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# Vertical Habitat Gradients: Comparing Phytoplankton Dynamics in Lakes with Low to Moderate Dissolved Organic Carbon Concentration

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**VERTICAL HABITAT GRADIENTS: COMPARING PHYTOPLANKTON DYNAMICS IN LAKES  
WITH LOW TO MODERATE DISSOLVED ORGANIC CARBON CONCENTRATION**

By

Matthew J. Farragher

B.S. State University of New York at New Paltz, 2016

A THESIS

Submitted in Partial Fulfillment of the

Requirements for the Degree of

Master of Science

(in Ecology and Environmental Science)

The Graduate School

The University of Maine

August 2021

Advisory Committee:

Jasmine Saros, Associate Director and Professor, Climate Change Institute and School of Biology and Ecology

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## THESIS ACCEPTANCE STATEMENT

On behalf of the Graduate Committee for Matthew Farragher I affirm that this manuscript is the final and accepted dissertation. Signatures of all committee members are on file with the Graduate School at the University of Maine, 42 Stodder Hall, Orono, Maine.

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Dr. Jasmine E. Saros, Professor of Biological Sciences

8/20/2021

Date

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**VERTICAL HABITAT GRADIENTS: COMPARING PHYTOPLANKTON DYNAMICS IN LAKES  
WITH LOW TO MODERATE DISSOLVED ORGANIC CARBON CONCENTRATION**

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Thesis Advisor: Dr. Jasmine Saros

An Abstract of the Thesis Presented  
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Degree of Master of Science  
(in Ecology and Environmental Science)  
August 2021

Concentrations of dissolved organic carbon (DOC) increased across lakes of Maine for several decades before stabilizing or decreasing in recent years. To investigate the seasonal effects of DOC on phytoplankton habitat structure, I assessed vertical gradients of temperature, oxygen, light, and chlorophyll in four lakes in Acadia National Park from under ice through fall turnover in 2020. Lake DOC concentrations ranged from low ( $\sim 2 \text{ mg L}^{-1}$ ) to moderate ( $\sim 4 \text{ mg L}^{-1}$ ). Low-DOC lakes were clearer, with greater mean Secchi depths (9-15 m) than moderate-DOC lakes (5-6 m). Moderate-DOC lakes experienced hypolimnetic anoxia in the summer and had more variable concentrations and vertical gradients of chlorophyll *a*. Seasonal variance of vertical habitat gradients were similar between low- and moderate-DOC lakes, but there was greater stability of chlorophyll *a* biomass and consistently deeper chlorophyll fluorescence peaks in the low-DOC lakes. Phytoplankton community structure was also assessed at three depths in one low- and one moderate-DOC lake on four dates over the sampling period. While the concentration and depth of chlorophyll *a* varied more in the moderate-DOC lake, there was greater turnover of phytoplankton community in the low-DOC lake, with Morisita-Horn dissimilarity slightly higher in low-DOC Jordan Pond ( $r^2 = 0.66$ ,  $p < 0.01$ ) than in moderate-DOC Seal Cove Pond ( $r^2 = 0.61$ ,  $p < 0.01$ ). Long-term trends in DOC concentration were correlated with Secchi depth across several lakes in Acadia National Park ( $r^2 = 0.76$ ,  $p < 0.001$ ), and DOC concentration was also related to changes in phytoplankton pigment assemblages in the sediment record of Seal Cove Pond ( $r^2 = -0.38$ ,  $p = 0.09$ ). DOC concentration was not related to diatom-inferred mixing depth in Seal

Cove Pond's sediment record, suggesting that DOC has a greater impact on light environment than on mixing depth in the moderate-DOC lake. Differences in the vertical habitat gradients and phytoplankton community structure of lakes ranging in DOC concentration from 2-4 mg L<sup>-1</sup> indicates that lakes are highly sensitive to changes in light environment, thermal structure, and other environmental drivers, particularly at low DOC concentrations. The greater sensitivity of low- to moderate-DOC lakes has important implications for broader ecosystem processes, including nutrient cycling, productivity, and water quality.

## ACKNOWLEDGEMENTS

I would first and foremost like to thank my wonderful thesis advisor Dr. Jasmine Saros for her patience and guidance. I couldn't have asked for a better mentor or a better opportunity. I would also like to thank my thesis committee members, Dr. Lee Karp-Boss and Dr. Amanda Klemmer, for their insight and expertise on how I could improve my research. Friends of Acadia funded this project through the Jordan Pond water quality monitoring grant, as well as my position as Aquatic Scientist. Additional funding was provided by the Gokcen fund, the Graduate Student Government grants, and my teaching assistantships with the School of Biology and Ecology. Václava Hazuková and Katherine Paul helped me for hundreds of hours in the field (usually for 12 to 14 hours at a time) but their contributions are immeasurable and without them this research would have been impossible. I thank the Saros lab past and present for additional fieldwork help, feedback, and friendship; Vendy, Joe Mohan, Rachel Fowler, Edna Pedraza Garzon, Simona Lukasik, Grayson Huston, Ben Burpee, and many others I haven't met but whose work I read and cited. Thank you to Bill Gawley, Jake Van Gorder, and Erica Doody, my collaborators at the National Park Service in Acadia. Thank you Scott Lariviere and Tamara Levitsky for assisting with chemical analysis in the Sawyer Water Research Laboratory. Thank you Becky Addressi and Betty Lee in the Climate Change Institute and Trish Costello in the School of Biology & Ecology for always helping with administrative tasks. I thank the maintenance staff in Sawyer for keeping the facilities clean and safe for myself and many others. Finally, I give my deepest gratitude and appreciation to Mom, Dad, Chris, and KP for all their love.

## TABLE OF CONTENTS

ACKNOWLEDGEMENTS .....	vi
LIST OF TABLES.....	viii
LIST OF FIGURES.....	ix
LIST OF EQUATIONS.....	x
Chapter	
1. INTRODUCTION .....	1
2. METHODS .....	4
2.1 Site Description .....	4
2.2 Seasonal data collection .....	7
2.2.1 Continuous monitoring .....	7
2.2.2 Manual sampling .....	7
2.3 Long-term data collection .....	10
2.4 Seasonal data analysis .....	11
2.5 Long-term data analysis .....	12
3. RESULTS .....	14
3.1 Continuous monitoring .....	14
3.2 Seasonal monitoring .....	14
3.2.1 Vertical habitat gradients .....	14
3.2.2 Chemistry and algal biomass .....	17
3.2.3 Phytoplankton community .....	20
3.3 Seal Cove Pond sediment core .....	22
4. DISCUSSION .....	23
REFERENCES .....	28
BIOGRAPHY OF THE AUTHOR .....	33



**LIST OF TABLES**

Table 1. Summary of physical and chemical data for each study lake in 2020 . . . . . 5

Table 2. Pairwise comparisons of vertical habitat gradients . . . . . 16

## LIST OF FIGURES

Figure 1.	Map of Mount Desert Island, Maine, USA and study lakes in Acadia National Park . . . . .	5
Figure 2.	Long-term trends in dissolved organic carbon and Secchi disk depth from 1995-2020 . . . . .	6
Figure 3.	Diagram of sampling methods for seasonal data collection . . . . .	9
Figure 4.	High-frequency continuous monitoring data of temperature, dissolved oxygen, and photosynthetically active radiation . . . . .	15
Figure 5.	Concentrations of algal biomass and nutrients for each season . . . . .	18
Figure 6.	Seasonal chlorophyll fluorescence and biomass . . . . .	19
Figure 7.	Chlorophyll fluorescence contours and vertical gradients . . . . .	19
Figure 8.	Phytoplankton community assemblages for each four dates in Jordan Pond and Seal Cove Pond . . . . .	20
Figure 9.	Non-metric multidimensional scaling of phytoplankton community dissimilarity in Jordan Pond and Seal Cove Pond . . . . .	21
Figure 10.	Extracted pigment concentrations, PCA Axis 1 and Axis 2, Cluster analysis, and diatom-inferred mixing depth index from Seal Cove Pond sediment core, with DOC concentrations . . . . .	22

## LIST OF EQUATIONS

Equation 1.	Calculation to estimate diffuse attenuation coefficients . . . . .	11
Equation 2.	Calculation for the depth of 1% photosynthetically active radiation . . . . .	11
Equation 3.	Calculation of diatom-inferred mixing depth index . . . . .	13

## CHAPTER 1

### INTRODUCTION

The vertical distribution of phytoplankton in lakes is determined by a suite of physical, chemical, and biological factors. Light and nutrients are essential to photosynthetic organisms and are temporally dynamic. Water clarity affects thermal structure and light attenuation (ultraviolet radiation, photosynthetically active radiation), in turn influencing phytoplankton habitat availability and community composition (Williamson et al., 1996; Fee et al., 1996; Saros et al., 2012). Both water quality and nutrient inputs are altered by precipitation (Carpenter et al., 2018; de Wit et al., 2016), internal convection and wind-driven mixing (MacIntyre & Romero, 2000; Strock et al., 2019) and basin morphometry (Kraemer et al., 2015). Together these variables structure lake ecosystems and shape phytoplankton communities.

In low productivity lakes, vertical habitat gradients are strongly controlled by dissolved organic carbon (DOC) concentrations which affect water clarity, thermal structure, and nutrient cycling (Gunn et al., 2001; Fee et al., 1996). Terrestrially-derived DOC is a group of compounds produced through the partial decomposition of organic matter which is transported into lakes and streams via surface waters. The drivers of increasing DOC are largely context dependent (Clark et al., 2010). Precipitation volume and composition can alter DOC inputs (Dillon & Molot, 2005; Hudson et al., 2003; Evans et al., 2006), such as reductions in acid precipitation following increased regulations of anthropogenic sulfur emissions after the Clean Air Act Amendment in 1990 (Monteith et al., 2007; Meyer-Jacob et al., 2019). The effects of DOC on water quality are well-studied; high-DOC lakes ( $> 5 \text{ mg L}^{-1}$ ) are “browned” or dark colored and absorb more heat in surface waters than in clear lakes, resulting in reduced epilimnion thickness in stratified lakes (Fee et al., 1996; Theodore, 2016). Light is attenuated at shallower depths in higher-DOC lakes, limiting habitat availability for phytoplankton (Jones, 1992; Morris et al., 1995; Williamson et al., 2015; Seekell et al., 2015). DOC can further constrain or facilitate the availability of nutrients through pathways of mineralization with iron (Hanson et al., 2011; Weyhenmeyer et al., 2014) or as a concomitant with compounds containing nitrogen (N) or phosphorus (P) (Maranger & Pullin, 2003; Findlay, 2005; Purdue et al., 1998).

DOC concentration is a critical factor in dynamic ecosystem processes, even at low concentrations. Snucins and Gunn (2000) found that deeper zones of clear lakes ( $\text{DOC} < 2 \text{ mg L}^{-1}$ ) are more sensitive to warming

than darker colored lakes ( $\text{DOC} > 4 \text{ mg L}^{-1}$ ). In a study of nearly 5,000 Swedish lakes, the greatest slope of increase in chlorophyll *a* biomass (a proxy for phytoplankton biomass) occurred as a positive relationship with increasing total organic carbon (TOC) in lakes ranging from 0 to  $5 \text{ mg L}^{-1}$  TOC (Isles et al., 2021). Increases in overall phytoplankton biomass as well as shifts in community composition from autotroph-dominated to mixotroph-dominated have also been observed by experimentally increasing DOC (Wilken et al., 2018). At higher DOC concentrations ( $4$  to  $12 \text{ mg L}^{-1}$ ), long-term DOC increases can shift dominant phytoplankton from diatoms to cyanobacteria to mixotrophs (Senar et al., 2021) and can reduce overall phytoplankton biomass (Deininger et al., 2017; Isles et al., 2021; Seekell et al., 2015). While high-DOC concentrations inhibit the growth of phytoplankton where light limitation outweighs the effects of nutrient subsidies, phytoplankton biomass is supplemented at low-DOC concentrations (Solomon et al., 2015; Seekell et al., 2015), with important impacts on community composition (Deininger et al., 2017; Klug, 2002). Clearly, DOC plays an important role in structuring lake habitat for phytoplankton.

A key question that arises is how changing lakewater DOC concentrations are affecting lake habitat structure for phytoplankton, particularly at the low end of the DOC gradient where even small changes in concentration can result in measurable changes in lake physical structure. Concentrations of DOC broadly increased across boreal lakes of North America and Europe between 1990 and 2005 (Monteith et al., 2007; Zhang et al., 2010), and over the last decade as well (Lapierre et al., 2021). Concurrently, DOC concentration varied in magnitude and direction across lakes of Maine, and within Maine lakes over time (Roesler & Culbertson, 2016; Brown et al., 2017; Strock et al., 2017). With variable DOC concentrations observed in Maine lakes over recent decades, my objective was to assess how vertical habitat gradients fluctuated across a set of lakes with low ( $< 5 \text{ mg L}^{-1}$ ) but variable DOC, and how this varied within and between seasons. From under ice to fall turnover, I investigated vertical gradients of temperature, oxygen, light, and chlorophyll across four lakes that differ in DOC concentration and morphometry, and I predicted 1) greater seasonal heterogeneity of vertical habitat gradients in the low-DOC lakes (i.e., more change in vertical habitat gradients over time). I also assessed phytoplankton community structure of one low- and one moderate-DOC lake, predicting 2) greater seasonal turnover of phytoplankton in the low-DOC lake. Low-DOC lakes are more sensitive to environmental drivers, resulting in more dynamic vertical habitat gradients like thermal structure and light environment (Longhi & Beisner, 2009; Snucins &

Gunn, 2000; Williamson et al., 2015), subsequently forcing higher species turnover as the phytoplankton community responds to changing conditions of light, mixing, and nutrients (Longhi & Beisner, 2009; Klug & Cottingham, 2001). Finally, I predicted that 3) long-term trends (~20 years) in DOC would correlate with changes in water clarity, thermal structure, and phytoplankton assemblages in sediment records. The effects of DOC concentration on ecosystem function have been well-studied in several research programs, but the role of DOC in structuring phytoplankton communities at low DOC concentrations requires additional investigation. Testing the degree to which DOC and related habitat gradients alter phytoplankton community structure in lakes at multiple temporal scales will lead to better understanding the consequences of long-term changes in DOC concentrations. The goal of this study was to expand the spatial and temporal breadth of existing DOC research to include nearly a full year of high-resolution sampling at multiple depths in the water column, and to implement a variety of methods to quantify phytoplankton dynamics, vertical gradients, and long-term trends.

## CHAPTER 2

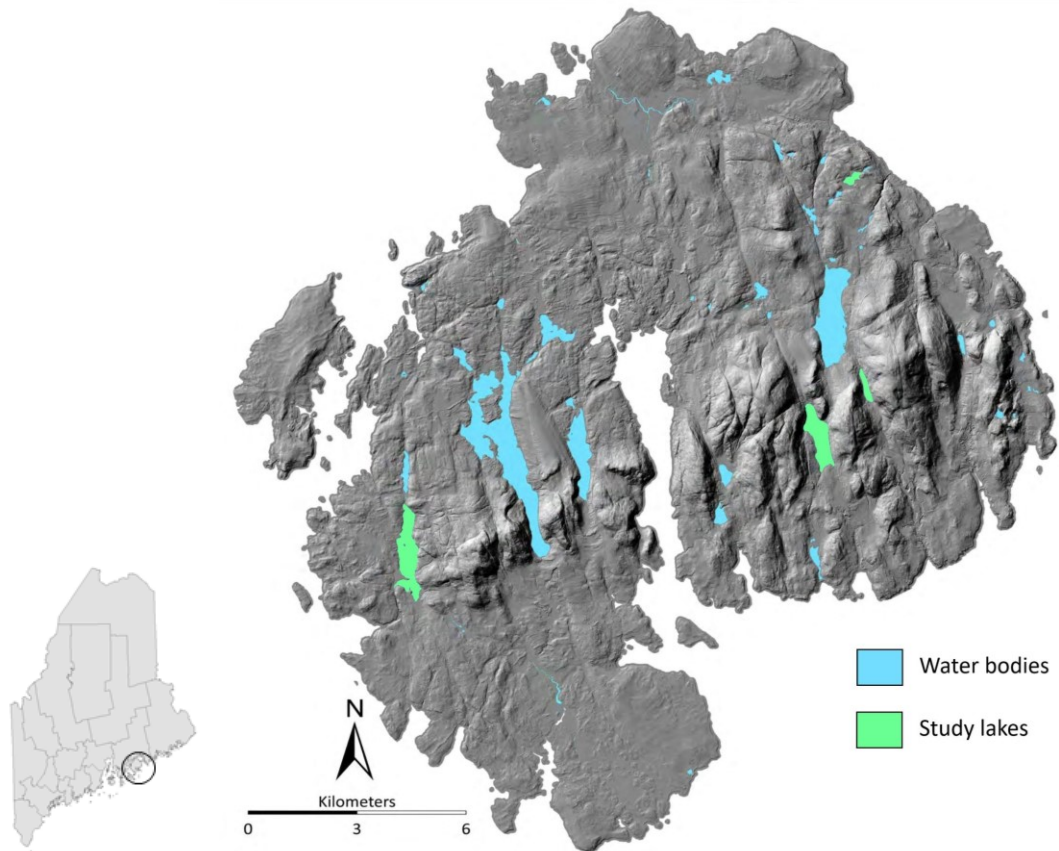
### METHODS

#### 2.1 Site description

Acadia National Park (ANP) is located primarily on Mount Desert Island in southeastern Maine, USA and comprises 141.6 km<sup>2</sup> of land, 10.5 km<sup>2</sup> of which is covered by freshwater lakes and ponds (Fig. 1). Forests are characteristic of both northern boreal and eastern deciduous ecoregions featuring spruce-fir forests, and stands of oak, maple, and beech. The predominant bedrock is granite that is overlain with shallow, well-drained soils derived from a mixture of glacial tills and clays, and many ANP lakes are glacial tarns (Gilman, 1988).

Four dimictic lakes in ANP were selected for this study based on their low to moderate DOC concentrations and comparable morphometry (Table 1). Bubble Pond, Jordan Pond, and Witch Hole Pond all lie completely within the national park boundary, while Seal Cove Pond occupies the extreme western edge of the park boundary and features private homes along the western shore. Jordan Pond and Bubble Pond are both drinking water sources, oligotrophic, and low-DOC (~2 mg L<sup>-1</sup>), while Seal Cove Pond and Witch Hole Pond are both mesotrophic with moderate-DOC concentrations (~4 mg L<sup>-1</sup>). Witch Hole Pond lies within a large area of the park that experienced a burn event in 1947.

Long-term datasets of DOC concentration and Secchi disk depth were obtained from the ANP National Park Service water quality monitoring program (Fig. 2). These data span from 1995 until 2020, where monitoring was conducted once per month from May until October of most years using a consistent sampling protocol (Gawley et al., 2015). From 1995 until 2010, DOC concentrations increased in Jordan Pond (0.3 mg L<sup>-1</sup>), Bubble Pond (0.5 mg L<sup>-1</sup>), and Seal Cove Pond (1.2 mg L<sup>-1</sup>), but decreased in Witch Hole Pond (1.5 mg L<sup>-1</sup>). DOC concentrations decreased across all lakes from 2010 until 2020. Secchi depth decreased considerably in Jordan Pond and Bubble Pond from 1995 until 2010 by 3.0 m and 2.0 m, respectively, after which Secchi depths remained consistent over the following decade. Over the entire 25 year period, Secchi depths in Seal Cove Pond and Witch Hole Pond remained unchanged. However, DOC and Secchi depth for all lakes are related by quadratic regression ( $r^2 = 0.76$ ,  $p < 0.001$ ).

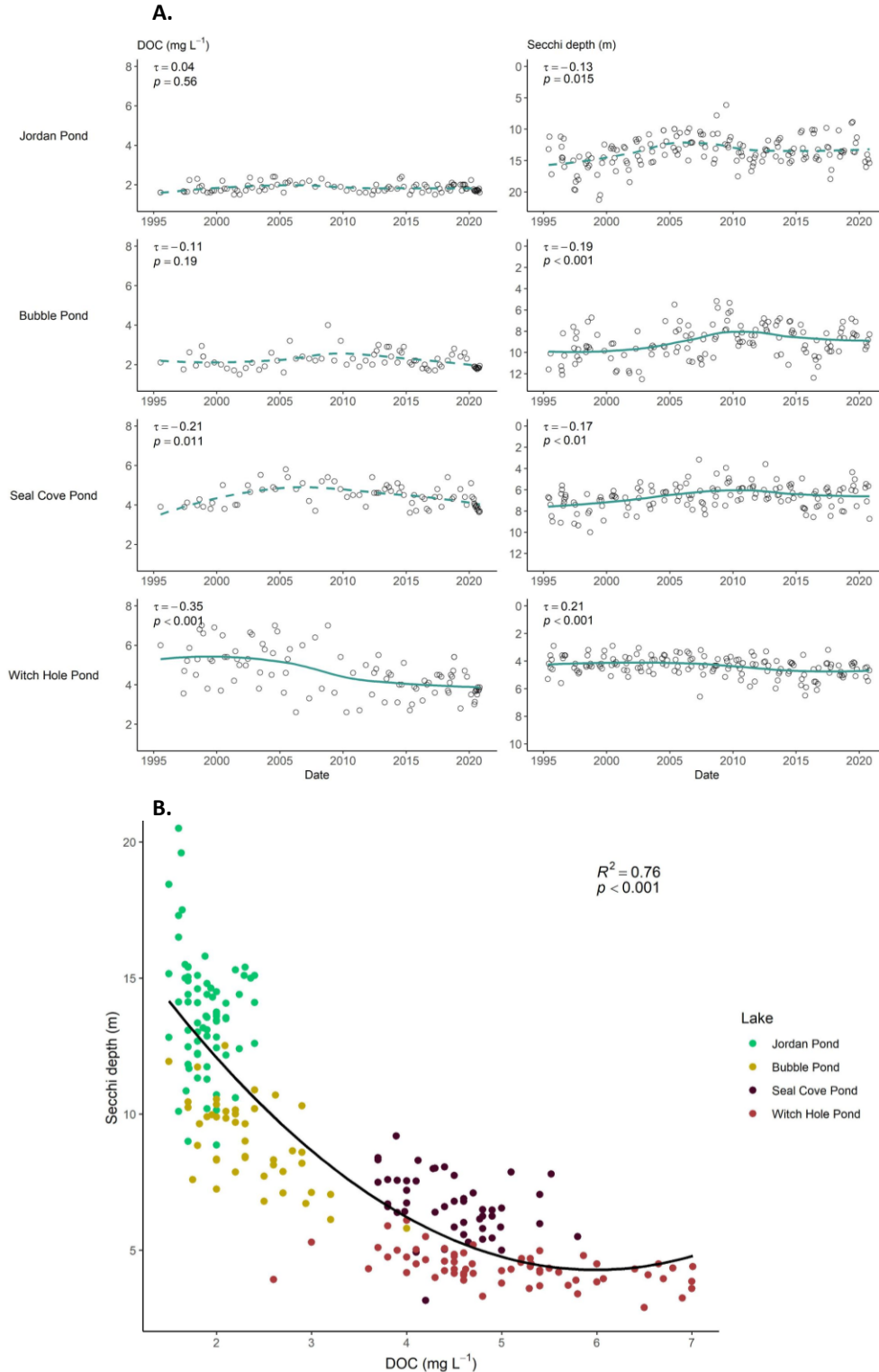


**Figure 1:** Map of Mount Desert Island in southeastern Maine, USA where Acadia National Park is located. Study lakes are colored green, all other water bodies are blue. Map modified with permission from Rodriguez-Padilla (2016).

**Table 1:** Mean and standard deviation of physical, chemical, and biological variables for each lake. DOC, chlorophyll *a* biomass (Chl *a*), and total phosphorus (TP) values from 2020 sampling season. Secchi depth values from ANP water quality monitoring 2020 sampling season.

Site	Area (ha)	Mean / Maximum depth (m)	DOC (mg L <sup>-1</sup> )	Chl <i>a</i> (ug L <sup>-1</sup> )	TP (ug L <sup>-1</sup> )	Secchi (m)
Jordan Pond	75.9	21.1 / 49.3	1.8 ± 0.2	0.9 ± 0.3	2.7 ± 1.1	15.1 ± 0.7
Seal Cove Pond	104.7	4.0 / 13.7	4.0 ± 0.4	2.3 ± 1.2	4.7 ± 1.4	6.6 ± 1.4
Bubble Pond	16.5	4.9 / 11.8	1.8 ± 0.1	1.5 ± 0.7	3.4 ± 1.0	9.1 ± 0.5
Witch Hole Pond	9.7	2.1 / 10.0	3.6 ± 0.4	4.0 ± 1.8	9.2 ± 3.0	4.9 ± 0.4





**Figure 2:** A) Long-term trends of DOC concentration (left) and Secchi depth (right) from 1995-2020. Data were fitted with locally weighted regression scatterplot smoothing (LOESS) trends with Mann-Kendall non-parametric trend tests using the function *MannKendall* from the R package *Kendall* (McLeod and Kendall, 2011).  $\tau$  indicates overall direction of change, and solid lines indicate significance ( $p < 0.01$ ). B) Quadratic regression of DOC concentration and Secchi depth. Data from Acadia National Park Service water quality monitoring program.

## **2.2 Seasonal data collection**

### **2.2.1 Continuous monitoring**

Each lake was outfitted with a string of sensors attached to a buoy for high-frequency, continuous monitoring for 9 months in 2020. The buoys were deployed in February 2020 through the ice and retrieved in October 2020. For Jordan Pond, Seal Cove Pond, and Witch Hole Pond, the buoys were deployed with one PME miniPAR® Logger positioned 2 m below the water surface, one PME miniDOT® Logger at 3 m below the water surface, and another PME miniDOT® Logger at 2 m above the lake sediment. The miniPAR loggers measured photosynthetically active radiation (PAR) and the miniDOT loggers measured dissolved oxygen concentration (DO). Additionally, Onset® HOBO Pendant MX Water Temperature Data Loggers were placed at 1 m intervals down the length of the line, recording temperature. The buoy in Bubble Pond had no PAR logger or DO loggers over the same time period as the other lakes, but was outfitted with Onset® HOBO Water Temperature Pro v2 Data Loggers every meter. All PAR sensors, DO sensors, and temperature sensors were synchronized to record data in 1-hour intervals. Buoys were deployed near the site of maximum depth in Bubble Pond (12 m), Seal Cove Pond (13 m) and Witch Hole Pond (9 m) and at 32 m in Jordan Pond. The buoy in Bubble Pond was managed by the Maine Department of Environmental Protection who contributed data as described above for this study.

### **2.2.2 Manual sampling**

Under-ice monitoring data were collected once in February 2020 in Jordan Pond, Seal Cove Pond, and Witch Hole Pond; ice-off occurred on Bubble Pond before I could conduct winter sampling there. Open water monitoring was performed every two weeks in all four lakes from May 2020 until November 2020 to capture the period from the onset of stratification through fall turnover. All manual samples were collected between the hours of 10:00 and 18:00 and at similar times for each individual lake. Sampling methods included data collection of vertical profiles and Secchi disk depth, and collection of water samples for chemistry, algal biomass, and phytoplankton (Fig. 3). Sampling dates were grouped into seasons for data visualization as follows: winter samples were collected under ice once between 21-25 Feb, while multiple dates were pooled in the other seasons, with spring sample dates from 26-May to 14-Jun, summer from 28-Jun to 19-Aug, and autumn from 05-Sep to 06-Nov.

### *Profiles*

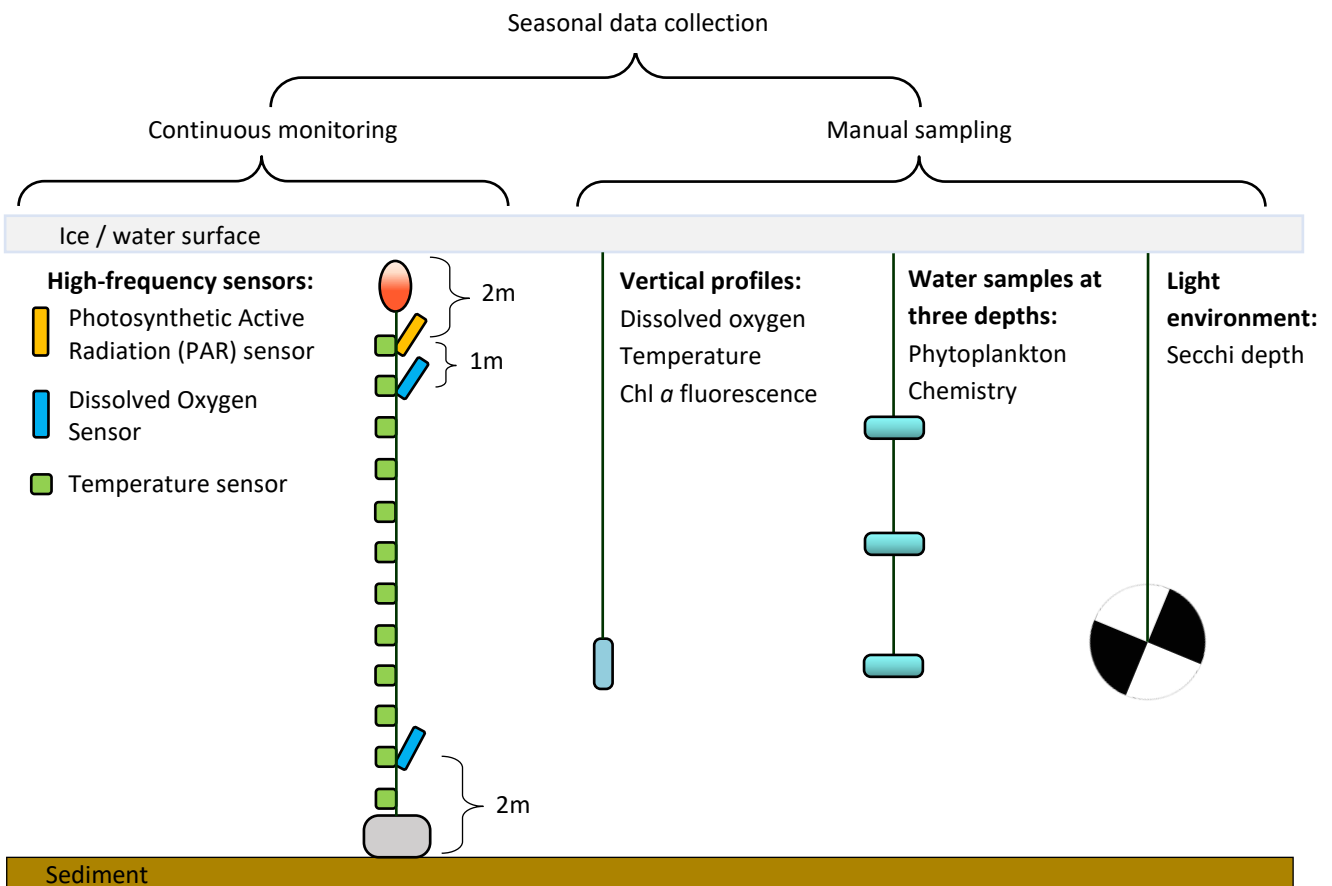
Continuous profiles of temperature and chlorophyll *a* fluorescence (fChl) were measured in each lake on each date using a Turner Designs C3™ Submersible Fluorometer. A YSI® EXO3 Multi-Parameter Water Quality Sonde was used to measure profiles of temperature and dissolved oxygen at 1 m intervals from the surface to within 1 m of the lake sediment for each lake except for Jordan Pond where profiles extended to 30 m. Secchi disk depth, a proxy for light attenuation, was recorded as the depth at which a 20-cm black and white Secchi disk was no longer visible when lowered down into the water column. Profiles were taken between the hours of 10:00 and 18:00 and at similar times for each individual lake to control for diel variation of light attenuation as well as non-photochemical quenching of fChl profiles. During daylight, non-photochemical quenching reduces fluorescence activity of chlorophyll in shallow zones of aquatic systems, forming the appearance of deeper chlorophyll peaks which may not accurately portray chlorophyll *a* biomass (Falkowski & Kolber, 1995). Extracted chlorophyll *a* biomass was also measured to substantiate chlorophyll profile characteristics, and is explained in detail below.

### *Chemistry & algal biomass*

Water samples were collected from three depths corresponding to the epilimnion, metalimnion, and hypolimnion. When lakes were not thermally stratified, top, middle, and bottom depths were selected. Depths are referred to hereafter as epilimnion, metalimnion, and hypolimnion for all samples regardless of stratification patterns. Total nitrate (TN) and total phosphorus (TP) concentrations were determined by persulfate digestion using unfiltered, whole water samples (American Public Health Association, 2000). Whole water samples were filtered through 0.7- $\mu\text{m}$  Whatman GF/F filters to determine concentrations of inorganic nutrients ( $\text{NH}_4^+$ ,  $\text{NO}_3^-$ ) and DOC.  $\text{NH}_4^+$ ,  $\text{NO}_3^-$ , and DOC concentrations were determined using the standard phenate, cadmium reduction, and catalytic oxidation methods, respectively (American Public Health Association, 2000). Chlorophyll *a* concentration (Chl *a*), a proxy for algal biomass, was measured by filtering whole water samples (kept in light-blocking bottles) through 0.7- $\mu\text{m}$  Whatman GF/F filters, after which the filters were frozen for more than 24 hours, placed in 90% acetone, and analyzed using a UV-VIS spectrophotometer within two weeks of collection using standardized methods (American Public Health Association, 2000). All water sample analyses were conducted at the University of Maine Sawyer Water Research Laboratory.

*Phytoplankton sampling*

Phytoplankton identification and enumeration in Jordan Pond (low DOC) and Seal Cove Pond (moderate DOC) were conducted at three depths on one sampling date from each season, corresponding to under-ice (inverse stratification), spring turnover, peak summer stratification, and fall turnover (Winter: 21-Feb; Spring: 28-May; Summer: 3-Aug and 4-Aug; Fall: 31-Oct and 06-Nov). Subsamples of the whole-water samples used for Chl *a* extraction were fixed in Lugol’s Iodine solution and stored in the dark until 20 to 25 ml was settled in an Utermöhl chamber for at least 12 hours. Phytoplankton were then counted along two transects at 600x magnification using a Nikon TS100 inverted microscope. Raw cell counts were converted to cell density mL<sup>-1</sup> based on subsample volume settled and the number of transects that were counted (Hillebrand et al., 1999). Individuals were identified to genus using Wehr et al. (2015) except for unidentified non-flagellated cells and unidentified cysts.



**Figure 3:** Diagram of sampling methods for seasonal data collection. Continuous monitoring was accomplished using high frequency sensors attached to buoys which were deployed in each lake for the duration of the study. Manual sampling consisted of taking vertical profiles, water samples, and Secchi disk depth.

## 2.3 Long-term data collection

### *Seal Cove Pond sediment core*

A sediment core was collected from Seal Cove Pond in 2016 to investigate long-term trends in algal pigments and diatom assemblages. These data were collected by a doctoral student, Rachel Fowler, for her dissertation work (Fowler, 2019); I present them here with a new data analysis, described below, but briefly describe the data collection methods here. The sediment core was retrieved using a gravity corer equipped with a 6.5-cm diameter tube at the deepest location in the lake. The core was 25.5 cm in length, and was sectioned in the field in 0.25-cm increments for the first 10 cm and 0.5-cm increments from 10 to 25.5 cm. Each section was dated using Pb<sup>210</sup> isotope ratios. Pigments were extracted using high-performance liquid chromatography following Chen et al. (2001). Sediment samples were stored at -80°C, then freeze-dried and extracted in an acetone:methanol:water solution (80:15:5) at -20°C. Extracts were filtered through 0.22-µm PTFE syringe filters and dried under N<sub>2</sub> gas, then re-dissolved in a 70:25:5 mixture of acetone, ion pairing reagent (0.75 g tetrabutylammonium acetate 80 and 7.7 g ammonium acetate in 100 ml H<sub>2</sub>O), and methanol prior to injection into the Agilent HPLC unit. Spectrum peaks were calibrated using commercial standards (DHI Denmark). Chl *a* was not included in this analysis due to its high rate of degradation in sediment samples (McGowan, 2007). Most pigments are subject to breakdown or consumption by microbes or macroinvertebrates before sedimentation (Cuddington & Leavitt 1999), and undergo degradation within lake sediments at varying rates due to temperature, light, and oxygen (Leavitt & Hodgson, 2002; McGowan, 2007). Despite these caveats, pigment assemblages in sediment records are a relative proxy for historical phytoplankton communities.

Diatom assemblages were identified and enumerated following Battarbee (2001), in which 10% HCl and 30% H<sub>2</sub>O<sub>2</sub> were used to digest carbonate and organic matter in each sediment subsample. Samples were then mounted onto slides with Naphrax<sup>®</sup> viewed on an Olympus BX51 microscope at 1000x magnification. A minimum of 300 valves per slide were identified and enumerated with taxonomic identification based on Krammer & Lange-Bertalot (1986-1991) and Camburn & Charles (2000).

## 2.4 Seasonal data analysis

### *Vertical habitat gradients*

To assess seasonal heterogeneity of vertical habitat gradients in the four lakes, I used pairwise comparisons of variables for each pair of lakes. While all lake pairs were tested in each analysis, I focused on comparing the two large lakes (Jordan Pond and Seal Cove Pond) to each other, as well as the two small lakes (Bubble Pond and Witch Hole Pond), where each pair has a low-DOC and moderate-DOC lake, but similar morphological characteristics. Lake morphometry was a focus of these pairings given its effect on lake thermal structure (Kraemer et al. 2015).

Thermal structure was described from lake temperature profiles by calculating mean temperature, Schmidt stability (SS), and the ratio of mixing depth to maximum lake depth ( $Z_{\text{mix}}:Z_{\text{max}}$ ) to afford meaningful comparisons between lakes with varying morphometry. Bathymetric maps of each lake were generated using ReefMaster® software and sonar data collected with a Humminbird 597ci GPS device. From these maps I calculated the whole lake volume as well as area and volume of each 1-m depth contour, which I then used to calculate SS. Mean DO % saturation was also calculated for each profile. Light attenuation was quantified as the ratio of the depth where 1% of photosynthetically active radiation ( $Z_{1\%PAR}$ ) remained to the lake's maximum depth ( $Z_{1\%PAR}:Z_{\text{max}}$ ).  $Z_{1\%PAR}$  was calculated following Morris et al. (1995) by first estimating the diffuse attenuation coefficient ( $K_d$ ) using concentrations of DOC and Chl  $a$  from epilimnion samples, then dividing by a constant:

$$\text{Equation 1: } K_d = 0.22[\text{DOC}] + 0.07[\text{Chl } a] - 0.05$$

$$\text{Equation 2: } Z_{1\%PAR} = K_d / 4.6$$

Vertical gradients of phytoplankton were quantified by calculating the mean and standard deviation of extracted Chl  $a$  for each lake profile. Additionally, the depth of the chlorophyll peak (DCP) was calculated by fitting generalized normal distributions to fChl profiles after Lofton et al. (2020; see also Leach et al., 2017). Ratios of DCP to maximum lake depth ( $\text{DCP}:Z_{\text{max}}$ ) were used to further investigate phytoplankton habitat structure. Means of vertical habitat gradient parameters were compared between lake pairs using T-tests, and the seasonal

heterogeneity of vertical habitat gradients were assessed using Levene's test to compare sample variances. Vertical gradients of nutrient concentrations were characterized by calculating the standard deviation of epi-, meta-, and hypolimnetic concentrations of DOC, TP, dissolved inorganic nitrogen (DIN, equal to the sum of  $\text{NH}_4^+$  and  $\text{NO}_3^-$ ), and DIN:TP for each lake profile.

### *Phytoplankton community*

To assess seasonal turnover of phytoplankton in the two lakes, phytoplankton community was visualized with non-metric multidimensional scaling (nMDS) using Morisita-Horn distances computed with the function *metaMDS* from the *vegan* package in R (Oksanen et al., 2017). Morisita-Horn distance emphasizes dominant species more than other similarity indexes, which is ideal for datasets with low-sample sizes (Jost et al., 2011). Samples from the winter (under-ice), spring, summer, and autumn were visualized for Jordan Pond and Seal Cove Pond with depths (epi-, meta-, hypolimnion) pooled together to better characterize the phytoplankton community of the entire lake, and to directly compare overall seasonal variability between lakes. Other nMDS plots were generated for each lake separately, with depths ungrouped to visualize vertical gradients in phytoplankton community structure. To test the differences in phytoplankton community composition between lakes/across seasons, and between depths/across seasons for each lake, I calculated within group distance between centroids using the *vegan* function *betadisper*, and additionally used PERMANOVA with 999 permutations using the *vegan* function *adonis2* (Anderson, 2017; Oksanen et al., 2017).

## **2.5 Long-term data analysis**

### *Seal Cove Pond sediment core*

I used the Seal Cove Pond sediment core data to assess whether changes in DOC concentrations over recent decades were correlated with changes in phytoplankton groups. Pigment concentrations were visualized using the R package *tidypaleo* (Dunnington, 2021). The *tidypaleo* functions *nested\_chclust\_coniss* and *nested\_prcomp* were used to portray results from both a principal components analysis (PCA) and a constrained

hierarchical clustering analysis (CONISS) alongside the pigment concentrations to identify breakpoints in the pigment assemblages over time (Dunnington, 2021). PCA scores were obtained using the *vegan* function *rda* (Oksanen et al., 2017). Additionally, mixing depth indexes (MDI) were calculated for each subsample using diatom assemblages with the following model from Stone et al. (2016):

$$\text{Equation 3: } \quad \text{MDI} = (M_k+1) / (M_j+1)$$

MDI was calculated as the ratio of relative abundances between the sum of *Aulacoseira* species ( $M_k$ ) and the sum of *D. stelligera* ( $M_j$ ), where greater sums of *Aulacoseira* (higher MDI) indicate deeper mixing depth, and greater sums of *D. stelligera* (lower MDI) indicate shallower mixing depth (Stone et al., 2016). MDI, along with monitored lakewater DOC concentration, were plotted alongside pigment assemblages, PCA Axis 1 and Axis 2, and the CONISS dendrogram. Correlations between DOC and MDI as well as PC Axis 1 scores and PC Axis 2 scores were determined using the R function *cor.test* (R Development Core Team, 2020). All statistical analysis described above was completed using R version 4.0.2 (R Development Core Team, 2020).



## CHAPTER 3

### RESULTS

#### 3.1 Continuous monitoring

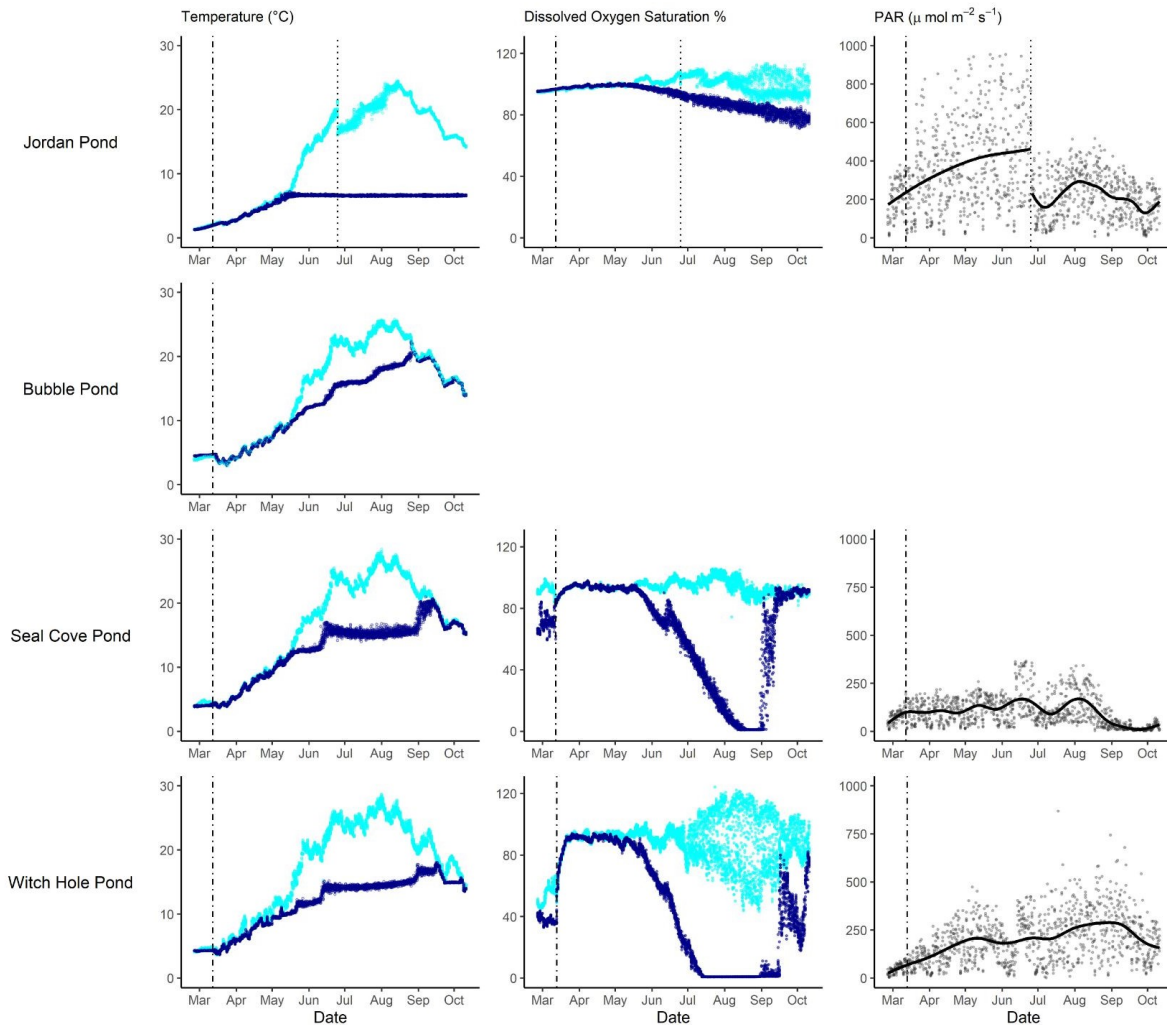
Data from high-frequency sensors captured thermal dynamics, benthic and pelagic oxygen content, and light environment from under-ice through fall turnover in Jordan Pond, Seal Cove Pond, and Witch Hole Pond (Fig. 4). Lake temperatures varied from 1°C below the ice in Jordan Pond to 25°C at 1 m depth in Witch Hole Pond during peak stratification (08-Aug). Inverse stratification occurred under ice, and onset of stratification occurred simultaneously across all four lakes in late-May. PAR steadily increased following ice-out until mid-July before decreasing in early-August. Moderate-DOC lakes Seal Cove Pond and Witch Hole Pond experienced hypoxia of the hypolimnion as early as 15-July, while Jordan Pond DO did not fall below 8 mg L<sup>-1</sup> at any point. The stratified layers in Bubble Pond, Seal Cove Pond, and Witch Hole Pond began to erode in early-September and were fully mixed by mid-October, while Jordan Pond remained stratified at the time of data retrieval from the buoys on 12-Oct and on the last manual sampling trip on 31-Oct.

#### 3.2 Seasonal monitoring

##### 3.2.1 Vertical habitat gradients

Jordan Pond had the greatest range of thermal stability, with SS varying from 1.6 J m<sup>-2</sup> under-ice to 2246.6 J m<sup>-2</sup> near the time of maximum temperature in early-August. Bubble Pond, Seal Cove Pond, and Witch Hole Pond had much lower mean SS (16.6 to 37.8 J m<sup>-2</sup>, Bubble Pond and Seal Cove Pond, respectively), reaching maximum stability (48.6 to 93.8 J m<sup>-2</sup>) over a month earlier than Jordan.  $Z_{\text{mix}}:Z_{\text{max}}$  ratios were lowest in Jordan Pond (mean  $Z_{\text{mix}}:Z_{\text{max}} = 0.25$ ,  $Z_{\text{mix}} = 12.4$  m) and the highest in Bubble Pond (mean  $Z_{\text{mix}}:Z_{\text{max}} = 0.67$ ,  $Z_{\text{mix}} = 8.04$  m). In the large lake pair,  $Z_{\text{mix}}:Z_{\text{max}}$  was lower in Jordan Pond than in Seal Cove Pond over the season ( $df = 10$ ,  $p < 0.001$ ), while it was similar in the small lake pair ( $df = 9$ ,  $p = 0.45$ ). The low-DOC lakes had higher mean DO concentration in both the large lake pair ( $df = 10$ ,  $p < 0.01$ ) and small lake pair ( $df = 9$ ,  $p < 0.001$ ). Secchi depth was deepest in the low-DOC lakes (Jordan Pond mean Secchi depth = 15.1 m, Bubble Pond mean Secchi depth = 9.1). Despite the high Secchi

depth values, Jordan Pond had lower  $Z_1:Z_{max}$  compared to Seal Cove Pond in the large lake pair (mean = 0.24, 0.35 respectively,  $p < 0.001$ ). Bubble Pond had the highest  $Z_1:Z_{max}$  of all lakes (mean = 0.87) with the highest estimated  $Z_{1\%PAR}$  extending to the lake sediment at a depth of 12 m, while moderate-DOC Witch Hole Pond had the lowest  $Z_1:Z_{max}$  where light was nearly completely attenuated at half of the lake's maximum depth (mean = 0.51,  $p < 0.001$  for small lake pair comparison).



**Figure 4:** High-frequency data for temperature, DO, and PAR from 26-Feb to 11-Oct 2020. In the temperature and DO plots, light blue indicates Top sensor data (~2 m below surface) and dark blue indicates Bottom sensor data (~2 m above sediment). PAR was positioned at 1 m below the surface in each lake. PAR values were smoothed with a generalized additive model (GAM), which better integrates trends in datasets where  $n > 1000$ . Only daytime PAR values between 10:00 and 14:00 are shown. Dashed lines indicate the estimated date of ice-off in each lake. The dotted line in both Jordan Pond plots indicates the date of “sensor drift”; on 25-Jun between 17:00 and 18:00, the buoy was unintentionally moved 20 m horizontally from where it was deployed to a position 3 m deeper, possibly due to a slumping event or other intrusive force. There is no DO or PAR data available for Bubble Pond.

Levene's test was used to assess the seasonal variance of each vertical habitat gradient by comparing the variances of each lake pair. There was no statistical difference in the seasonal heterogeneity of vertical habitat gradients between lake pairs except for SS where all lake pairs that included Jordan Pond were significant (Table 2). The variance of  $Z_{mix}:Z_{max}$ ,  $Z_1:Z_{max}$ , and  $DCP:Z_{max}$  between all lake pairs were not different, despite having different means for several lake pairs via Student's T-test. Considering only the large and small lake pairs (Jordan Pond:Seal Cove Pond, Bubble Pond:Witch Hole Pond), seasonal variance of vertical habitat gradients (SS,  $Z_{mix}:Z_{max}$ ,  $Z_1:Z_{max}$ , and  $DCP:Z_{max}$ ) were highest in the higher-DOC lakes of each pair except Jordan Pond SS variance was higher than that of Seal Cove Pond, and Bubble Pond  $Z_1:Z_{max}$  variance was higher than that of Witch Hole Pond.

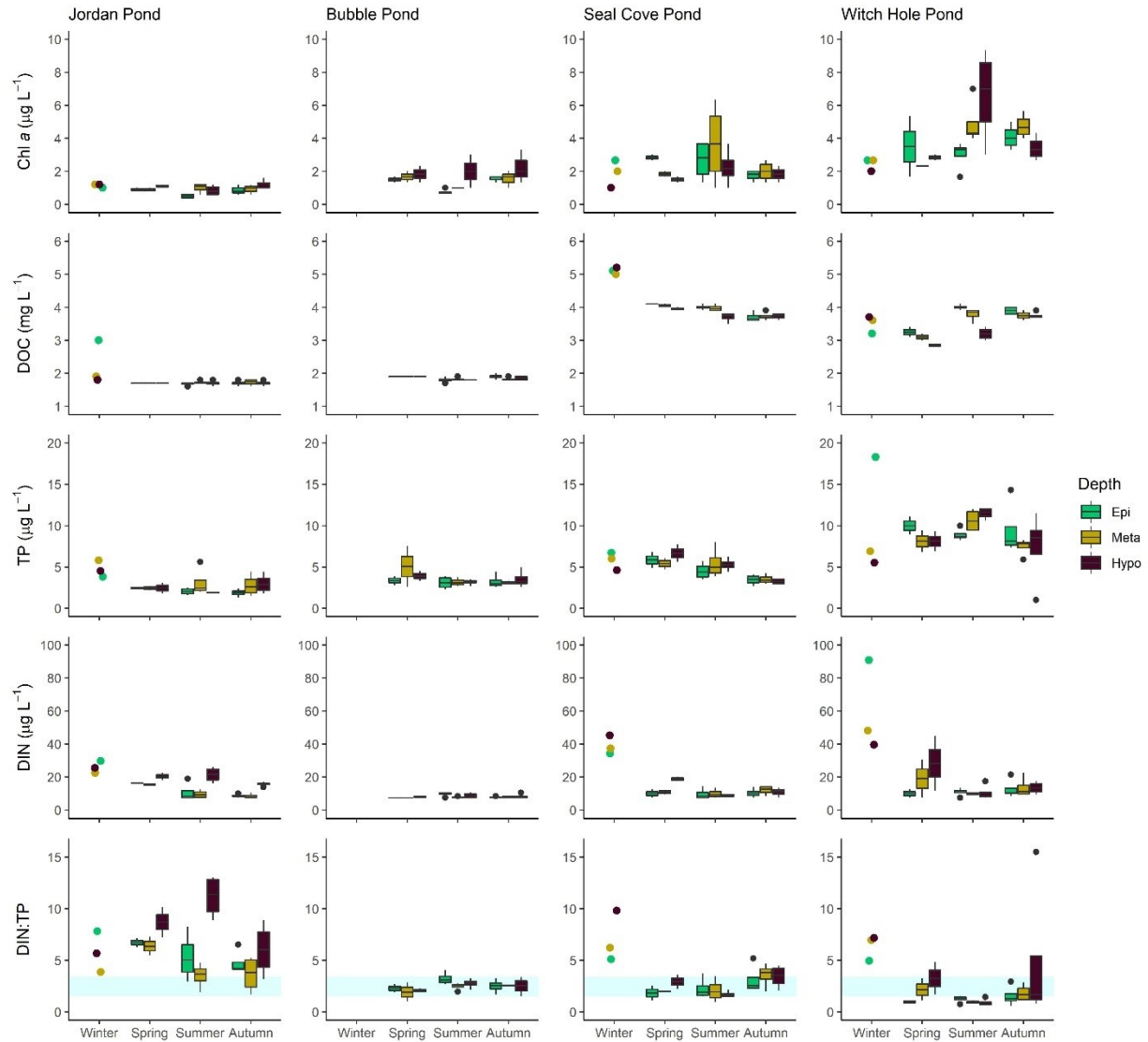
**Table 2:** Comparison of vertical habitat gradients between lake pairs. Levene's test  $p$  values are shown, assessing the seasonal heterogeneity of variances for each vertical habitat gradient parameter, where \* denotes significant differences of variances by Levene's test and + denotes significant differences ( $p < 0.00625$ ) between means of each parameter by independent T-test after Bonferroni correction. Mean DOC, TP, Chl  $a$ , and DO were calculated for each sampling event, as was Schmidt stability (SS) and ratios of mixing depth ( $Z_{mix}$ ), depth of 1%PAR ( $Z_1$ ), and the depth of the chlorophyll peak (DCP) to maximum lake depth ( $Z_{max}$ ). These values were then tested independently for each lake pair, where  $n = 11$  for Jordan Pond (JP), Seal Cove Pond (SC), and Witch Hole Pond (WH) but  $n = 10$  for Bubble Pond (BB).

Lake pair	DOC	TP	Chl $a$	DO	SS	$Z_{mix}:Z_{max}$	$Z_1:Z_{max}$	$DCP:Z_{max}$
JP-SC	0.225+	0.207+	0.068+	0.004*	< 0.001*+	0.170+	0.317+	0.680
BB-WH	0.039+	0.087+	0.093+	0.000*+	0.322	0.525	0.298+	0.307+
JP-BB	0.345	0.487	0.068	0.314	< 0.001*+	0.364+	0.034+	0.696+
JP-WH	0.183+	0.173+	0.012+	0.000*+	< 0.001*+	0.138	0.316+	0.532
SC-BB	0.096+	0.056	0.349	0.008*	0.037	0.879	0.062+	0.407+
SC-WH	0.846	0.577+	0.472+	0.475	0.127	0.546	0.604+	0.819

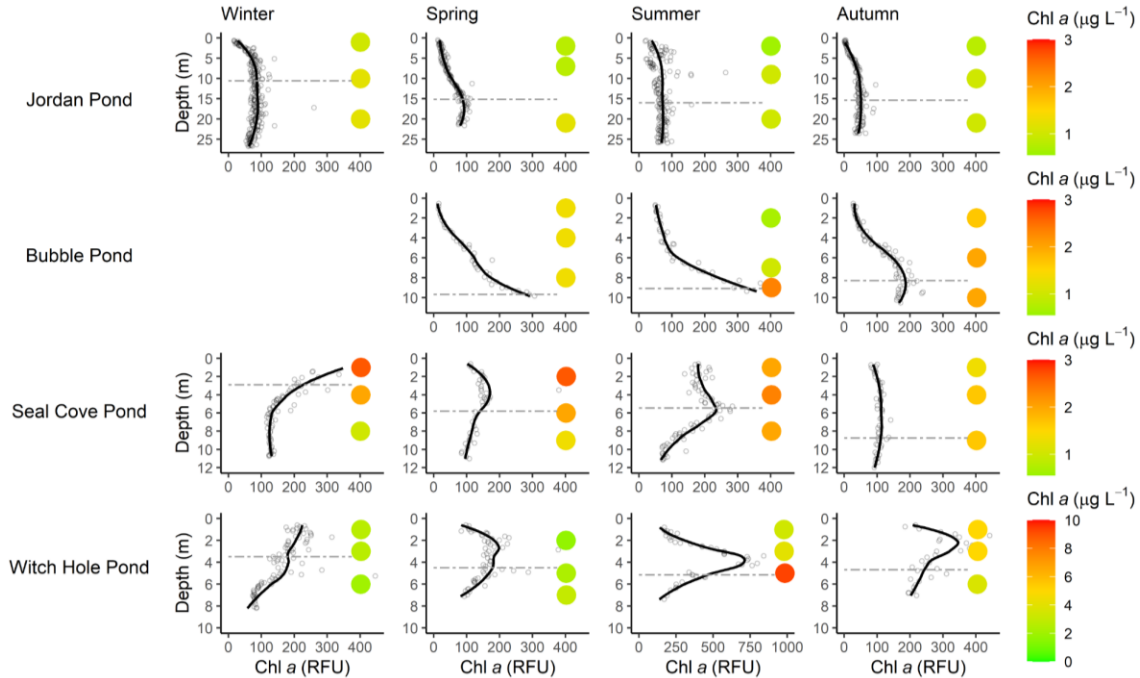
### 3.2.2 Chemistry & algal biomass

DOC concentrations were all highest under-ice in Jordan Pond and Seal Cove Pond before steadily decreasing over the season (Fig. 5). DOC concentrations in Witch Hole Pond increased until mid-summer. TP was highest across all lakes early-summer before generally decreasing, and DIN was highest under-ice for the three lakes sampled in winter, and during the first sampling period mid-spring for Bubble Pond. DIN decreased mid-spring, often below detection limits ( $\text{NH}_4^+$ :  $5 \mu\text{g L}^{-1}$ ,  $\text{NO}_3^-$ :  $2.5 \mu\text{g L}^{-1}$ ). DIN:TP was highest in Jordan Pond throughout the season, indicating P limitation (Bergström et al., 2010). Witch Hole Pond and Seal Cove Pond were P-limited under ice, before DIN:TP decreased in the spring.

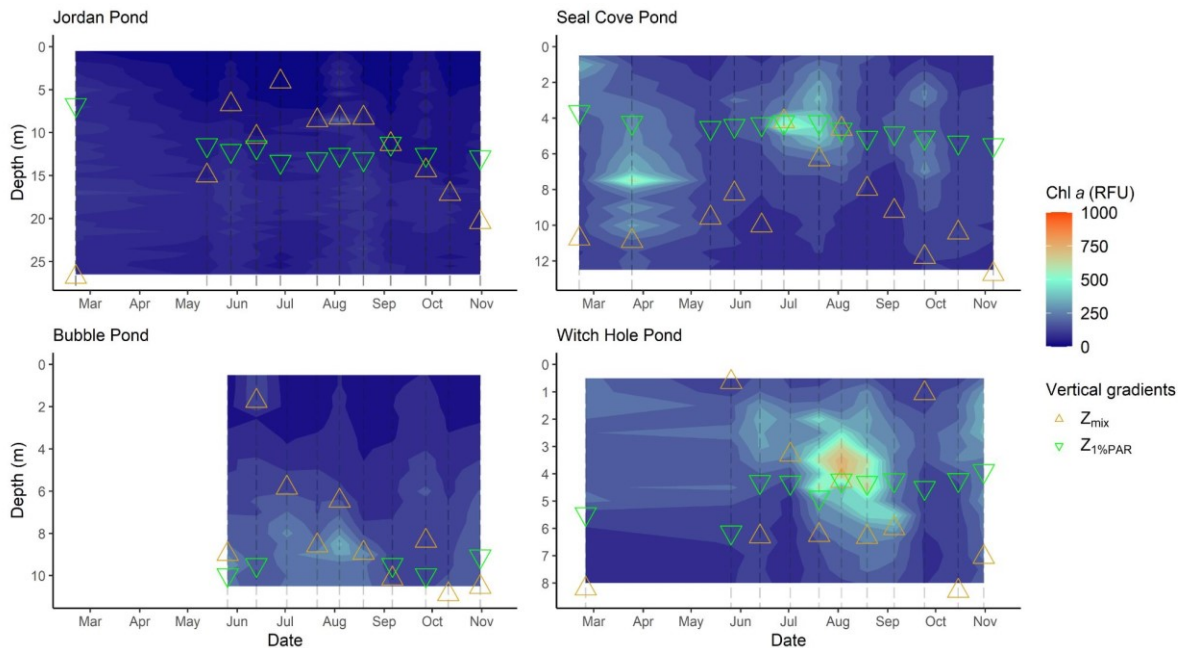
In both the large and small lake pairs, Chl *a* was higher throughout the season in the moderate-DOC lakes. Jordan Pond had the lowest algal biomass with mean value of  $0.9 \mu\text{g L}^{-1}$  Chl *a*, compared to Seal Cove Pond (mean =  $2.3 \mu\text{g L}^{-1}$ ,  $p = 0.001$ ). Algal biomass in Bubble Pond was lower than in Witch Hole Pond (mean =  $1.5$  and  $4.0 \mu\text{g L}^{-1}$ ,  $p < 0.001$ ). Vertical heterogeneity of algal biomass was also greater in the moderate-DOC lakes. Standard deviations of the epi-, meta-, and hypolimnion Chl *a* values in Jordan Pond and Seal Cove Pond were  $0.22$  and  $0.42$  respectively, while Bubble Pond and Witch Hole Pond values were  $0.40$  and  $0.96$ . *P* values for the large lake pair ( $0.049$ ) and small lake pair ( $0.019$ ), along with the low number of samples constituting standard deviation ( $n = 3$ ) suggests this metric may not be significant. However, the depth of the chlorophyll peaks were greater in the low-DOC lakes for both lake pairs (Figs. 6 and 7). Expressed as a ratio of  $\text{DCP:Z}_{\text{max}}$ , Jordan Pond and Seal Cove Pond were similar (mean =  $0.36$  and  $0.29$ ), whereas Bubble Pond had higher mean values than Witch Hole Pond (mean =  $0.76$  and  $0.31$ ,  $p < 0.001$ ).



**Figure 5:** Concentrations of chlorophyll *a* (Chl *a*), DOC, total phosphorus (TP), and dissolved inorganic nitrogen (DIN), and DIN:TP for three depths (epi-, meta-, hypolimnion), with samples pooled for each season; Winter ( $n = 1$  except in Bubble Pond), Spring ( $n = 2$ ), Summer ( $n = 4$ ), and Autumn ( $n = 4$ ). Light blue rectangles in DIN:TP plots span values from 1.5 and 3.4 which indicate N and P co-limitation, DIN:TP < 1.5 indicates N limitation, and DIN:TP > 3.4 indicates P limitation (Bergström et al., 2010).



**Figure 6:** Seasonal chlorophyll *a* fluorescence profiles (relative fluorescence units, RFU) with LOESS curves and chlorophyll *a* biomass (Chl *a*) on the right-hand side of each plot at sample depth. The upper 0.5 m of each profile was excluded from this analysis due to noise at the water surface in some profiles. Note that Witch Hole Pond has a different scale for Chl *a* (0-10  $\mu\text{g L}^{-1}$ ) than the other lakes (0-3  $\mu\text{g L}^{-1}$ ), and that Witch Hole Pond summer has different fChl scale (0-1000 RFU) than all other plots (0-400 RFU). Winter data not available for Bubble Pond.

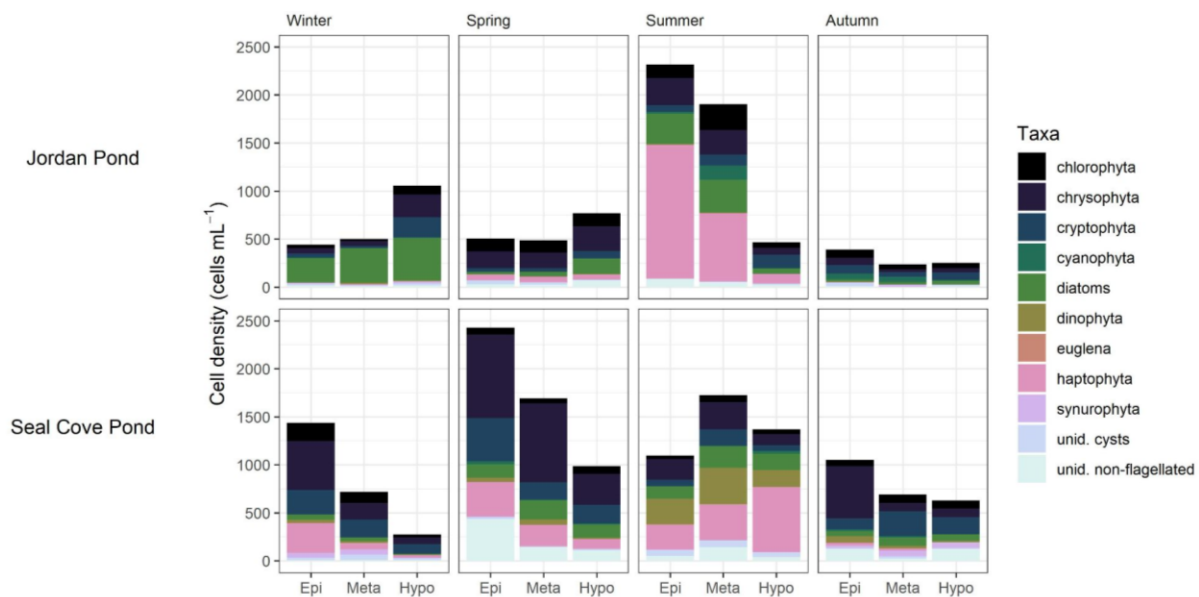


**Figure 7:** Mean chlorophyll *a* fluorescence (Chl *a* RFU) of 0.5-m profile contours on all sampling dates, indicated by vertical dashed lines. Mixing depth ( $Z_{\text{mix}}$ , gold triangle) and depth of 1% PAR ( $Z_{1\%PAR}$ , green inverted triangle) are also shown. Profiles from 25-Mar and 13-May for Seal Cove Pond and 13-May for Jordan Pond were included here but excluded from all other analyses and figures because profiles did not extend to maximum depths. The upper 0.5-m of each profile was excluded from this analysis due to noise at the surface in some profiles.

### 3.2.3 Phytoplankton community

In low-DOC Jordan Pond, phytoplankton cell density increased with depth under ice, with density at 20 m nearly two-fold of that at 1 m and 10 m (Fig. 8). This pattern occurred in the spring as well, although with lower overall cell density. The highest cell density occurred in the summer and the lowest in autumn, with greater densities in the surface samples than at lower depths for those seasons. The majority of phytoplankton under ice in Jordan Pond were diatoms, particularly *Rhizosolenia*, whereas chlorophytes and chrysophytes were dominant in the spring. Jordan Pond experienced a bloom of the haptophyte *Chrysochromulina* in the summer epi- and metalimnion, accompanied by the chlorophyte *Oocystis*, *Rhizosolenia*, and cyanobacterium *Aphanocapsa*. The three depths in autumn were similar and each had high evenness with no dominant taxa.

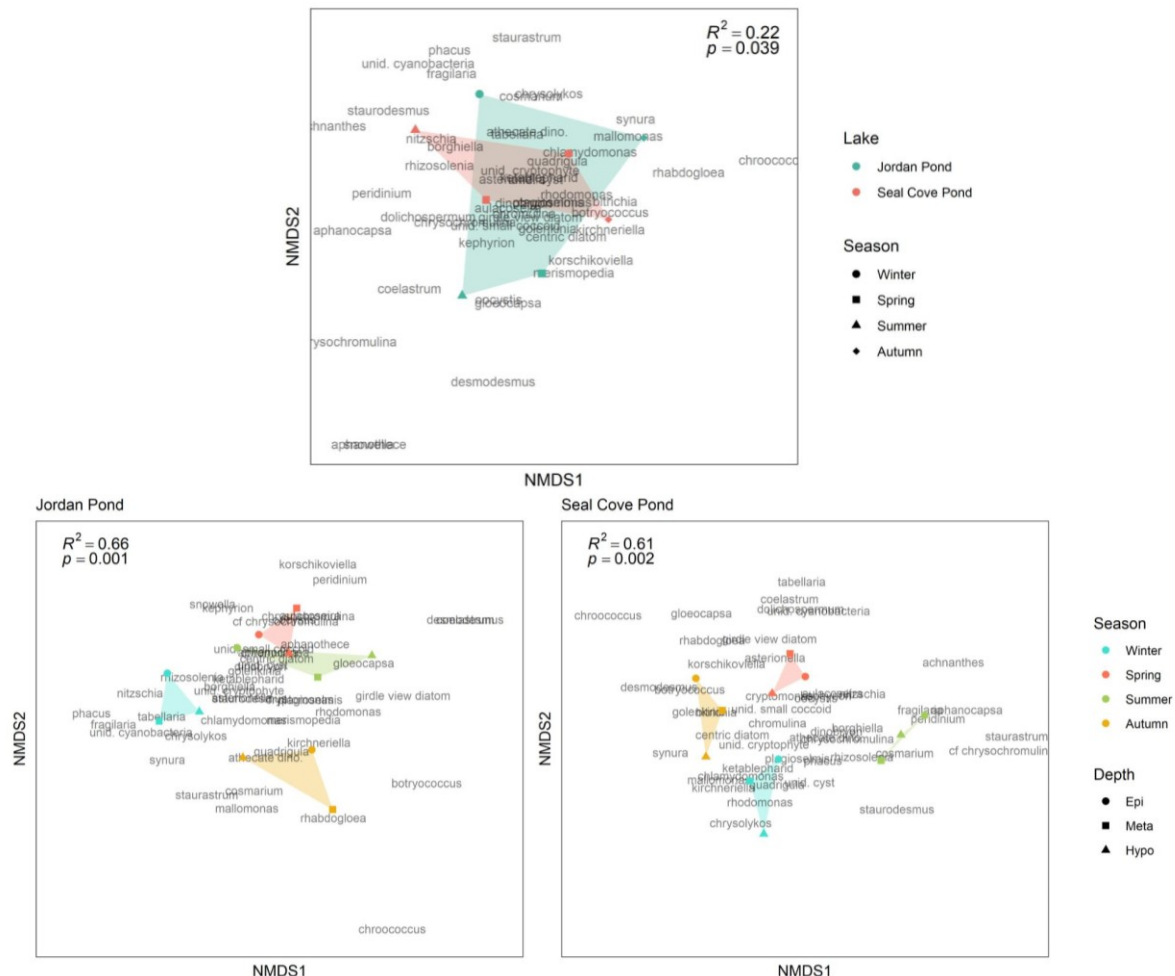
Moderate-DOC Seal Cove Pond had higher cell densities in surface waters in all seasons except summer, where densities were higher in the meta- and hypolimnion. The greatest cell density occurred in the spring epilimnion, and the lowest density during winter at the greatest depth. The under ice community had over 25 taxonomic groups present, with twice the cell density at 1 m than at 4 m depths. Chrysophytes, haptophytes, and cryptophytes had the highest densities in the 1 m under-ice sample, which persisted through spring turnover. The chrysophyte *Chromulina* dominated the spring water column, until blooms of *Chrysochromulina* and dinoflagellate



**Figure 8:** Phytoplankton community assemblages for three depths (epi-, meta-, and hypolimnion) on one date from each season (dates matching Fig. 6). Raw cell counts were converted to estimate cell density per ml. Unidentified cysts (unid. cysts) and unidentified non-flagellated taxa (unid. non-flagellated) also included.

*Borghiella* occurred alongside chrysophytes in the summer. Autumn phytoplankton community was similar to the winter community beneath the ice except for a slight increase in centric diatoms in the autumn.

Jordan Pond and Seal Cove Pond were somewhat distinct from one another when dates and vertical layers were grouped in the PERMANOVA model ( $r^2 = 0.22$ ,  $p = 0.053$ ) (Fig. 9). Morisita-Horn distances were larger between dates in Jordan Pond than in Seal Cove Pond, indicating greater differences of phytoplankton community composition over the season in Jordan Pond. Despite relatively low sample sizes, PERMANOVA tests were also performed on individual lakes; with dates ungrouped, seasonal dissimilarity was moderate for both Jordan Pond ( $r^2 = 0.66$ ,  $p = 0.001$ ) and Seal Cove Pond ( $r^2 = 0.61$ ,  $p = 0.002$ ).

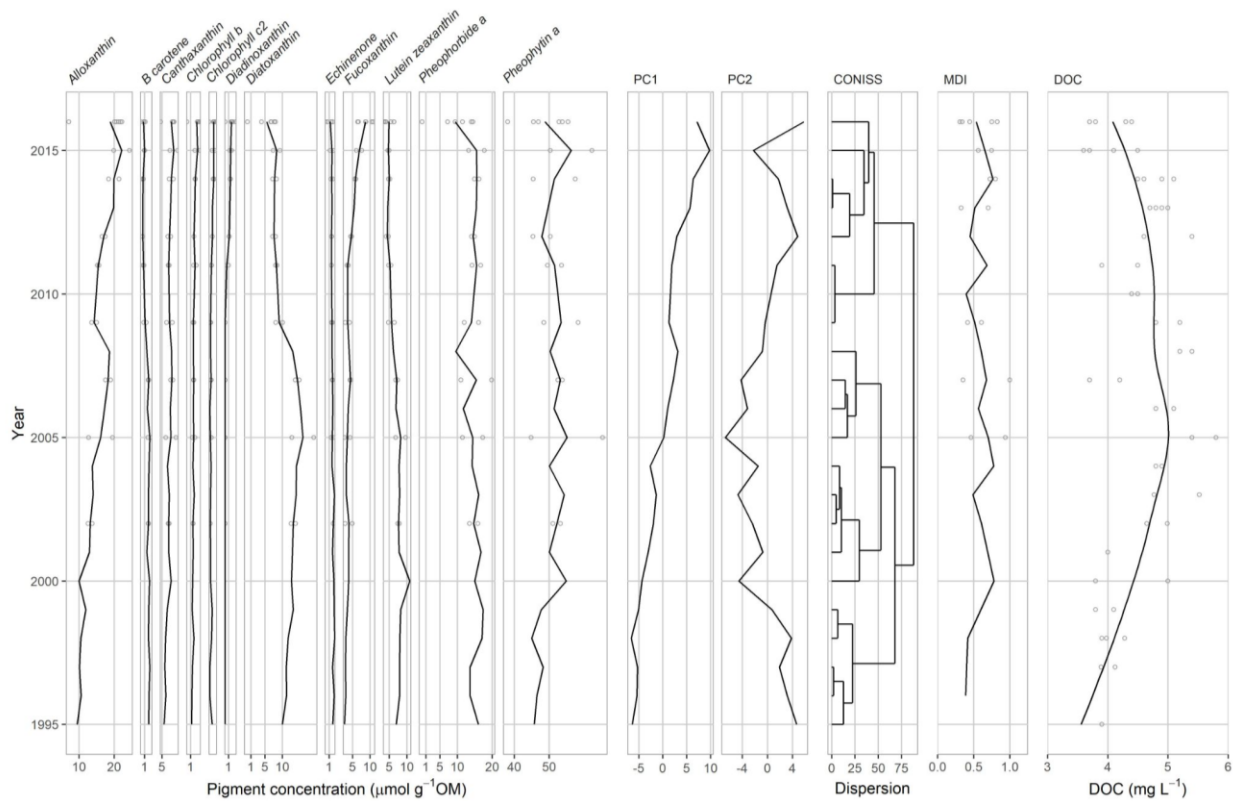


**Figure 9:** Non-metric multidimensional scaling of Morisita-Horn dissimilarity distances comparing phytoplankton communities of Jordan Pond and Seal Cove Pond. The top panel shows all four sample dates of both lakes where vertical layer samples are grouped together. The bottom panels show ungrouped layers from each sampling date for within-lake comparisons of phytoplankton community. Sample dates match those in fig. 6 and fig 8. PERMANOVA  $r^2$  and  $p$  values included on each plot to show similarity between groups.



### 3.3 Seal Cove Pond sediment core

From 1995 to 2016, concentrations of alloxanthin (cryptophytes), canthaxanthin (cyanobacteria), and fucoxanthin (phaeophyceae, diatoms, other heterokonts) all generally increased, while lutein-zeaxanthin (chlorophytes, cyanobacteria) decreased (Fig. 10). Between 2005 and 2010, diatoxanthin (diatoms) decreased by 52% and lutein zeaxanthin decreased by 63%. These decreases were reflected in the cluster analysis, which shows the largest dispersion of algal pigments occurring between 2005-2010. PCA scores were moderate predictors of pigment variance, with 51% variance explained by PCA Axis 1, and 80% explained by PCA Axis 1 and Axis 2 combined. PC Axis 1 and DOC concentration were not correlated ( $r^2 = 0.16$ ,  $p > 0.1$ ) but PC Axis 2 and DOC were somewhat negatively correlated ( $r^2 = -0.38$ ,  $p = 0.09$ ). MDI increased slightly from 0.39 to 0.54 from 1995-2016 with high variance ranging from 0.39 in 1996 to 0.78 in 2000. MDI and DOC were not correlated ( $r^2 = 0.03$ ,  $p > 0.1$ ).



**Figure 10:** Pigment concentrations in Seal Cove Pond sediment core spanning 1995-2016. Vertical lines represent mean yearly values for pigments and mixing depth index (MDI); without determining the date of each subsample beyond year, values belonging to the same year could not be plotted vertically (time axis) and were instead plotted horizontally (concentration axis). DOC concentration was plotted similarly, with monthly values instead plotted as points for each year, and the trend was fitted with a LOESS smoothed curve. Results of PCA Axis 1 and Axis 2 (PC1, PC2) and clustering analysis (CONISS) are included.

## CHAPTER 4

### DISCUSSION

#### *Higher stability of vertical gradients in low-DOC lakes, but greater community turnover*

Differences in phytoplankton biomass and community structure were observed between lakes with low but varying DOC concentrations. Low-DOC lakes had lower temporal variability of vertical habitat gradients including thermal stability, mixing depth, oxygen concentration, and light attenuation, as well as more homogenous vertical distributions of chlorophyll *a* fluorescence profiles and chlorophyll *a* biomass at three depths. These findings contrast my first prediction that low-DOC lakes would have greater seasonal heterogeneity of vertical habitat gradients over the 2020 sampling season than moderate-DOC lakes. This finding differs from other studies where darker, higher-DOC lakes had greater stability in thermal structure (Longhi & Beisner, 2009; Snucins & Gunn, 2000), light attenuation (Williamson et al., 2015), and oxygen concentration (Williamson et al., 2015; Knoll et al., 2018). However, my observation of greater stability of Chl *a* concentrations and vertical distribution in the low-DOC lakes is consistent with previous surveys and whole-lake manipulations (Longhi & Beisner, 2009; Lofton et al., 2020; Christensen et al., 1996). Also in agreement with others, I observed that algal biomass was more concentrated in the epilimnion or metalimnion in the higher DOC lakes which resulted in larger, more narrow peaks of chlorophyll, whereas low-DOC lakes had lower total biomass overall but deeper chlorophyll peaks that often extended into the hypolimnion and spanned a larger range of depths (Carpenter & Pace 2018; Leach et al., 2017). More narrow Chl *a* peaks in the moderate-DOC lakes (Fig. 6) suggests that phytoplankton face constraints on the availability of suitable habitat above or below the DCP, especially during the height of summer stratification, likely due to a combination of temperature, nutrient availability, and predation (Leach et al., 2017; Lofton et al., 2020; Girdner et al., 2020).

While algal biomass and DCPs were more variable in the moderate-DOC lakes, I found that phytoplankton community composition was more variable over the season in low-DOC Jordan Pond than in moderate-DOC Seal Cove Pond, in agreement with my second prediction. Greater seasonal heterogeneity of phytoplankton communities in the clearer lake is consistent with previous studies, albeit at higher DOC concentrations than in this study (Longhi & Beisner, 2009; Deiningner et al., 2017). Winter phytoplankton communities were especially

different between the two lakes, where phytoplankton biomass increased with depth in Jordan Pond but decreased in Seal Cove Pond, likely due to differences in nutrient and light availability, and grazing pressure (Hrycik & Stockwell, 2021). However, vertical gradients in community structure remained similar across seasons in Seal Cove Pond while Jordan Pond did not. The discrepancy of higher phytoplankton turnover in Jordan Pond despite higher stability of vertical habitat gradients may be reconciled by low sample size, large differences in mean and maximum depth between Jordan Pond and Seal Cove Pond, or chemical characteristics. N and P are major drivers of phytoplankton structure and composition in boreal lakes, particularly when considering the nutrient limitation patterns of each lake (Daggett et al., 2015; Bergström & Karlsson, 2019). For example, the summer haptophyte bloom in Jordan Pond was accompanied by phosphorus decreasing below detection limit and the highest DIN:TP ratio of the season, indicating P-limitation (Bergström, 2010). Jordan Pond was P-limited for most of the sampling period, while Seal Cove Pond was primarily co-limited by N and P. Phytoplankton biomass is clearly controlled by nutrients and DOC to varying extents depending on lake trophic status and nutrient limitation patterns (Leach et al., 2019; Daggett et al., 2015; Bergström & Karlsson, 2019).

Previous studies of vertical habitat gradients note the absence of phytoplankton taxonomy data entirely (Longhi & Beisner, 2009; Williamson et al., 2015; Christensen et al., 1996) or lack of samples from multiple depths other than the mixed layer (Lofton et al., 2020; Klug & Cottingham, 2001). These studies instead rely on fluorescence spectra of algal pigments and/or extracted chlorophyll *a* biomass to characterize phytoplankton dynamics. In this study, I used a combination of chlorophyll *a* fluorescence profiles, extracted biomass for all lake profiles from three depths, and phytoplankton cell counts for two lakes from each season at three depths. This approach allowed us to find that phytoplankton diversity and total algal biomass responded differently to concomitant environmental drivers (Weyhenmeyer et al., 2013). For phytoplankton biomass to remain lower and more stable throughout the season in the low-DOC lake while undergoing higher turnover than the higher-DOC lake suggests that small changes in nutrient and light availability are more impactful on community composition at lower DOC concentrations. Higher species turnover in the low-DOC lake may be explained by the slight decrease of nutrients that occurred during the summer. Nutrient depletion (N and P, other essential nutrients) favors certain taxa over others on the basis of their functional traits, as does light deficiency, temperature fluctuation, and mixing (Girdner et al., 2020; Reynolds, 2006). Functional traits, particularly trophic mode, are linked to resource

limitation; lower nutrient levels can favor mixotrophic taxa like dinoflagellates and other buoyancy regulating taxa that are able to compete for nutrients, engulf smaller algae, and generally maintain similar chlorophyll *a* concentrations (Girdner et al., 2020; Reynolds, 2006). Decreases in N favors diazotrophs (N-fixing taxa) like cyanobacteria (Litchman et al., 2015) while N increases favor mixotrophs (Deininger et al., 2017), providing another link between trophic mode and nutrient cycling, and more specifically through N-deposition (Litchman et al., 2015; Daggett et al., 2015).

*Does DOC explain long-term trends in vertical habitat gradients and phytoplankton communities?*

I predicted that long-term trends of DOC concentration would correlate with trends in water clarity, thermal structure, and phytoplankton communities. The major period of inflection in both the long-term data and the sediment record occurred between 2005 and 2010, where diatoxanthin and lutein zeaxanthin pigment concentrations decreased by 50% or more (Fig. 10), while DOC concentrations decreased in three out of four lakes (Fig. 2A). DOC concentration was directly related to changes in water clarity (Fig. 2B) in agreement with previous studies of ANP lakes (Roesler & Culbertson, 2016), and the pigment decreases were reflected in the cluster analysis as well as in PC Axis 2 which showed a moderate negative correlation with DOC concentration. However, DOC and diatom-inferred mixing depth were not correlated, suggesting that DOC had a larger effect on light environment than on mixing depth in Seal Cove Pond. Water clarity was therefore a major driver of phytoplankton community based on the relationship between water clarity, DOC, and pigment assemblages, while mixing depth may have been controlled primarily by wind speed (Strock et al., 2019). The timeframes of pigment and diatom assemblages were truncated in 1995 to match the long-term dataset for DOC concentration, but the oldest sediment sections dated to 1861. Without reliable DOC data before 1995, I could not extend my long-term analysis prior to 1995. With a longer time series I may have seen similar trends as previous studies where DOC was related to thermal structure (Brown et al., 2017; Strock et al., 2017; Williamson et al., 2015). An additional option would be employing the predictive model described by Roesler and Culbertson (2016) that estimates DOC concentrations from Secchi depth.

## *Conclusions*

It is likely that the combined effects of DOC concentration, nutrient availability, and light environment were responsible for structuring phytoplankton habitats across the study lakes throughout the season and over the last two decades. Differences in vertical habitat gradients between low- and moderate-DOC lakes elicited unique phytoplankton community characteristics that varied from under ice through fall turnover, with slightly greater seasonal heterogeneity of phytoplankton community in low-DOC Jordan Pond. The low-DOC lake had more dynamic phytoplankton community structure than vertical habitat gradients as measured in this study, but there is suitable evidence to claim that low-DOC lakes are more sensitive to changes in environmental drivers, signified by higher phytoplankton turnover. Williamson et al. (1996) also suggested an increased sensitivity to even small fluctuations in light attenuation for lakes with DOC concentrations below  $2 \text{ mg L}^{-1}$ , and the evidence presented here supports this prediction.

There are several consequences of the higher sensitivity of low DOC lakes, namely the potential impact on water quality. Jordan Pond and Bubble Pond are both sources of drinking water, and 48% of public drinking water in Maine is sourced from just 45 lakes (<https://www.maine.gov/dhhs/mecdc/environmental-health/dwp/consumers/surfaceWater.shtml>). Increases in DOC concentration can directly impair drinking water quality (Ledesma et al., 2012, Warner & Saros, 2019). Generally, lakes integrate physical, chemical, and biological signals from upstream water bodies, but also from the airshed and watershed. As indicators of change for a multitude of ecosystems, studying lakes can allow scientists and managers to understand and predict future challenges (Williamson et al., 2009). Lakes are sensitive to internal and external forces, low-DOC lakes especially so, indicating that drinking water management will be especially challenging as extreme precipitation events have been occurring more frequently in the northeastern United States in recent decades (Howarth et al., 2019). Drinking water treatment would require more chemical treatment to reach legislated drinking water standards (Kritzberg et al., 2020).

Pronounced differences between the vertical habitat gradients and phytoplankton community structures of lakes ranging in DOC concentration from  $2\text{-}4 \text{ mg L}^{-1}$  suggests that small differences in or changes to DOC concentration can lead to substantial ecological consequences. Nutrient cycling, thermal structure, and other environmental drivers directly or indirectly related to DOC concentration elicit significant changes to both

phytoplankton community and habitat structure, particularly at lower DOC concentrations, and the greater sensitivity of these lakes has important implications for broader ecosystem processes.

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