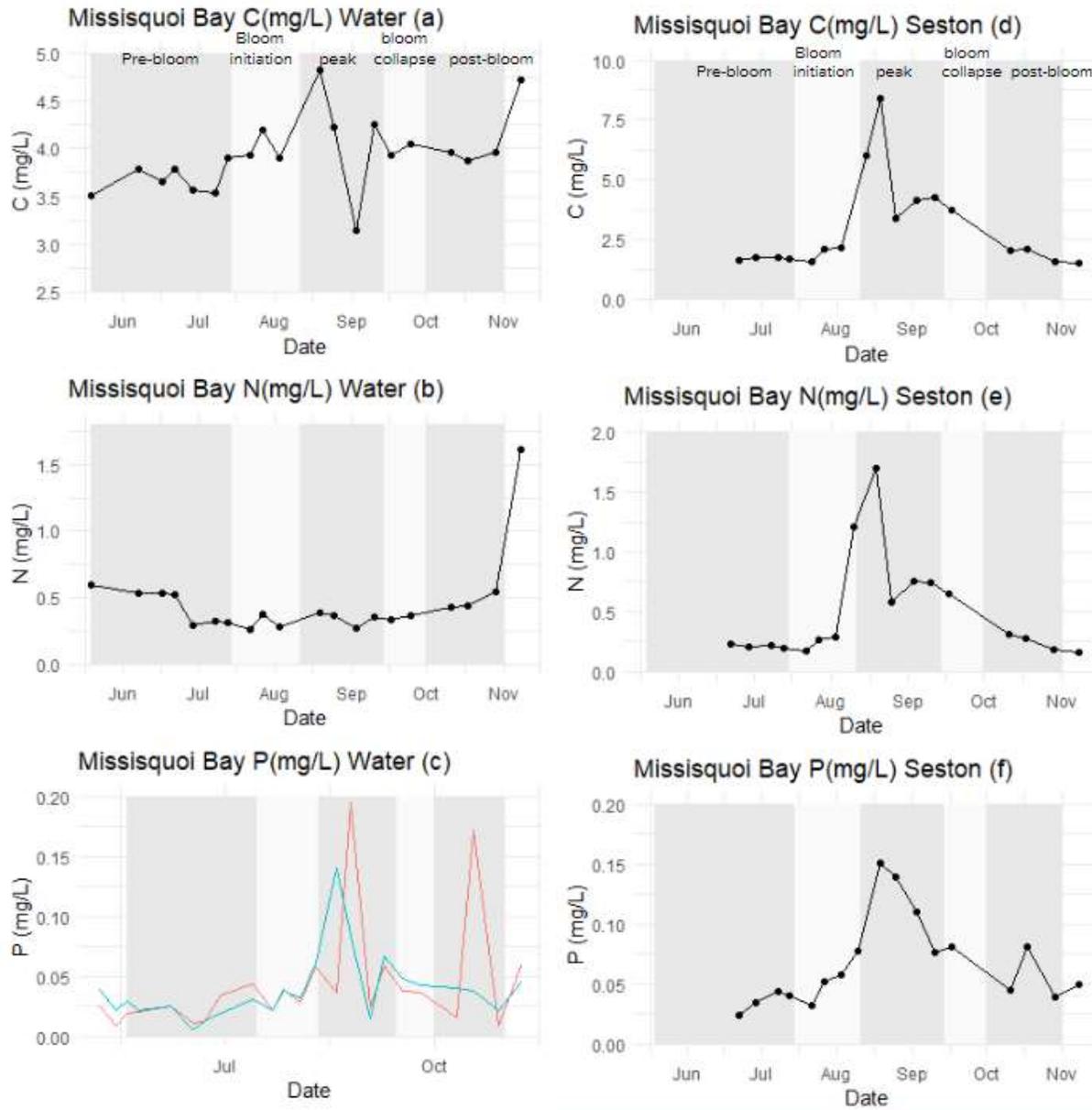


Figure 2 (a-f): Time series of Missisquoi nutrient concentrations. Left panels a, b, and c are water samples; right column d, e, and f are seston. In figures b and c, blue= surface P, orange=bottom P.

In Missisquoi Bay, water column C:N increased pre-bloom and decreased post-bloom, while seston had the opposite trend (Figures 3a and 3d). Water column C:P and N:P remained

stable during the bloom, but both seston C:P and N:P spiked just before the bloom (Figures 2b, e, c, and f).

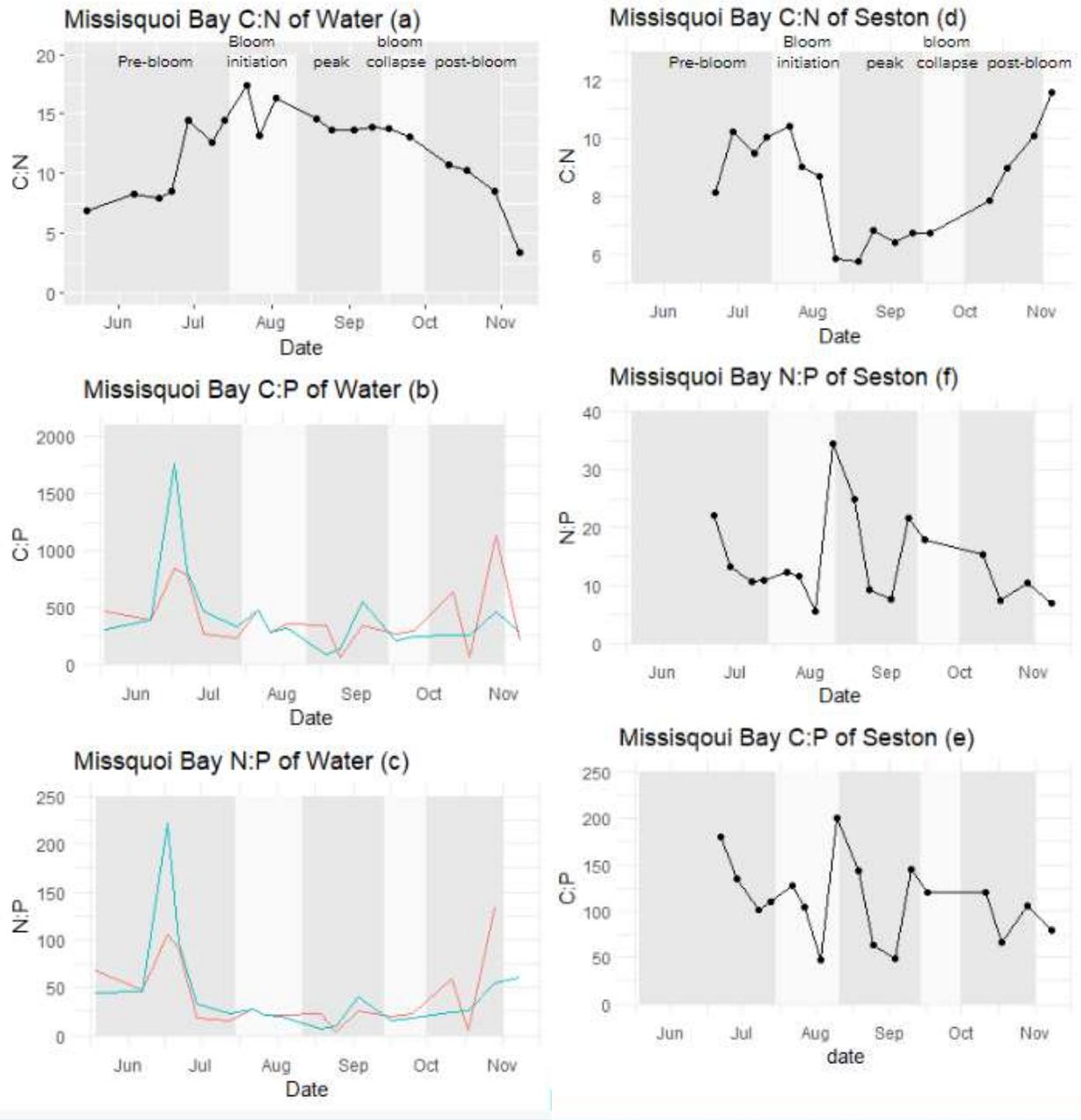


Figure 3 (a-f): Time series of Missisquoi Bay C:N:P elemental stoichiometry. Left panels a, b, and c are water samples; right panels d, e, and f are seston. In figures b and c, blue=surface P, orange=bottom P.

Ambient DOC and TDN in St. Albans Bay surface water had the highest values in spring (late May) and were relatively stable over the remainder of the study period (Figures 4a and b). Water

column P was much more variable, with an increase from approximately $10 \mu\text{g P L}^{-1}$ in late July to $>75 \mu\text{g P L}^{-1}$ in surface water just before the bloom began to develop. Like Missisquoi Bay, we saw depletion of P in surface water during the bloom, then a spike in hypolimnetic P after the bloom subsided (Figure 4c). Seston C, N, and P all spiked concurrently with water column P in early August when the bloom initiated, then decreased gradually through fall (Figures d, e, and f).

Water column C:N in St. Albans spiked just before the bloom, also concurrent with the increase in ambient P (Figure 5a). C:P and N:P in surface and hypolimnetic water samples, however, were highest in mid-June with additional smaller increases just before the bloom and in late fall (Figure 5b and c). Seston C:N decreased substantially during the bloom (Figure 5d), while C:P and N:P increased at bloom initiation, decreased during bloom growth, then crashed when the bloom senesced (Figure 5e and f).

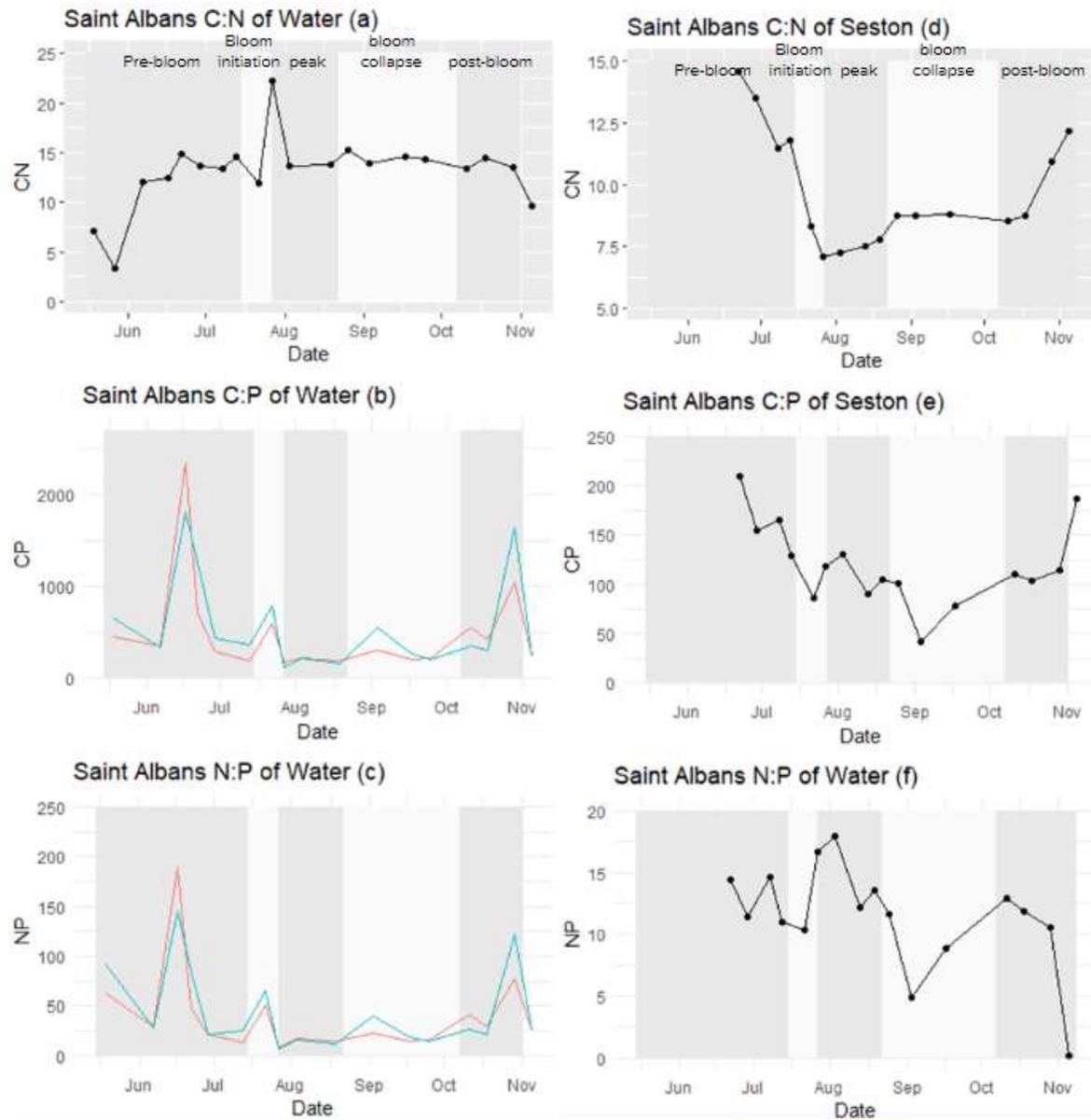


Figure 5 (a-f): Time series of Saint Albans Bay C:N:P elemental stoichiometry. Left panels a, b, and c are water samples; right panels d, e, and f are seston. In figures b and c, blue= surface P, orange=bottom P.

Discussion

On average, we found that seston C:N:P was close to the optimal Redfield ratio at both sites over the study period, with the greatest divergence during bloom conditions. While seston and water column ratios are known to vary from Redfield and still be under optimal conditions (Oliver, et al., 2012), some conclusions can be speculated from these season-long trends. In this

case, it appears that seston are likely fixing atmospheric nitrogen, as seston P tracked closely to resource P (water column), but seston N increased substantially over ambient concentrations during blooms. We found that ambient water ratios were higher than the seston ratios in every instance and were up to approximately 5x higher in the case of C:P in Saint Albans (Table 1). This suggests that the seston is selective of the nutrients in its environment, as it varies from the water nutrients available. Ultimately, since the same low N:P ratio is not seen in the water column, it can be determined that the seston has retained some homeostasis in its elemental composition against the nutrient fluxes in the aquatic environment (Sterner & Elser, 2002).

We observed one distinct bloom in both Missisquoi Bay and Saint Albans Bay (Figure 1). The Saint Albans bloom occurred chronologically before the Missisquoi Bay bloom, which can potentially be attributed to differences in watershed characteristics (drainage primarily of mountain snowmelt versus agricultural land). In addition, Missisquoi Bay is shallower than Saint Albans, which could make it more susceptible to internal loading (Isles, et al., 2015). Here, it is important to note that both bays have different bloom patterns, but follow the same trend of low pre-bloom phycocyanin, fairly sudden/sharp bloom growth leading into a clear peak bloom period, followed by sharp bloom collapse, and then relatively level values for the post-bloom period (Figure 1).

In Figures 2-5, there are many possible trends to consider between the two bays, nutrient ratios, and nutrient concentrations. First, it is important to note that surface phosphorus and bottom phosphorus concentrations, while not being exactly the same in the data here, follow roughly similar trends (Figures 3c, 5c). In Missisquoi Bay, we found that surface P spiked at bloom initiation, and hypolimnetic P spiked immediately after the bloom subsided, indicating P release to bottom waters as dying cells sank and degraded.

In figures 2 and 4, trends in the concentrations of the nutrients carbon, nitrogen, and phosphorus can be observed. In both bays, the seston nutrients fairly consistently peaked in the bloom peak (in the first bloom, for Missisquoi Bay), and then dropped off and leveled off. Increase of all nutrients in seston would be anticipated during a bloom, as there is simply more seston present, and therefore more nutrients. In the water samples from Missisquoi Bay, both carbon and phosphorus peaked in bloom 1 and had a minimum shortly after, but interestingly the nitrogen levels were fairly consistent. Since water samples here include the seston, peaks of carbon and phosphorus in the water column when there is a higher concentration of those nutrients in the seston makes sense. It is interesting to consider the lack of a peak in nitrogen in the water column here, because there was a peak in seston nitrogen concentration. One possible explanation for this is that the cyanobacteria in the bloom was nitrogen limited by the environment and thus required atmospheric N via N-fixation in order for the bloom to occur. This would mean that, even if there are low inputs of nitrogen into the lake from the surrounding environment, that does not mean the cyanobacteria will be nitrogen limited-- they can utilize N from the atmosphere in order to meet nitrogen demands. Finally, the water samples from Saint Albans had stable concentrations of carbon and phosphorus, with small peaks around the bloom, suggesting as stated above, that the variability of nutrients in the seston, which is in the water column, corresponds to fluxes in the water column nutrient concentrations.

In Figures 3 and 5, trends in the nutrient stoichiometry throughout the season can be distinguished. In the water samples in Missisquoi Bay and Saint Albans, all ratios (C:N, C:P, and N:P) had some sort of increase around the peak bloom period, and then decreased afterwards. This would suggest increased carbon and nitrogen, as compared to phosphorus. This makes sense, as phytoplankton are fixing carbon and likely nitrogen as they assimilate bioavailable P from the

water column. In the seston in Missisquoi Bay and also in Saint Albans Bay, C:N was high before the bloom, then dropped during the bloom, then increased again, and similar trends are seen for C:P and N:P. This suggests that during blooms the seston are pulling in more nitrogen and phosphorus from their environment, either through direct uptake or fixation. It is interesting that the water and seston trends are almost opposite, suggesting, like with the nutrient concentration trends, the seston are selective of what nutrients in their environment they consume.

Conclusion and Future Research

Throughout all the data collected here, a few key trends have been observed. The seston appears to be selective of the nutrients in its environments, reflected in both mass concentration and stoichiometry diverging from ambient water column measurements. Our results point to variability in nutrient limitation, over the sampling period, where blooms were initiated following a phosphorus spike (P-limitation), but likely sustained as available N from N-fixation was utilized, and then ultimately depleted (meaning N limitation or N-P co-limitation at the time of the bloom peak). Understanding how the variation in nutrients in Lake Champlain relates to changes in seston growth/cyanobacteria blooms can help to better predict when there will be blooms. For example, an increase in phosphorus concentrations in seston during the summer could be an indicator that there is about to be a bloom, and then community members that utilize the lake can be informed in advance on when the lake will be unsafe for swimming/consumption. Based on this research, the seston/cyanobacteria do have a level of homeostasis that stabilizes elemental composition in response to changing nutrient concentrations the water column, but overall increases in nutrients do appear to relate to cyanobacteria blooms.

Similar trends have been discerned in other studies. For example, in Heslen, et al., they noted that C:P ratios in seston increased with increased water temperatures, as blooms were forming (2005). Multiple studies have also noted the importance of focusing on both N and P in order to reduce toxic cyanobacteria blooms, and have detailed the contributions and importance of both of these nutrients, as well as other environmental factors, for blooms (Pearl, Havens, et al., 2020; Levy, 2017). In these studies they have observed that both N and P together influence cyanobacteria blooms, and they should be studied together, and solutions should be made to decrease both of these nutrient inputs into lakes. This aligns with this research, as a switch in limitation (P to N/N-P limitation) was observed. Also in align with this research it has been noted that atmospheric N from nitrogen-fixation could be contributing notable amounts of N to cyanobacteria blooms (Levy, 2017).

In a study specifically in Missisquoi Bay, it was observed that nutrients in the lake tended to increase after large rain events, but this flux of nutrients only resulted in blooms later in the season, when lake temperature increased (Celikkol, et al., 2021). Both N and P fluxes were contributing to a cyanobacteria bloom, but the temperature and storm events were critical influences as well (Celikkol, et al., 2021). This significance of temperature and storm events was also noted in other lakes, like Lake Erie (Levy, 2017). With this in mind, this research could benefit from also looking at storm events and temperature in relation to nutrient fluxes and bloom formation, to see if similar trends are observed.

To further expand upon these observed trends, it would be critical to analyze the variations in water and seston stoichiometry in the lake over multiple years, and between both locations. It would also be interesting to look at how the nutrient stoichiometry varies between each bloom period, to see how significantly different the peaks and minimums are. Finally, it would be

interesting to analyze not just when there are cyanobacteria blooms, but which cyanotoxins are present when. Then, the nutrient stoichiometry of the different toxins could also potentially be observed, and more trends about ratios and the abundance of harmful blooms/toxins could be studied.

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