

Assessing spatial patterns and temporal trends in lake response to rapid permafrost thaw in the Scotty Creek basin

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Abstract

Aquatic ecosystems at the southern limit of permafrost are highly sensitive to climate warming, including dramatic alterations of the landscape resulting from thawing of permafrost. In the southern Northwest Territories (NT), permafrost is typically restricted to forested peat plateaus, that are elevated above the surrounding wetland complex. As mean annual air temperatures approach 0°C, permafrost thaw can result in collapsed peat plateaus and waterlogged trees. These landscape changes can alter the connections between water bodies and the amount of terrestrial organic matter that enters these ecosystems, potentially contributing to the “browning” of lakes. Understanding how lakes in the southern NT have been responding to the acceleration of permafrost degradation is challenged by the scarcity of monitoring records. The Scotty Creek basin, southern NT, is an ideal location to study linkages among shallow lake limnology, landscape hydrology, and landscape change in thawing permafrost peatlands as three decades of field research has provided a unique long-term perspective on watershed changes rarely available for remote regions. For this dissertation, paleolimnological methods were applied to indirectly reconstruct long-term environmental change, using chemical and biological proxy data preserved in lake sediments from lakes in or near the Scotty Creek basin. Modern diatom ecology was assessed to improve diatom-based paleolimnological inferences of changes over time, and applied in a multi-proxy paleolimnological approach to investigate regional lake ecosystem changes over the past few hundred years. Two key findings emerged from the research: (1) dissolved organic carbon (DOC) quality, rather than DOC quantity, was a key driver of spatio-temporal variability in lake change; and (2) most lakes experienced only modest changes despite the widespread prevalence of permafrost degradation. This research presents a necessary step for integrating lakes into the ecohydrological research network at the Scotty Creek Research Station.

For Maddy

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Table of Contents

Abstract	ii
Dedication	iii
Acknowledgements	iv
Table of Contents	vi
List of Tables	x
List of Figures	xi
Acronyms	xvi
Chapter 1: General Introduction	1
Permafrost thaw in discontinuous permafrost peatlands	1
Impacts of permafrost thaw on dissolved organic carbon in lakes	3
Paleolimnological insights into thawing discontinuous permafrost peatlands.....	5
The Scotty Creek Research Station	7
Dissertation Goals and Objectives	8
Chapter 2: Limnology and diatom ecology of shallow lakes in a rapidly thawing discontinuous permafrost peatland.....	11
Abstract	12
Introduction	13
Methods	16
Field methods	16

Water chemistry analyses	18
Physical Landscape Characterization	19
Subfossil Diatom Analysis	20
Data Analysis.....	20
Results	23
High Temporal Resolution Assessment of Goose Lake and First Lake.....	23
Characterization of aquatic ecosystems in the Scotty Creek Basin.....	24
Diatom communities.....	26
Discussion	29
Seasonal temperature and oxygen dynamics in Goose Lake and First Lake.....	29
Spatial patterns in lake water chemistry	31
Diatom ecology in permafrost wetlands and lakes of the Scotty Creek basin	32
Tables	35
Acknowledgements	45
Chapter 3: Divergent trajectories of ecological change in shallow thermokarst lakes of a rapidly thawing discontinuous permafrost peatland.....	46
Abstract	47
Introduction	48
Methods.....	51
Study site description.....	51

Core collection and dating	52
Diatom preparation and analysis	52
Diatom species data analyses	53
Results and Discussion.....	54
Core chronologies.....	54
Diatom-inferred lake change	54
Conclusions and Future Directions	62
Tables	63
Figures	65
Chapter 4: Examining trajectories of ecological change in five small lakes along a gradient of hydrological connectivity in a rapidly thawing discontinuous permafrost peatland	70
Abstract	71
Introduction	72
Methods.....	76
Site Description	76
Core collection and chronology establishment.....	77
Sedimentary analyses	78
Results	79
Sediment core chronologies.....	79
Diatom and elemental/isotopic analyses.....	80

Discussion	86
Goose Lake (hydrologically well-connected, headwater lake)	86
First Lake (hydrologically well-connected, second lake in the cascade)	89
Next Lake (hydrologically well-connected, last lake in cascade)	92
SC5 (hydrologically isolated).....	92
SC8 (hydrologically isolated).....	94
Conclusion.....	96
Tables	98
Figures	99
Chapter 5: General Conclusions	110
References	115
Appendices.....	136

List of Tables

Table 2.1: Physical characteristics and modern water chemistry statistics for 16 lakes in the Scotty Creek and surrounding basins, collected July 2018.

Table 2.2: Spearman's correlation coefficients of water chemistry variables and physical lake characteristics for 16 lakes in the Scotty Creek basin. * $p < 0.05$, ** $p < 0.01$

Table 2.3: Dominant diatom species identified in lake substrate samples. Percentage of chrysophyte cysts and protozoan plates, in relation to diatom valves, also included.

Table 3.1: Physical characteristics and modern water chemistry statistics for 15 lakes in the Scotty Creek and surrounding basins, collected July 2018.

Table 3.2: Table 2: Lake depth, lake area, dissolved organic carbon (DOC) concentrations, and true colour of 15 lakes in the Scotty Creek and surrounding basins, collected July 2018.

Table 4.1: Modern water chemistry of 5 lakes in the Scotty Creek basin, collected July 2018.

List of Figures

Figure 2.1: Map of study area. (A) Approximate location of site within Canada, (B) approximate location of site within Taiga Plains ecozone, (C) location of all study lakes, (D) Enlarged map of study lakes highlighted in (C) and includes wetland sample sites (white dots). Yellow markers are locations of data loggers.

Figure 2.2: Lake depth, temperature, dissolved oxygen and light absorption recorded every 30 minutes from June 7th to August 22nd 2019 from Goose Lake's north basin (A), Goose Lake's main basin (B) and First Lake (C). Precipitation data was recorded from Pluvio totalizing station located near Goose Lake.

Figure 2.3: Land classifications of the Scotty Creek basin based on classifications established in Chasmer et al. 2014. 250 m buffer zones are added to each lake, with the bog and fen environments within the buffer zones shown in red and yellow, respectively. Inset shows an example of the 250 m buffer zone around lake SC3, in detail.

Figure 2.4: Principal components analysis (PCA) of select water chemistry variables and physical characteristics of 16 shallow lakes in the Scotty Creek basin (A) and select water chemistry variables and areal proportion of collapse scar environment (Bog250m) and fen environment (Fen250m) within 250 m of lakes shorelines for 9 lakes included in landscape classification analyses (B). Dashed lines represent variables plotted passively. Area = lake area, D_L = shoreline development index.

Figure 2.5: Relative abundance diagram displaying the most common diatom taxa in the modern sediments retrieved from 16 shallow lakes in the Scotty creek and neighbouring basins. Species were grouped based on similar ecology. Species or ecological groups present at less than 2%

relative abundance were removed. Lakes were ordered using diatom PCA axes scores. Ratio of chrysophyte cysts to diatom valves and protozoan plates to diatom valves are also displayed.

Figure 2.6: Redundancy analysis (RDA) ordination triplot illustrating relationships between diatom species and environmental variables. Environmental variables are represented by arrows. Lake sites are in black. Diatoms species codes (red) are listed in Appendix A.

Figure 2.7: Ground-level photographs of wetland sites and corresponding list of dominant diatom species identified in a sample retrieved from the site. Percentage of chrysophyte cysts and protozoan plates, in relation to diatom valves, are also listed.

Figure 3.1: Map of study area. (A) Approximate location of site within Canada, (B) approximate location of site within Taiga Plains ecozone, (C) location of all study lakes in the Scotty Creek and neighbouring basins.

Figure 3.2: (A) Principal components analysis (PCA) biplot of diatom species in 15 shallow lakes in the Scotty Creek basin across three different time periods (~1850, ~1950, ~2018). Species names and vectors were removed the ordination to highlight the degree and direction of change in species composition between ~1850-1950 and ~1950-2018 for each lake. (B) Enlarged section of the ordination highlighted in (A).

Figure 3.3: Relative abundance diagram displaying the most common diatom taxa in three time periods (~1850, ~1950, and 2018) from 15 shallow lakes in the Scotty creek and neighbouring basins. Species were grouped based on similar ecology. Species or ecological groups present at less than 2% relative abundance were removed

Figure 3.4: Scatterplots with 1:1 line showing changes in A) Small *Navicula* species (*sensu lato*); B) Small benthic *Fragilaria* species (*sensu lato*); C) *Encyonopsis* species; D) Large

Navicula species; and E) Planktonic species, between ~1850 and ~1950 (left), and ~1950 and 2018 (right)

Figure 4.1: Map of study area. (A) Approximate location of site within Canada, (B) approximate location of site within Taiga Plains ecozone, (C) location of all study lakes: Goose Lake, First Lake, Next Lake, SC5, and SC8.

Figure 4.2: Relative abundance diagram for Goose Lake, displaying the most common diatom species. Species were grouped based on similar ecology. Species or ecological groups present at less than 2% relative abundance were removed. Hills N2 diversity scores, ratio of chrysophyte cysts to diatom valves and protozoan plates to diatom valves are also displayed. Horizontal red lines delineate diatom biostratigraphic zones.

Figure 4.3: Relative abundance diagrams of total mercury (Hg), stable isotopes of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$), and elemental ratios of organic carbon to nitrogen (C/N) for Goose Lake.

PCA values were calculated from diatom species assemblages displayed in Figure 4.2.

Horizontal red lines delineate diatom biostratigraphic zones.

Figure 4.4: Relative abundance diagram for First Lake, displaying the most common diatom species. Species were grouped based on similar ecology. Species or ecological groups present at less than 2% relative abundance were removed. Hills N2 diversity scores, ratio of chrysophyte cysts to diatom valves and protozoan plates to diatom valves are also displayed. Horizontal red lines delineate diatom biostratigraphic zones.

Figure 4.5: Relative abundance diagrams of total mercury (Hg), stable isotopes of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$), and elemental ratios of organic carbon to nitrogen (C/N) for First Lake.

PCA values were calculated from diatom species assemblages displayed in Figure 4.4.

Horizontal red lines delineate diatom biostratigraphic zones.

Figure 4.6: Relative abundance diagram for Next Lake, displaying the most common diatom species. Species were grouped based on similar ecology. Species or ecological groups present at less than 2% relative abundance were removed. Hills N2 diversity scores, ratio of chrysophyte cysts to diatom valves and protozoan plates to diatom valves are also displayed. Horizontal red lines delineate diatom biostratigraphic zones.

Figure 4.7: Relative abundance diagrams of total mercury (Hg), stable isotopes of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$), and elemental ratios of organic carbon to nitrogen (C/N) for Next Lake.

PCA values were calculated from diatom species assemblages displayed in Figure 4.6.

Horizontal red lines delineate diatom biostratigraphic zones.

Figure 4.8: Relative abundance diagram for SC5, displaying the most common diatom species.

Species were grouped based on similar ecology. Species or ecological groups present at less than 2% relative abundance were removed. Hills N2 diversity scores, ratio of chrysophyte cysts to diatom valves and protozoan plates to diatom valves are also displayed. Horizontal red lines delineate diatom biostratigraphic zones.

Figure 4.9: Relative abundance diagrams of total mercury (Hg), stable isotopes of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$), and elemental ratios of organic carbon to nitrogen (C/N) for study lake SC5.

PCA values were calculated from diatom species assemblages displayed in Figure 4.8.

Horizontal red lines delineate diatom biostratigraphic zones.

Figure 4.10: Relative abundance diagram for SC8, displaying the most common diatom species. Species were grouped based on similar ecology. Species or ecological groups present at less than 2% relative abundance were removed. Hills N2 diversity scores, ratio of chrysophyte cysts to diatom valves and protozoan plates to diatom valves are also displayed. Horizontal red lines delineate diatom biostratigraphic zones.

Figure 4.11: Relative abundance diagrams of total mercury (Hg), stable isotopes of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$), and elemental ratios of organic carbon to nitrogen (C/N) for study lake SC8. PCA values were calculated from diatom species assemblages displayed in Figure 4.10. Horizontal red lines delineate diatom biostratigraphic zones.

Acronyms

CONISS: CONstrained Incremental Sum of Squares

D_L: Shoreline development ratio

DO: Dissolved oxygen

ICP-OES: Inductively Coupled Plasma – Optical Emissions Spectroscopy

ICP-MS: Inductively Coupled Plasma – Mass spectrometry

DOC: dissolved organic carbon

LTER: Long-term ecological research

NWT: Northwest Territories

PCA: Principal components analysis

RDA: Redundancy analysis

TCU: True colour units

THg: Total Mercury

TN: Total nitrogen

TP: Total phosphorus

VIF: Variance inflation factor

Chapter 1: General Introduction

Permafrost thaw in discontinuous permafrost peatlands

Sporadic discontinuous permafrost peatlands (i.e., permafrost underlies 10-50% of land area) are highly vulnerable to irreversible thaw as mean annual air temperatures approach a critical threshold of 0°C (Carpino et al., 2021; Quinton et al., 2019; Wright et al., 2022). Significant losses in geographic extent of discontinuous permafrost peatlands are predicted by 2060, with some models suggesting that tipping points may have already been reached for the southern-most permafrost peatlands (ICCI, 2022). Throughout the Holocene, permafrost aggradation and degradation in discontinuous permafrost peatlands has occurred as part of a natural cyclical process taking place over centennial to millennial timescales, driven by changes in hydrology, autogenic succession, and forest fire (Olefeldt, et al., 2021a; Zoltai, 1993). As air temperatures continue to warm in response to anthropogenic climate change, degradation will outpace aggradation, leading to a net decrease in permafrost extent (Swindles et al., 2015). The loss of permafrost has already resulted in pronounced changes to discontinuous permafrost peatland landscapes (Carpino et al., 2021; Chasmer & Hopkinson, 2017; Quinton et al., 2019; Wright et al., 2022).

Discontinuous permafrost peatland landscapes are a mosaic of peat plateaus, channel fens, and bogs (also called collapse scars), interspersed with mineral uplands and numerous small, shallow lakes. Permafrost is typically restricted to forested (black spruce, *picea mariana*) peat plateaus that are slightly elevated (~1 meter) above the surrounding wetland complex due to the presence of ground ice. Peat plateaus act as run-off generators, while the primary role of bogs is water storage (although they can also be ephemerally connected to other wetlands) and channel fens transmit water to the drainage outlet and therefore influence the surface water connectivity of the

landscape (Connon et al., 2015; Hayashi et al., 2004). Ground subsidence caused by the thawing of permafrost leads to the development of small permafrost collapse scars as forested plateaus become waterlogged and are converted from forest into wetland. Discontinuous permafrost peatland landscapes are becoming increasingly interconnected hydrologically as a result of the development of taliks (perennially unfrozen ground) and channel fen development due to permafrost thaw. However, this may be a transient stage only, as thaw may eventually lead to landscape drainage as the number and depth of flow paths increases, followed by the establishment of permafrost-free forests (Carpino et al., 2021; Chasmer & Hopkinson, 2017; Devoie et al., 2019). Forest fires, which are becoming more frequent and severe in response to climate change, can accelerate the loss of permafrost (Coleman et al., 2015; Connon et al., 2018; Devoie et al., 2019; Gibson et al., 2018; Robinson & Moore, 2000; Yoshikawa et al., 2002).

The rapid thawing of permafrost and subsequent alteration of hydrological pathways has the potential to mobilize large reserves of previously frozen terrestrial organic matter into downstream waterbodies. This has substantial implications for surface water quality and aquatic ecosystem function, including the small, shallow permafrost peatland lakes that are abundant across the landscape, and represent ~18% of total lake area in boreal and tundra landscapes across the circumpolar North (Olefeldt et al., 2021b). Small, shallow lakes are important sites for the active processing of carbon, capable of both emitting and sequestering carbon mobilized from thawing permafrost, as well as acting as links to downstream waterbodies for connected lakes (Cole et al., 2007). Historically, inland waters have been ignored in estimations of carbon budgets, and small lakes and wetlands continue to be underrepresented in the scientific literature despite their abundance and importance for global biogeochemical cycling (Cole et al., 2007; Jones et al., 2017; Tranvik et al., 2009).

Impacts of permafrost thaw on dissolved organic carbon in lakes

Landcover and hydrological connectivity exert important controls over the quality and quantity of materials (e.g. carbon, nutrients, mercury) that are exported from the terrestrial environment into aquatic ecosystems. Dissolved organic carbon (DOC) is of particular concern, due to the important role DOC plays in carbon and mercury biogeochemical cycling at local to global scales, and as a key control on aquatic ecosystem function (Olefeldt, et al., 2021b; Vonk et al., 2015). DOC is operationally defined as the fraction of organic carbon that passes through a filter, typically with a pore size of 0.45 μm (Pagano et al., 2014). The DOC pool in aquatic ecosystems represents a complex mixture of aliphatic (open-chain) and aromatic (unsaturated ring) organic carbon molecules that vary in their reactivity and susceptibility to transformation (He et al., 2016; Pagano et al., 2014). The composition (i.e. “quality”) of the aquatic DOC pool reflects the predominant sources (e.g. autochthonous vs allochthonous) of DOC, and how it is processed (e.g. photo-oxidation, microbial degradation). Autochthonous (i.e. aquatic) DOC sources are produced within lakes, and are typically labile. Allochthonous (i.e. terrestrial) DOC sources typically have higher aromaticity, which produces the yellow-reddish colour often associated with high DOC waters (Pagano et al., 2014). Increases in allochthonous DOC transport to lakes has been associated with “lake browning”, a darkening of waters of impacted lakes that has been documented across the northern hemisphere in response to a variety of external forcings (Coleman et al., 2015; Pagano et al., 2014; Wauthy et al., 2018).

Climate change can impact the composition of materials exported to lakes through several avenues, creating challenges in predicting how lakes will respond with continued warming. For example, as permafrost thaws, terrestrial organic matter previously stored in frozen soils is released and becomes available for transport into aquatic ecosystems. The composition of

permafrost soils widely varies, from highly organic soils to soils with a high mineral content, which directly influences the composition of materials exported through the catchment and into lakes. Additionally, as peat plateaus collapse and transition to fens, the hydrologic connectivity of the landscape increases (Connon et al., 2014), drastically altering land-to-lake linkages. For example, water stored in bogs typically had higher aromatic DOC, and therefore higher colour (Olefeldt et al. 2012; personal observation). The connection of previously isolated bogs to the channel fen network that has been documented to occur following permafrost thaw (referred to as ‘bog capture’; Connon et al., 2014) has the potential to increase the export of highly-coloured water to connected lakes. Increasing active layer depth can also influence DOC composition, as deepening flow paths can put flowing water in contact with more humified, and therefore more aromatic carbon (Burd et al., 2018). Finally, lake residence time (the average time water spends in a lake) can impact DOC composition, as this influences the time that DOC is exposed to solar radiation (leading to photobleaching and colour reduction), microbial degradation (reducing the DOC pool), and/or evaporative concentration of DOC (Kothawala et al., 2014; Lindell et al., 2000; Molot & Dillon, 1997).

An added consequence of DOC mobilization is the potential for transport of contaminants bound within the organic matrix that enter lakes along with DOC. Mercury has been accumulating in permafrost soils over millennia, and can be released to waterbodies along with carbon as the permafrost thaws (Obrist et al., 2017; Schuster et al., 2018). Several studies have found evidence that links increased mercury export to thawing permafrost (Klaminder et al., 2008; Korosi et al., 2015; Rydberg et al., 2010). For example, a thawing palsamire had notably lower mercury concentrations in a thawing permafrost peat hummock that was inundated by water compared to a nearby non-degrading hummock, indicating that mercury was leaching from the thawing

hummock (Klaminder et al., 2008). Dated lake sediment cores from Sweden and the Northwest Territories documented a high correlation between inferred terrestrial matter and mercury concentrations, suggesting a terrestrial export of mercury from soils is the primary control on mercury in lake sediments (Korosi et al., 2015; Rydberg et al., 2010). Peatlands are hotspots for the microbial transformation of mercury into its highly toxic methylmercury form (Gordon et al., 2016; Wright et al., 2022); although there is some evidence to indicate that small lakes may act as sites for mercury demethylation (Thompson et al., 2023).

High concentrations of coloured DOC have been observed in lakes affected by permafrost thaw, indicating that permafrost degradation may lead to widespread lake browning (Wauthy et al., 2018). However, a paucity of long-term data available across northern regions limits our ability to assess how permafrost thaw is altering lake water quality, including DOC, as permafrost landscape heterogeneity and complex hydrological responses to thaw make it challenging to make predictions about future changes. Indirect methods involving the use of paleoenvironmental archives are critical for addressing knowledge gaps regarding trajectories of change.

Paleolimnological insights into thawing discontinuous permafrost peatlands

Paleolimnology is the science that uses chemical, physical, and biological proxy data preserved in lake sediments to reconstruct environmental change (Smol, 2008). Paleolimnology has made important contributions to our understanding of the nature of permafrost, rates of change, and associated water quality and ecological changes (Bouchard et al., 2017; Korosi et al., 2022).

Among the bioindicators, the diatoms (unicellular algae of the Class Bacillariophyceae) with are particularly useful for studying the effects of climate change on lakes, due to high species

diversity and well characterized species-environment relationships (Smol, 2008). Diatoms have been shown to be useful for tracking changes in benthic habitat, water depth, length of the ice-free season, thermal stratification, and water quality variables such as pH and chromophoric (i.e. coloured) DOC (Coleman et al., 2015; Hargan et al., 2015; Michelutti et al., 2003; Pienitz & Smol, 1993).

High concentrations of coloured DOC have been observed in lakes in permafrost thaw-affected catchments across the circumpolar north, suggesting a link between permafrost degradation and lake browning (Wauthy et al., 2018), but this is based on spatial trends with limited long-term data to support it. My MSc research used paleolimnological methods to reconstruct environmental change over the last several hundred years in two small lakes in sporadic discontinuous permafrost peatlands near Kakisa, Northwest Territories, Canada (Coleman et al., 2015). Remotely-sensed images indicated that substantial permafrost thaw had been extensive in both lake catchments since 1950, yet only one lake recorded recent increases in chromophoric DOC based on diatom subfossil assemblage changes (Coleman et al., 2015). The increase in DOC began prior to the availability of remotely sensed imagery, and followed a sedimentary charcoal peak indicating a fire event (Coleman et al., 2015). Diatom-inferred DOC increases corresponded to an increase in lignin-derived phenols from terrestrial carbon sources (Korosi et al., 2015). Divergent trends in lakes in close proximity was also documented in a paleolimnological study of two subarctic lakes in Sweden, where diatom assemblages in one lake appeared to be responding to changes in terrestrial organic carbon, while organic carbon and diatom assemblages remained relatively stable in the other lake (Rosén et al., 2009). The difference in response of the Swedish lakes was attributed to differences in catchment

hydrological connectivity and complex interactions between several climate-related variables (Rosén et al., 2009).

While I identified hydrological connectivity as a potential explanation for the divergent trends in the two study lakes near Kakisa, NT, from my MSc, no hydrological data was available for the lake catchments to explore the role of hydrological connectivity in more detail. The Scotty Creek Research Station is located ~300 km northwest of Kakisa, and has been a site of long-term, field-based ecohydrological research going back decades (Quinton et al., 2019; Wright et al., 2022). Much of our understanding of the impacts of permafrost thaw on discontinuous permafrost peatland hydrology has come from research conducted at the Scotty Creek Research Station (Carpino et al., 2021; Quinton et al., 2019; Wright et al., 2022). Therefore, Scotty Creek presents several opportunities to gain insights into the impacts of permafrost thaw on lakes, as well as the underlying drivers of this change.

The Scotty Creek Research Station

The Scotty Creek Research Station is located in the Dehcho region of the Northwest Territories, Canada, in the Taiga Plains ecoregion (Ecosystem Classification Group 2007). The Taiga Plains is characterized by open-water and peatland-rich, highly organic flat terrain underlain by sporadic discontinuous permafrost (Quinton et al., 2019; Wright et al., 2022). Scotty Creek is representative of sporadic discontinuous permafrost peatlands across the North. Researchers working in remote regions are challenged by the lack of long-term monitoring stations, and therefore a scarcity of data; however, the Scotty Creek basin, has been the focus of monitoring and field studies for over three decades. Scotty Creek is also integrated into the National Aeronautics and Space Administration Arctic-Boreal Vulnerability Experiment (NASA

ABOVE), a large-scale study of environmental change and its implications for social-ecological systems that links field-based, process-level studies with geospatial data products derived from airborne and satellite sensors. Together with the Dehcho First Nations, the Scotty Creek Research Station has also formed the Dehcho Collaborative on Permafrost, which aims to work together to improve permafrost thaw monitoring, adaptation, process understanding, and prediction (Quinton et al., 2022).

Although the Scotty Creek basin is one of the most well-studied permafrost peatland catchments in the subarctic, very little research has been done on the many small, shallow lakes found at or near the research station.

Dissertation Goals and Objectives

The goal of my PhD research is to assess spatial patterns and temporal trends in lake response to rapid permafrost thaw in the Scotty Creek basin, and to evaluate underlying drivers that might explain variability in lake response. Such knowledge is required in order to derive insights into future trajectories of change. My research leverages the knowledge and data products available for Scotty Creek, and combines lake monitoring techniques, remote sensing, and paleolimnological methods to provide a foundation for advancing our understanding of the limnology of permafrost peatland lakes and their role as sentinels of broader landscape change.

This thesis is divided into three data chapters (Chapters 2, 3 and 4), written as manuscripts for publication in peer-reviewed journals. Chapter 2 aimed to characterize spatial variation in limnological characteristics and assess relationships with hydrological parameters, as well as to investigate drivers of diatom assemblages to facilitate their use as paleolimnological indicators of changes over time. I collected water samples and sediment cores from 16 lakes at or near the

Scotty Creek Research Station. Water chemistry variables analyzed included DOC, lake colour, total phosphorus, and dissolved metals. Landscape classification was available for a subset of nine lakes, and I used this to classify lake shorelines based on the prevalence of channel fens, bogs, and peat plateaus as an indicator of hydrological connectivity. I deployed temperature, oxygen, and light data loggers in two lakes at the Scotty Creek Research Station to monitor high-resolution temporal trends from early June to end of August, 2019. I had originally planned for three years of data collection at the Scotty Creek Research Station, but I was only able to complete one year because of circumstances related to COVID-19. I analyzed surface sediment samples from the 16 lakes, as well as surface samples from bog and fen environments at the Scotty Creek Research Station, to assess modern diatom ecology and improve diatom-based paleolimnological inferences of ecosystem changes. Specifically, this chapter aims to answer the following questions: (1) What are the water chemistry variables that drive variation across lakes? (2) how do key water quality variables (temperature, oxygen, light) change through the open-water season? (3) What are the underlying drivers of variation in diatom assemblages across the 15 lakes? (4) Is there a relationship between limnological characteristics (diatoms, water chemistry) and hydrological connectivity? This chapter provided the foundation for Chapters 3 and 4.

Chapter 3 investigated regional lake ecosystem changes inferred from diatom assemblage in 15 lakes, providing a snapshot of change between 1850, 1950, and present-day. In this assessment, three sediment samples were analyzed from dated sediment cores corresponding to three periods of time: (1) present-day conditions; (2) ~1950, just prior to rapid acceleration of permafrost in 1970; and (3) ~1850, prior to the onset of anthropogenic climate change. This is a modified version of the “top-bottom paleolimnological approach”, a commonly used technique for

regional assessments of change (Smol, 2008). Chapter 4 investigated trajectories of lake ecosystem change over the last several hundred years at high temporal resolution, in five lakes that represent a range in hydrological connectivity. For Chapter 4, I paired a diatom-based paleolimnological assessment with reconstructions of changes in biogeochemical proxies indicative of aquatic-terrestrial linkages, including total mercury, carbon content, atomic carbon to nitrogen ratios (to infer organic matter sources), and stable isotopes of carbon and nitrogen ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$). This allowed me to explore the timing and nature (e.g. gradual or abrupt) of lake changes, and linkages between ecological changes inferred from diatoms and changes in terrestrial organic matter inputs to lakes. Three of the five lakes are connected along a hydrological cascade, and the remaining two lakes are hydrologically isolated, allowed me to investigate the potential role of hydrological connectivity in influencing trajectories of lake ecosystem change.

The characterization of the limnology of small lakes in the Scotty Creek basin (Chapter 2), and ecosystem changes over time (Chapters 3 and 4), is a necessary step for integrating lakes into the ecohydrological research network at the Scotty Creek Research Station. This dissertation therefore provides foundational knowledge for future research at the Scotty Creek Research Station to unravel the mechanisms behind lake ecosystem responses to permafrost thaw.

Chapter 2: Limnology and diatom ecology of shallow lakes in a rapidly thawing discontinuous permafrost peatland

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Author's Contributions

KAC, JBK, and WLQ conceived of research ideas and acquired funding, GNH and LC created landscape classifications and analysed landscape data, KAC and JRT conducted field work and acquired all samples for analysis. KAC conducted all other analyses and led the writing of the manuscript. All authors contributed to manuscript drafts and gave approval for submission to Inland Waters for publication.

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Abstract

Shallow lakes are abundant features across southern discontinuous permafrost peatlands, which are highly sensitive to even modest warming of air temperatures. This study provides a foundation for advancing our process-based understanding of the drivers of lake ecological change by characterizing the limnology of shallow lakes in the Scotty Creek basin (Northwest Territories, Canada), a site of long-term ecohydrological monitoring near the southern extent of permafrost. High temporal resolution oxygen and temperature recordings in two lakes over a growing season indicate no development of a thermal gradient, but record periods of low oxygen. Analysis of landscape characterization and modern lake water chemistry suggests that the presence of nearshore collapse scar wetlands and fens may be important drivers of lake water chemistry, but relationships are not straightforward. Sedimentary diatom relationships with water chemistry suggest they may be useful in paleolimnological studies tracking permafrost thaw in peatlands and associated changes in chromophoric dissolved organic carbon. This study also highlights the importance of continued high temporal resolution monitoring integrated with paleolimnological studies to better predict how shallow lakes will respond to future warming in this dynamic thermokarst landscape.

Introduction

Shallow lakes play a critical role in the cycling of water and chemical constituents across landscapes, acting as both sentinels and agents of environmental change. Consequently, changes to lake ecosystem structure and function are relevant to our broader understanding of landscape ecohydrology and biogeochemical cycling. Shallow lakes are abundant features across southern discontinuous permafrost peatlands, part of a landscape mosaic that also includes permafrost peat plateaus (or palsas) and thermokarst collapse scars and fens. Discontinuous permafrost landscapes are highly sensitive to even modest warming of air temperatures (Kettles & Tarnocai, 1999; Spence et al., 2020), and models project that 40% of the world's permafrost could be lost by 2100 (SOCR 2021), with sensitive sporadic permafrost regions potentially permafrost-free by mid-century (Chasmer & Hopkinson, 2017).

Permafrost thaw can change the thickness of the seasonally thawed (i.e. active) layer, generate a layer of talik separating the underlying permafrost from the overlying active layer, and produce thermokarst terrain. While changes in active layer thickness occur slowly (press disturbance), thermokarst development from the thawing of ice-rich permafrost manifests as a rapid (or pulse) disturbance (Vonk et al., 2015). In southern permafrost peatlands, thermokarst processes result in the conversion of forests into wetlands (Quinton et al., 2019). This transition alters the hydrologic connectivity of the landscape by increasing the number, duration, and depth of flow paths (Karlsson et al., 2012; Quinton et al., 2019; Smith et al., 2007). The hydrological connectivity of a landscape exerts a strong control over transportation of sediment, organic matter, and nutrients, and shallow lakes play a critical role in the processing of these materials along hydrological cascades.

A change in watershed hydrology as a result of permafrost thaw can alter the quality and quantity of dissolved organic carbon (DOC) exported to downstream aquatic ecosystems (Vonk et al., 2015). For example, increased ground thaw depth, and therefore lower water table depth, results in deeper flow paths that could impact DOC composition because flowing water can have greater contact with deeper, more humified carbon (Burd et al., 2018). Increased areal wetland coverage and hydrological connectivity, coupled with increased availability of terrestrial organic matter liberated from thawed soils, has the potential to increase the export of terrestrial organic carbon to lakes. As terrestrial organic carbon is typically highly coloured, increased export of carbon from the catchment can result in a phenomenon known as lake browning (Wauthy et al., 2018). Lake browning has implications for lake ecology and biogeochemistry as a result of changes in light penetration, thermal regime, and oxygen dynamics (Porcal et al., 2009; Vonk et al., 2015). Carbon budgets for inland waters (lakes, rivers, and reservoirs) suggest that these freshwater ecosystems play a critical role in the carbon cycle, with twice as much carbon being exported from the land to inland waters than the land to the ocean (Cole et al., 2007). It has been estimated that over half of the carbon entering inland waters is either buried or returned to the atmosphere (Cole et al., 2007), highlighting the importance of these ecosystems in processing carbon.

Increases in lake DOC concentrations are predicted with continued permafrost thaw (Vonk et al., 2015; Wauthy et al., 2018), yet paleolimnological reconstructions of thermokarst lakes have provided mixed results regarding trajectories of lake DOC concentrations (Bouchard et al., 2013; Coleman et al., 2015; Thienpont et al., 2013; Vonk et al., 2012). This may be due, at least in part, to localized differences in catchment ecohydrological characteristics. In permafrost peatlands, collapsed scar wetlands, and channel fens perform unique hydrological and biogeochemical functions that influence downstream transport of carbon (Connon et al., 2014; Gordon et al.,

2016; Olefeldt & Roulet, 2012). Understanding the impact of permafrost thaw on lake DOC therefore requires consideration of how such thaw affects the hydrological and biogeochemical functioning of the surrounding catchment. A better understanding of the influence of hydrological connectivity and catchment vegetation on the limnological characteristics of shallow lakes is needed to predict future lake ecosystem changes in rapidly thawing discontinuous permafrost peatlands.

The Scotty Creek basin, located in the lower Liard River Valley of the Taiga Plains ecozone, Northwest Territories, is an ideal location to study linkages among shallow lake limnology, landscape hydrology, and landscape change in discontinuous permafrost peatlands. Field research on permafrost hydrology, vegetation changes, wetland biogeochemistry has been ongoing at Scotty Creek since the late 1990s and has provided a unique long-term perspective on watershed changes rarely available for remote subarctic regions (Quinton et al. 2019). The Scotty Creek basin is also included in the study area for the NASA ABoVE program, which provides a comprehensive dataset of airborne and satellite imagery for Scotty Creek and much of the larger ecoregion. To date, however, little or no research has been conducted on the many small lakes and ponds found within the Scotty Creek basin. The large wealth of climatological, biogeochemical, and ecohydrological research, as well as the established field research infrastructure available at the Scotty Creek research station, makes the Scotty Creek basin an ideal site to study drivers of limnological change in shallow thermokarst lakes.

In this paper, we provide the first limnological characterization of shallow lakes in the Scotty Creek basin. We examined relationships between nearshore landscape characterization, lake water chemistry (DOC, colour, nutrients, and metals), and sedimentary diatom (*Bacillariophyta*) species assemblages to derive new insights into terrestrial-aquatic linkages at Scotty Creek, and

to refine the use of diatoms as (paleo)ecological indicators of permafrost thaw. Finally, we present high-resolution temporal data over the ice-free season of 2019 to document short-term dynamics of lake depth, lake water oxygen levels, light penetration, and thermal gradients in two lakes in the Scotty Creek basin that we propose as candidate sites for the establishment of a long-term lake monitoring program. This study provides a foundation for advancing our process-based understanding of the drivers of limnological change in rapidly thawing discontinuous permafrost peatlands.

Methods

Field methods

The Scotty Creek basin (61°180 N, 121°180 W) is within the sporadic discontinuous permafrost zone near the boundary with the extensive discontinuous zone and is characterized by low-relief and extensive peatlands (Quinton et al., 2019). Warming air temperatures since the 1970s has resulted in a rapidly evolving landscape and is predicted to be permafrost-free by mid-century (Chasmer & Hopkinson, 2017). Permafrost exists beneath treed peat plateaus, while surrounding wetlands, including channel fens and collapse scar wetlands (hereafter “collapse scars”), are predominately treeless and permafrost-free. Recently, “treed wetlands” were documented and described by Disher et al. (2021) who proposed that they represent a transitional stage as treeless wetlands evolve into forest.

In 2018, a sampling survey was conducted on small lakes within the Scotty Creek and neighbouring basins, followed by a more intensive study of a few lakes and surrounding wetland ecosystems in June 2019. 16 lakes were accessed by helicopter in mid-July 2018 (Figure 2.1).

This season ice-off occurred between May 4 and 10. Conductivity and pH were measured at the surface, at all sites *in situ* using a Hanna multiprobe, taken from the center of the lake. Oxygen measurements were not recorded due to equipment malfunction. Lake depths were measured using an acoustic depth sounder; however, depths were not used in analyses as a result of challenges establishing depths due to interference of dense moss mats and macrophytes established on many lake bottoms, which prevented stabilized readings of the depth sounder (for many lakes readings fluctuated by 10s of cm, which is significant for these shallow systems). For all sites, water samples were collected from the surface in two pre-sterilized 1-litre polyethylene bottles. One litre was filtered through 0.45µm cellulose acetate filters, within 24 hours of collection for analysis of dissolved organic carbon (DOC) and total nitrogen (TN). Unfiltered water was poured into 250 mL glass bottles containing 0.5 mL nitric acid, including a field blank using DI water, and sent to SGS Laboratories for elemental analysis, including total phosphorus (TP) (Montreal, QC, Canada). Sediment cores were collected from lakes using a Uwitec gravity corer with an internal diameter of 8.6 cm and sectioned into 0.5 cm intervals using a modified Glew (1988) extruder. The top 0.5 cm of each core was used for the analysis of modern diatom assemblages.

Intensive sampling was conducted while stationed at the Scotty Creek Research Station in June 2019, including water and sediment sampling of Goose Lake and First, as well as six wetland sites (five fen sites and one collapse scar site) (Figure 2.1D). Additionally, substrate samples (submerged vegetation, submerged peat, sediment, and grasses) were collected from shoreline environments around Goose Lake, and from a benthic moss mat in the centre of the north basin of Goose Lake (~1m depth). Water samples were collected in two 1-litre polyethylene bottles, pre-rinsed using the subject lake's water. Similar to the 2018 lake survey, one litre was filtered

through 0.45 μ m cellulose acetate filters, within 24 hours of collection. Using a Hanna Multiprobe conductivity, pH, and dissolved oxygen were measured in Goose Lake, First Lake, and wetland sites. Buoys equipped with HOBO Pendant wireless temperature and light data loggers, Onset HOBO U26 dissolved oxygen (DO) data loggers and Onset HOBO U20 depth loggers were deployed in both the main basin and northern basin of Goose Lake and center of First Lake (Figure 2.1D) on June 7th (~a month past ice-off) and removed August 22nd 2019. Each buoy was connected to a rope which was anchored to the sediment using 20 lb weights. An additional rope was suspended from the buoy, upon which three temperature/light loggers, and one oxygen logger were attached. The depth logger was attached to the weight to keep it stationary in the water column in relation to the sediments and was kept afloat using empty 2L bottles. Precipitation data was collected using a Pluvio totalizing station, located at the Scotty Creek research station adjacent to Goose Lake, and was corrected for undercatch. Precipitation was recorded every 30 minutes to examine the impact of precipitation on other time-series data (e.g. light and depth).

Water chemistry analyses

DOC and TN were analyzed from filtered water using a Shimadzu-TOC5000 Series TOC-L analyzer using the combustion catalytic oxidation method and non-dispersive infrared detection. Standards were made using potassium hydrogen phthalate for instrument calibration and performance. Samples were acidified using HCl and sparged to purge DIC. True colour was measured using colourimetry, using the platinum-cobalt method on a Genesys 10S UV-Vis spectrophotometer (APHA, 2011). Alkalinity was analyzed by titrating samples with 0.02N H₂SO₄ following (APHA, 1998). Samples were sent to SGS Laboratories (Montreal, QC, Canada) for elemental analysis, including total phosphorus and total metals, using ICP-MS and

ICP-OES. Although perchloric acid digestion followed by colorimetry is the more common for analysis of total phosphorus, good agreement has been found between this method and ICP-MS (Ivanov et al., 2012), as used here.

Physical Landscape Characterization

Shoreline Development and Lake Area

The shoreline development (D_L) ratio is an index that describes how close a lake is to a perfect circle. Lakes with a D_L close to 1 have circular shapes, while lakes with high D_L have more jagged and crenulated shapes. D_L is the ratio of the perimeter of the lake to the perimeter of a circle with the same area

$$D_L = \frac{S_L}{2\sqrt{\pi A_0}} \quad (1)$$

where S_L is shoreline length, and A_0 is the area of the lake. Lakes with a higher D_L have higher potential for the development of littoral communities and increase the exposure of lakes to the surrounding shorelines. Lake area and perimeter were calculated using the polygon function in Google Earth.

Buffer and Overlay Landscape Analysis

Nine of the 16 study lakes were selected from the Scotty Creek basin for the buffer and overlay landscape analysis. These lakes were selected as they are within a region that has previously been classified by (Chasmer et al., 2014), using airborne LiDAR data and high spatial resolution multi-spectral data from WorldView-2 satellite acquired in 2010. The buffer and overlay

analyses were done in ArcMap version 10.7.1 using a raster file of the Scotty Creek study area. Individual shapefiles were created for each land classification (channel fen, collapse scars, water, moraine/upland, and permafrost) and the water layer was separated into individual lakes. A buffer of 250 m was applied to each of the nine lakes followed by an overlay analysis to determine how much fen and collapse scar area fell within each buffer. The outputted layers included shapefiles only of the collapse scars and fens that overlapped within the 250m buffer. The areas of extracted collapse scars and fens were then calculated within 250 m of each lake.

Subfossil Diatom Analysis

Diatom slides were prepared following Battarbee et al., 2001 using the hydrogen peroxide method, and mounted using Naphrax. Diatom valves were identified using an Amscope B690C-PL microscope and multiple reference texts (Krammer and Lange-Bertalot 1997; Krammer and Lange-Bertalot 1999; Krammer and Lange-Bertalot 2000; Fallu et al. 2000) and online databases (Guiry and Guiry, 2021; Spaulding et al. 2022). Between 300 to 500 valves were counted per site, except for Fen 4 and the collapse scar site which had markedly low diversity (Hill's $N_2 < 4$), in which case a minimum of 175 valves were counted. Diatom species were grouped based on similar ecologies (Appendix A) and were displayed as relative abundances. Chrysophyte cysts, which can form in response to changing environmental conditions, and protozoan plates, which can provide information on moisture levels, were also present on diatom slides and enumerated and displayed on figures as percent, relative to the sum of all diatom valves.

Data Analysis

Data retrieved from data loggers was plotted using the ggplot package (Wickham 2019) in R (R Core Team 2020). Light absorption (A) between sensors was calculated by the equation

$$A = 100 \frac{I_0 - I_z}{I_0} \quad (2)$$

where I_0 is the irradiance recorded in the shallowest sensor, and I_z is the irradiance recorded in the deepest sensor. Total light absorption was divided by total number of cm between the two sensors to get light absorption per cm. Anomalous negative values, caused by higher irradiance values recorded in the deeper sensor than the shallower sensor were removed, and likely a result of shading of the shallower sensor by the buoy. A LOESS smoothed line was included in the figures using the `stat_smooth` function in `ggplot` in R.

Water chemistry variables that had concentrations below detection were not included in any analyses (mercury, silver, arsenic, beryllium, boron, bismuth, molybdenum, nickel, antimony, selenium, tin, thallium, zirconium, and zinc). Variables were also removed if there was evidence of contamination, based on anomalously high field blank concentrations (aluminum, cadmium, cobalt, chromium, copper, iron, lead, titanium, uranium, and vanadium). Spearman's correlation analyses, used here due to the non-normal distribution of most variables, were calculated on remaining variables to determine statistically significant relationships between water chemistry variables [pH, dissolved organic carbon (DOC), total nitrogen, filtered (TN), true colour (colour), phosphorus (TP), conductivity, alkalinity, calcium (Ca), potassium (K), lithium (Li), magnesium (Mg), manganese (Mn), sodium (Na), silicon (Si), and strontium (Sr)] and physical lake features (lake area (Area) and shoreline development (D_L)).

Principal components analyses (PCA) were used to visualize limnological variation among lakes. Variables were standardized using the “scale” function in the `vegan` package (Oksanen et al. 2019) in R. A PCA was generated for all 16 lakes to examine variation between lakes with respect to lake area (Area) and shoreline development (D_L), and select water chemistry variables

(pH, DOC, TN, colour, conductivity, Li, and Mn). Area and D_L were plotted passively. Highly correlated variables were removed from the PCA. For example, conductivity was correlated with alkalinity, calcium (Ca), potassium (K), magnesium (Mg), and strontium (Sr). The remaining variables were selected due to their importance in structuring biological communities (pH, DOC, TN, TP, colour, and conductivity), usefulness as a lithogenic tracer (Li), or sensitivity to redox conditions (Mn). Li, TP, and Area were normalized using a log transformation, and D_L and conductivity were normalized using a loglog transformation. A PCA was also generated for the subset of 9 lakes used in landscape analyses to visually examine relationships between the same water chemistry variables as above, and collapse scar or fen coverage within 250 m of the lake. Collapse scar and fen coverage was plotted passively, and Mn was normalized using a log transformation.

Direct ordination [Redundancy analysis (RDA)] was used to evaluate relationships between diatom community composition and environmental variables. Lake area and conductivity were log transformed to normalize distribution, and species data were Hellinger transformed. A variance inflation factor (VIF) test was run to assess multicollinearity. Variables with high VIFs were sequentially removed from analysis until all environmental variables had VIFs below 10. Variables retained in the analysis were pH, colour, DOC, area, and conductivity. Significance of the RDA was determined using an ANOVA-like permutations test. Correlation analyses were conducted using the Hmisc package (Harrell, 2021), and PCAs, VIFs, RDAs and permutation tests were conducted using the Vegan package (Oksanen et al., 2019) in R.

Results

High Temporal Resolution Assessment of Goose Lake and First Lake

Depth measurements obtained from depth loggers deployed in First Lake and the two main basins of Goose Lake (Figure 2.1D) from June 7th to August 22nd showed good agreement between all three loggers, and suggest water levels of these shallow (~1 m) lakes fluctuated by ~30-40 cm throughout this time period (Figures 2A, 2B, and 2C). Water levels appear to have fluctuated through June and July and began to stabilize towards the end of the recorded period. Lowest water levels occurred in early to mid-June, and mid-July. Bottom dissolved oxygen (DO) measurements ranged from 5 to 12.5 mg/L in Goose Lake, both in the north basin (Figure 2.2A), and the main basin (Figure 2.2B). In First Lake, DO measurements appear to have dropped to 0 mg/L for periods of time, however this is likely a result of the logger dropping into the sediments, as the logger records these anoxic conditions during periods of lower water levels (Figure 2.2C). The consistency between temperature readings at different depths suggests that the entire water column in both lakes was mixed throughout the recorded time period (Figure 2.2). Temperature measurements were consistent between lakes and fluctuate between 10 and 25°C throughout the recorded period, and all lakes recorded warmer periods in mid-June and late July/early August. The calculated % absorption of light per cm is similar between Goose Lake and First Lake, and shows that light penetration might fluctuate through time, but no clear seasonal trends were apparent (Figure 2.2). However, in Goose Lake, periods of higher light absorption (e.g. in late July) coincided with warmer temperatures (Figures 2A and 2B). Rainfall events occurred sporadically throughout the season, with the largest rainfall event occurring on July 18th with 12.4 mm of rain falling over an hour. Lake depth increased by ~20 cm in Goose

Lake and First Lake after this rainfall event with maximum depth occurring on July 23rd (Figure 2.2).

Characterization of aquatic ecosystems in the Scotty Creek Basin

Morphology and water chemistry of 16 thermokarst lakes

In 2018, lake depths of the 16 surveyed lakes ranged from ~0.9 to 2.1 m however dense macrophyte stands or benthic moss mats likely interfered with sonar measurements, as measurement readings in some lakes would not stabilize and would fluctuate by tens of centimetres. Lake area ranged from 11 to 244 ha, with a notably larger lake with an area of 713 ha (FS1)(Table 2.1). Lakes were circumneutral to slightly alkaline (pH = 7.85 – 8.75), and alkalinity ranged from 28-124 mg/L CaCO₃. DOC in these lakes ranged from 12.96 to 23.74 mg/L, and water colour ranged from 18-463 TCU (Table 2.1). TN (filtered) ranged from 0.54 to 1.54 mg/L, TP (unfiltered) ranged from 8 to 38 µg/L, and conductivity ranged from 55.5 to 244.2 uS/cm.

Near-shore Landscape characterization of 9 selected thermokarst lakes

Landscape coverage of fen environments varied between 0 and 34% within 250 m of the shorelines of the 9 lakes included in the landscape characterization analyses, while collapse scars were more extensive, covering between 13.4 and 48.9% of the landscape within 250 m of these lakes (Figure 2.3). Lakes were generally well connected through channel fen networks, however two lakes, SC5 and SC8 were more isolated. SC8 had no fen environment within 250 m of the lake indicating it may be hydrologically isolated and while SC5 had a fen-like environment containing grasses and sedges along the western edge of its shoreline, this fen was not hydrologically connected to a channel fen network (Figure 2.3).

Water chemistry of wetland environments

The five fen environments had lower pH ranges than sampled lakes, were circumneutral to slightly acidic (5.97-7.40), and had higher DOC concentrations than lakes ranging from 23.08 to 33.7 mg/L. In comparison to this study, Gordon et al. (2016) previously reported lower pH values (5.15-5.46), and higher DOC values (~42-49 mg/L) for fens in the Scotty Creek basin. Similar to lakes, water colour in these five sites was variable and ranged from 54 to 459 TCU. Alkalinity was lower than lakes and ranged from 26 to 50 mg/L CaCO₃, TN was slightly lower than lakes and ranged from 0.52 to 0.91 mg/L, and conductivity was lower than lakes and ranged from 25 to 82 uS/cm. DO ranged from 2.06 to 9.27 mg/L or 17.6 to 89.7% saturation, and was slightly lower than what had been recorded by data loggers in Goose Lake and First Lake (see below). The one sampled collapse scar had high DOC (46.8 mg/L), which was within the range of values reported by Gordon et al. (2016) (~32-47 mg/L), and also had high colour (522 TCU), low pH (5.33), low alkalinity (4 mg/L CaCO₃) and low conductivity (25 uS/cm). TN (0.59 mg/L) and DO (6.35 mg/L; 58.5% saturation) were within the range of water chemistry variables measured in fen environments.

Analysis of relationships between water chemistry and landscape features

Principal components analysis (PCA) axis 1 explained 50% of the variation in water chemistry in the 16-lake dataset, largely driven by conductivity, lithium (Li), manganese (Mn), total nitrogen (TN), and colour, while PCA axis 2 explained 23% of the variation in the data set and was largely driven by DOC and TP (Figure 2.4A). Generally, lakes are well dispersed throughout the ordination space, however, SC3, SC8, SC1, SC2, Next Lake, SC4, SC9, SC11 are well dispersed along PCA axis 2, but not axis 1 indicating these lakes differ in water chemistry variables associated with axis 2 (DOC and TP). Some lakes appear to have similar water chemistry (e.g.

SC2 and Next Lake; Figure 2.4A), despite being relatively far apart in physical space (Figure 2.1). PCA ordination of the 9-lake dataset (Figure 2.4B) illustrates the relationship between the same water chemistry variables examined in Figure 2.4A and proportion of collapse scar and fen environments within 250 m of lakes. Here PCA axis 1 explained 46% of the variation in the dataset and was driven by conductivity, Mn, TN, Li, and TP while PCA axis 2 explained 21% of the dataset and was driven by pH, colour, and DOC (Figure 2.4B).

Correlation analyses suggest that in this region lake area is strongly ($r > 0.6$) and positively correlated to conductivity, ($r = 0.79$, $p < 0.01$), alkalinity ($r = 0.85$, $p < 0.01$), major ions such as Ca ($r = 0.74$, $p < 0.01$), Mg ($r = 0.77$, $p < 0.01$), and K ($r = 0.78$, $p < 0.01$) and moderately ($0.3 < r < 0.6$) and positively correlated with TN ($r = 0.54$, $p < 0.05$), Mn ($r = 0.53$, $p < 0.05$), and Sr ($r = 0.57$, $p < 0.05$) (Table 2.3). Lake area was also found to be strongly and negatively correlated to colour ($r = -0.85$, $p < 0.01$) (Table 2.2). Shoreline development index is moderately and positively correlated with conductivity ($r = 0.50$, $p < 0.05$) and Mg ($r = 0.48$, $p < 0.05$) (Table 2.2). DOC is moderately and positively correlated to both TN ($r = 0.52$, $p < 0.05$) and TP ($r = 0.58$, $p < 0.05$) (Table 2.2). TN is not significantly correlated to TP ($r = 0.48$, $p > 0.05$) (Table 2.2). Colour is moderately, and negatively correlated to pH ($r = -0.54$, $p < 0.05$), and strongly and negatively related to TN ($r = 0.69$, $p < 0.01$), while TN is moderately and positively related to lithium ($r = 0.50$, $p < 0.05$) (Table 2.2). DOC and colour are not correlated in these lakes ($r = 0.16$, $p = 0.55$) (Table 2.2).

Diatom communities

Lakes

With a few exceptions, two common diatom assemblages were identified in the small lakes within the Scotty Creek and surrounding basins. The first assemblage, identified in SC9, SC3, SC2, SC1, SC5, and SC11, was dominated by small benthic *Fragilaria* species *sensu lato*, which

includes mainly *Pseudostaurosira brevistriata*, *P. parasitica*, *Staurosira construens*, and *S. venter*, and small *Navicula* species *sensu lato*, which includes *Navicula minima*, and *Sellaphora seminulum* (Figure 2.5). The second assemblage, identified in SC4, SC6, SC12, Next Lake, FS2, Goose Lake, and SC10 was dominated by *Encyonopsis* species (*E. cesatii* and *E. descripta*), and large *Navicula* species (*N. cryptocephala*, *N. cryptotenella*, and *N. radiosa*). Many of these lakes (SC12, Goose Lake, SC10, Next Lake, and FS2) also had high abundances of *Brachysira* species (*B. styriaca*, *B. vitrea*, and *B. zellensis*) (Figure 2.5). There were a few exceptions to these common groupings: The assemblage in FS1 was dominated by *Achnantheidium minutissimum*; the assemblage in SC8 was dominated by *Achnantheidium minutissimum*, large *Navicula* species, *Nitzschia* species, and *Brachysira* species; and the assemblage in First Lake was dominated by *Achnantheidium minutissimum*, large *Navicula* species, *Nitzschia* species (mainly *N. fonticola* and *N. palea*), and centric planktonic species (*Lindavia michiganiana*, and *Discotella pseudostelligera*) (Figure 2.5). The abundance of chrysophyte cysts relative to diatom valves was variable, ranging from 0 to ~20%. Higher abundances were found in SC3 (~20%) and SC11 (~19%) and absent in FS1 and SC9. Protozoan plates were present in low abundance in most lakes (~0.2-4.6%), and absent in SC9 and SC10 (Figure 2.5). Redundancy analysis (RDA) of diatom assemblages and pH, colour, dissolved organic carbon, lake area, and conductivity was statistically significant ($F=1.8422$, $p<0.05$). The selected variables collectively explained 47.9% of the variance in the diatom assemblages, 40% of which was explained in the first two RDA axes (Figure 2.6). Some species preferences were identified in the RDA. For example, *Brachysira vitrea* was found to be associated with lakes with greater surface area. *Navicula cryptocephala*, *N. radiosa*, *Encyonopsis cesatii*, *E. descripta*, *Kobayasiella jaagi*, *Cymbella incerta*, and *Brachysira styriaca* were all found to be associated with lakes with higher DOC,

while *Staurosira construens*, *Staurosira venter*, and *Pseudostaurosira brevistriata* were associated with high colour. Lakes SC1, SC2, SC3, SC5, and SC9 had a similar diatom assemblage, while Next Lake, Goose Lake, and lakes SC4, SC6, SC10 and SC12 had similar assemblages. FS2, SC8, and First Lake also had a similar assemblage (Figure 2.6).

Wetland diatom assemblages

Diatom assemblages identified in the wetland samples were variable but exhibit notable differences from lake diatom assemblages. The most abundant diatoms found in fen environments were *Eunotia* species (mainly *E. bilunaris* and *E. subarcuatoides*), *Gomphonema* species (mainly *G. parvulum*), and *Tabellaria flocculosa*. *Rossithidium pusillum*, *Achnanthidium minutissimum* (Figure 2.7), *Nitzschia* species (mainly *N. fonticola* and *N. palea*), large *Navicula* species (mainly *N. cryptocephala*, *N. cryptotenella*, and *N. radiosa*), *Kobayasiella subtilissima*, and planktonic *Fragilaria* (mainly *F. tenera*) species were also present (Figure 2.7). The relative abundances of chrysophyte cysts (7-36%) and protozoan plates were variable (2-37%), but generally higher in fens than lakes (Figure 2.7). The diatom assemblage in the collapse scar sample was dominated by *Kobayasiella subtilissima* (95%). The highest relative abundances of both chrysophyte cysts and protozoan plates were found in the collapse scar sample (both at 42% relative abundance) (Figure 2.7)

Diatom assemblages identified in lake substrate samples

In the lake substrate samples *Tabellaria flocculosa* and Large *Navicula* species (mainly *N. cryptocephala*, *N. cryptotenella*, and *N. radiosa*) were the most abundant diatom species identified. *Tabellaria flocculosa* was present in high abundances in grass (~48%) and submerged vegetation (~71%) samples and was also present in the submerged peat sample (~11%) (Table 2.3). Large *Navicula* species were found in high abundance in the sediment (~38%), submerged

peat (~30%) and benthic moss mat (~39%) samples (Table 2.3). In addition to the large *Navicula* species, the diatom assemblage identified in the sediment sample also consisted of planktonic *Fragilaria* species (mostly *F. tenera*), *Encyonema* species (mostly *E. silesiacum*) and *Brachysira* species (*B. styriaca* and *B. vitrea*) (Table 2.3). In addition to large *Navicula* species and *T. flocculosa*, the submerged peat sample also consisted of planktonic *Fragilaria* species, and *Encyonopsis* species (*E. descripta* and *E. cesatii*). In addition to *T. flocculosa*, the grass sample also consisted of *Gomphonema* species (mostly *G. parvalum*) and *Achnantheidium minutissimum*, while the benthic moss mat sample consisted of Large *Navicula* species, *Encyonopsis* species and *Brachysira* species (*B. styriaca* and *B. vitrea*) (Table 2.3). Chyrosphyte cyst abundances are generally low in the substrate samples (2 to 6%), with the exception of submerged peat which has higher abundances (26%). Protozoan plates are almost entirely absent in these samples (~0 to 0.25%) (Table 2.3).

Discussion

Seasonal temperature and oxygen dynamics in Goose Lake and First Lake

Goose Lake and First Lake did not develop a thermal gradient over the 76-day period the loggers were deployed. Paleolimnological records indicate that thermal stability has been increasing in lakes across the circumpolar Arctic in response to climate change (Rühland et al., 2015).

Although development of thermal gradients in shallow lakes is rare, they have been observed in shallow lakes with high DOC concentrations, as DOC can absorb more solar radiation and increase surface water temperatures (Bouchard et al., 2011; Deshpande et al., 2017). Shallow boreal lakes may also be more prone to periodic thermal gradient development where trees provide shelter from wind mixing (Klaus et al., 2021).

Oxygen availability at the sediment-water interface is a fundamental control on lake biogeochemical cycling. For example, methanogenesis, the production of methane as a respiratory by-product, occurs in anoxic conditions, and furthermore may be fueled by the addition of terrestrial sources of organic carbon (Grasset et al., 2018). Increased thermal stability, in combination with increased bacterial consumption of high terrestrial carbon inputs, have resulted in prolonged periods of anoxia in some subarctic lakes in Northern Quebec (Deshpande et al., 2017). Small subarctic lakes in Norway similarly experienced decreasing oxygen concentrations with increasing DOC inputs (Couture et al., 2015). These changes could have important consequences for the carbon cycle as increased export of terrestrial carbon and longer periods of thermal stability may result in shallow subarctic lakes becoming important emitters of methane (Grasset et al., 2018). In contrast, high DOC subarctic lakes in Siberia had oxygen concentrations at equilibrium with the atmosphere (Shirokova et al., 2013). Oxygen levels near the sediment-water interface in Goose Lake and First Lake ranged between 5 and 12.5 mg/L and would be considered low for the protection of aquatic life (for reference, 9.5 mg/L is considered the lowest acceptable dissolved oxygen concentration for early life stages; CCME 1991). As both Goose Lake and First Lake have high DOC concentrations (23.74 and 21.93 mg/L, respectively) high rates of microbial respiration may be responsible for lower oxygen levels as there is no evidence of thermal gradient development.

Peatlands cover approximately 19% of the circumpolar permafrost region (Tarnocai et al., 2009), yet high temporal resolution data on lakes within peatlands is scarce and is a notable gap in lake monitoring networks such as GLEON (Global Lakes Ecological Observation Network). As permafrost wetland complexes near the southern extent of permafrost are particularly vulnerable to rising air temperatures, the Scotty Creek basin offers an ideal location for a long-term

ecological research (LTER) site. Lake monitoring data collected here could be combined with ongoing landscape and hydrological research at the Scotty Creek Research Station, as well as high spatial resolution aerial images provided by the NASA ABoVE program, to provide a more holistic understanding of changes in terrestrial-aquatic linkages with permafrost thaw.

Spatial patterns in lake water chemistry

We expected the relative proportion of collapse scars and channel fens within 250 m of the lake shoreline to be an important driver of water chemistry in the Scotty Creek basin because of the differential roles these landscape features play in the biogeochemical processing and transport of materials from land to lake. In this landscape, channel fens act as water conveyors, while collapse scars act predominately as water storage (Quinton et al. 2019) and may be important sources of chromophoric DOC as they were identified in this study as having high DOC and high colour (522 TCU). Our results, however, show limited evidence for the role of channel fens and collapse scars in driving lake water chemistry. For example, SC5 and SC8 are hydrologically isolated from the channel fen network, and both have high colour, which may suggest that channel fens have a role in flushing terrestrial DOC from lakes; however, Next Lake has relatively high colour despite being well-connected hydrologically. We postulate that temporal dynamics in a rapidly changing landscape could explain why we do not see strong evidence for the importance of fen and collapse scar prevalence in influencing lake water chemistry. An increase in fen development may initially increase colour in lakes due to a phenomenon known as “bog capture” (Connon et al. 2014), where previously isolated collapse scar wetlands become connected to the expanding fen network as permafrost plateaus continue to degrade. The highly coloured water is then conveyed to nearby lakes through the fen network. With time, coloured DOC may ultimately be flushed from Next Lake and other lakes recently influenced by the

capture of collapse scars. Paleolimnological approaches that reconstruct DOC trajectories in lakes in combination with a time series of remotely sensed images could be used in future studies to test this. Diatoms, which have been used to track changes in lake habitat, water depth, and water quality variables such as pH, DOC, and colour (Coleman et al., 2015; Hargan et al., 2015; Michelutti et al., 2003; Pienitz et al., 1999; Pienitz & Smol, 1993) may be particularly useful for tracking changes related to permafrost thaw in the Scotty Creek basin, as described below.

Diatom ecology in permafrost wetlands and lakes of the Scotty Creek basin

Two different diatom assemblages were observed in 13 of the 16 lakes sampled. The first assemblage, identified in 6 lakes, is comprised of small benthic *Fragilaria* species (*sensu lato*) and small *Navicula* species (*sensu lato*), which were found in this study to be associated with higher colour. A similar assemblage has been identified in a lake with high colour located southeast of the Scotty Creek basin near Tathlina Lake (Coleman et al. 2015; Korosi et al. 2015). Small benthic *Fragilaria* (*sensu lato*) have been used as indicators of harsher, low light conditions and tend to decrease in abundance with warming (Bouchard et al., 2013; K. Rühland et al., 2008). Although primarily benthic, they have also been identified as tychoplanktonic (E.g. Velez et al. 2021), and can move into the water column with mixing. However, their absence in Goose Lake and First Lake, which appear to be well mixed at least during the ice-free season of 2019 suggests that their presence is not related primarily to column mixing.

The second assemblage, recorded in 7 lakes, is comprised of *Encyonopsis* species and large *Navicula* species. These species were found to be associated with high DOC and lower pH (though note the pH gradient is narrow, ranging from 7.85 - 8.75). The species assemblages in these lakes are similar to the assemblage found in the benthic moss mat sampled from Goose Lake. While large *Navicula* species have been associated with higher DOC (Coleman et al.,

2015; Rühland et al., 2003), *Encyonopsis* species are epiphytic and often associated with mosses (Bahls, 2013). Therefore, a main driver of diatom assemblages in these lakes may be the presence of a benthic moss mat, which is dependent on light being able to penetrate to the benthic zone of these lakes. Light penetration is reduced in highly coloured waters (Seekell et al. 2015), which could limit the growth of moss and associated epiphytes in these lakes. In contrast, the high DOC, and lower colour in some of these lakes may be a signature of extensive moss and macrophyte growth, as autochthonous aquatic sources of DOC are generally lower in colour (Pagano et al., 2014).

The species assemblages that were present in high abundances in wetlands are different from assemblages that were identified in lakes. Three of the most common species or groups of species, were *Eunotia* species, *Gomphonema* species, and *Tabellaria flocculosa*. *Eunotia* species in particular are commonly identified in paleoecological studies using peat cores and have lower pH optima (e.g. Hargan et al., 2015). *T. flocculosa* has been found in a wide variety of freshwater habitats, including lakes and peatlands, and have broad morphological variations in terms of size, but shorter varieties as found here have often been observed in peatlands and attached to vegetation (DeColibus, 2013). This is consistent with the assemblages identified in the substrate samples, as *T. flocculosa* was found in high abundances in the grasses and submerged vegetation. The diatom assemblage identified in the collapse scar site was found to be different from both lakes and fens and was dominated by *Kobayasiella subtilissima* (95%). Hargan et al. (2015) also found that *K. subtilissima* had higher prevalence in collapse scar habitats. Collapse scars also have the highest abundance of cysts and protozoan plates compared to both fens and lakes.

The two different assemblages of diatoms that were identified in these shallow subarctic lakes are likely driven by differences in benthic production, which is impacted by the ability of light to

penetrate the water column. As increasing coloured DOC concentrations can reduce light penetration, paleolimnological studies using diatoms as a paleoindicator may be useful for examining the trajectory of lake browning with continued permafrost thaw. The low abundances of common wetland species that were identified in lakes suggests that we are not seeing a strong biological signal of these environments in the lakes. We can therefore be confident that the diatom assemblages recorded in lakes are indicative of that lake's conditions and have not been transported from other locations. It is, however, important to note that changing lake depth will also influence the relative importance of benthic production in lakes and decreases in lake depth are expected with drying of wetlands with on-going thaw and loss of permafrost (Carpino et al., 2021; Chasmer & Hopkinson, 2017). This highlights the importance of continued high temporal resolution monitoring in addition to paleolimnological studies of these lakes to better predict how these lakes will change with future warming in this dynamic landscape.

Tables

Table 2.1: Physical characteristics and modern water chemistry statistics for 16 lakes in the Scotty Creek and surrounding basins, collected July 2018.

	Mean	SD	Min	Max	Median
Depth (m)	1.3	0.4	0.9	2.1	1.2
Area (km ²)	1.06	1.69	0.11	7.13	0.32
Shoreline Development Index	1.18	0.21	1.02	1.75	1.09
pH	8.23	0.27	7.85	8.75	8.20
DOC (mg/L)	18.79	3.13	12.96	23.74	18.35
True Colour (TCU)	176	124	18	463	174
TP (µg/L)(unfiltered)	18.3	7.9	8.0	38.0	17.0
TN (mg/L)(filtered)	0.90	0.28	0.54	1.54	0.79
Conductivity (uS/cm)	106.9	58.5	55.5	244.2	83.1
Alkalinity (CaCO ₃)(mg/L)	54	29	28	124	43
Calcium (mg/L)	15.4	6.5	7.9	29.8	13.3
Potassium (mg/L)	0.61	0.65	0.19	2.49	0.34
Lithium (µg/L)	1.4	0.8	0.7	3.2	1.2
Magnesium (mg/L)	4.67	3.08	2.24	12.70	3.51
Manganese (µg/L)	17.3	8.3	4.9	35.1	15.5
Sodium (mg/L)	2.35	1.93	0.74	7.25	1.62
Silicon (mg/L)	1.52	0.98	0.27	4.33	1.21
Strontium (µg/L)	61.1	36.0	28.5	149.0	45.3

Table 2.2: Spearman's correlation coefficients of water chemistry variables and physical lake characteristics for 16 lakes in the Scotty Creek basin. * $p < 0.05$, ** $p < 0.01$

	Area	DL	pH	DOC	TP	TN	Colour	Conductivity	Alkalinity	Ca	K	L	Mg	Mn	Na	Si	Sr
Area	1.00	0.45	0.21	-0.06	-0.07	0.54	-0.85**	0.79**	0.85**	0.74**	0.78**	0.29	0.77**	0.52	0.36	-0.06	0.57*
DL		1.00	-0.07	0.12	-0.19	0.22	-0.23	0.50*	0.47	0.43	0.35	0.35	0.48	0.12	0.30	0.49	0.42
pH			1.00	-0.16	0.10	0.45	-0.54	0.48	0.46	0.37	0.63**	0.16	0.51*	0.48	0.42	-0.09	0.49
DOC				1.00	0.58*	0.52*	0.16	-0.01	-0.06	-0.01	-0.06	0.17	-0.04	0.22	-0.02	-0.28	-0.04
TP					1.00	0.48	-0.06	-0.21	-0.11	-0.28	-0.05	0.20	-0.20	0.51*	0.29	-0.38	-0.21
TN						1.00	-0.69**	0.53	0.52*	0.49	0.65**	0.50*	0.51*	0.52*	0.53*	-0.37	0.58*
Colour							1.00	-0.76**	-0.81**	-0.68**	-0.84**	-0.38	-0.74**	-0.54*	-0.55*	0.25	-0.65**
Conductivity								1.00	0.94**	0.95**	0.83**	0.32	0.99**	0.54*	0.33	0.07	0.80**
Alkalinity									1.00	0.89**	0.85**	0.36	0.95**	0.57*	0.48	0.12	0.76**
Ca										1.00	0.74**	0.37	0.94**	0.47	0.28	0.14	0.86**
K											1.00	0.19	0.84**	0.43	0.44	-0.10	0.75**
Li												1.00	0.29	0.29	0.82**	0.17	0.55*
Mg													1.00	0.52*	0.37	0.14	0.77**
Mn														1.00	0.27	-0.18	0.29
Na															1.00	0.17	0.51*
Si																1.00	0.15
Sr																	1.00

Table 2.3: Dominant diatom species identified in lake substrate samples. Percentage of chrysophyte cysts and protozoan plates, in relation to diatom valves, also included.

	Sediment	Submerged Peat	Grasses	Submerged vegetation	Benthic Moss Mat
Location	Shoreline	Shoreline	Shoreline	Shoreline	~ 1 m depth, north basin
Dominant Diatom Species	Large Navicula (~38%)	Large Navicula (~30%)	Tabellaria flocculosa (~48%)	Tabellaria floccuosa (~71%)	Large Navicula spp (~39%)
	Planktonic Fragilaria (~9%)	Tabellaria flocculosa (~11%)	Gomphonema spp (~21%)		Encyonopsis spp (~14%)
	Encyonema spp (~8%)	Planktonic Fragilaria spp (~9%)	Achnantheidium minutissimum (~11%)		Brachysira spp (~11%)
	Brachysira (~7%)	Encyonopsis spp (~9%)			Achnanthes spp (~10%)
Cysts	Cysts (%): 4%	Cysts (%): 26%	Cysts (%): 2%	Cysts (%): 2%	Cysts (%): 6%
Protozoan Plates	Plates (%): 0.24%	Plates (%): 0%	Plates (%): 0%	Plates (%): 0%	Plates (%): 0.25%

Figures

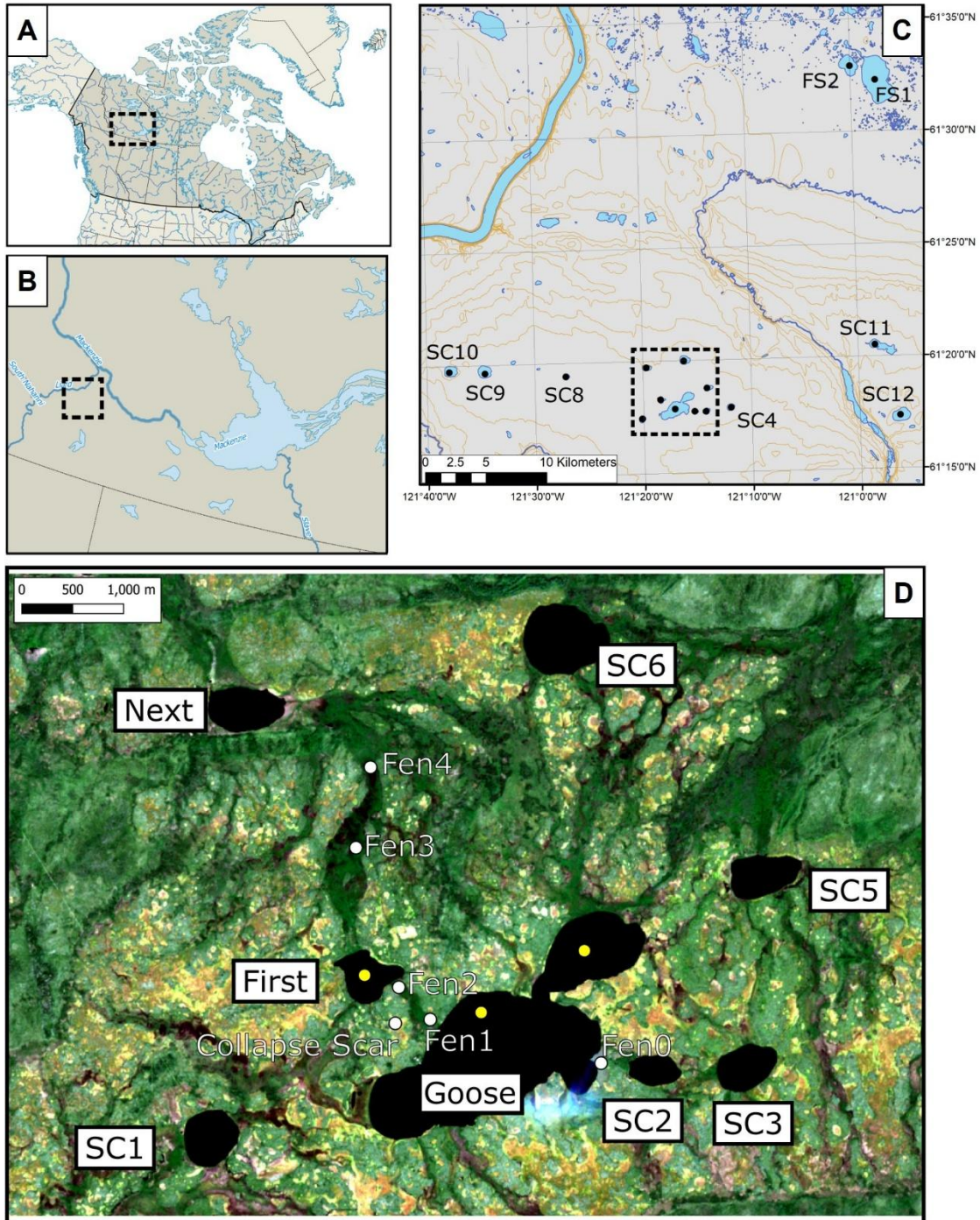


Figure 2.1: Map of study area. (A) Approximate location of site within Canada, (B) approximate location of site within Taiga Plains ecozone, (C) location of all study lakes, (D) Enlarged map of study lakes highlighted in (C) and includes wetland sample sites

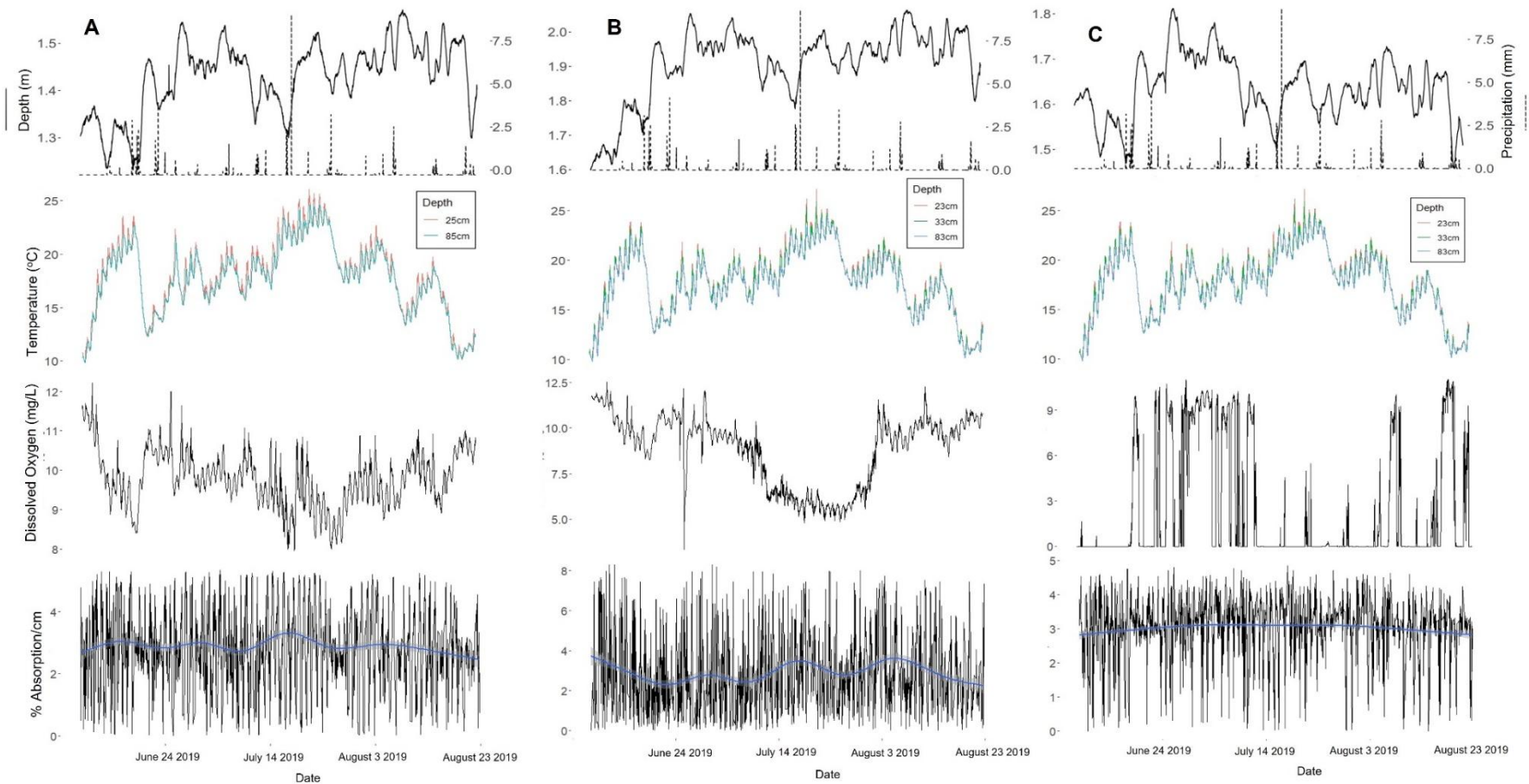
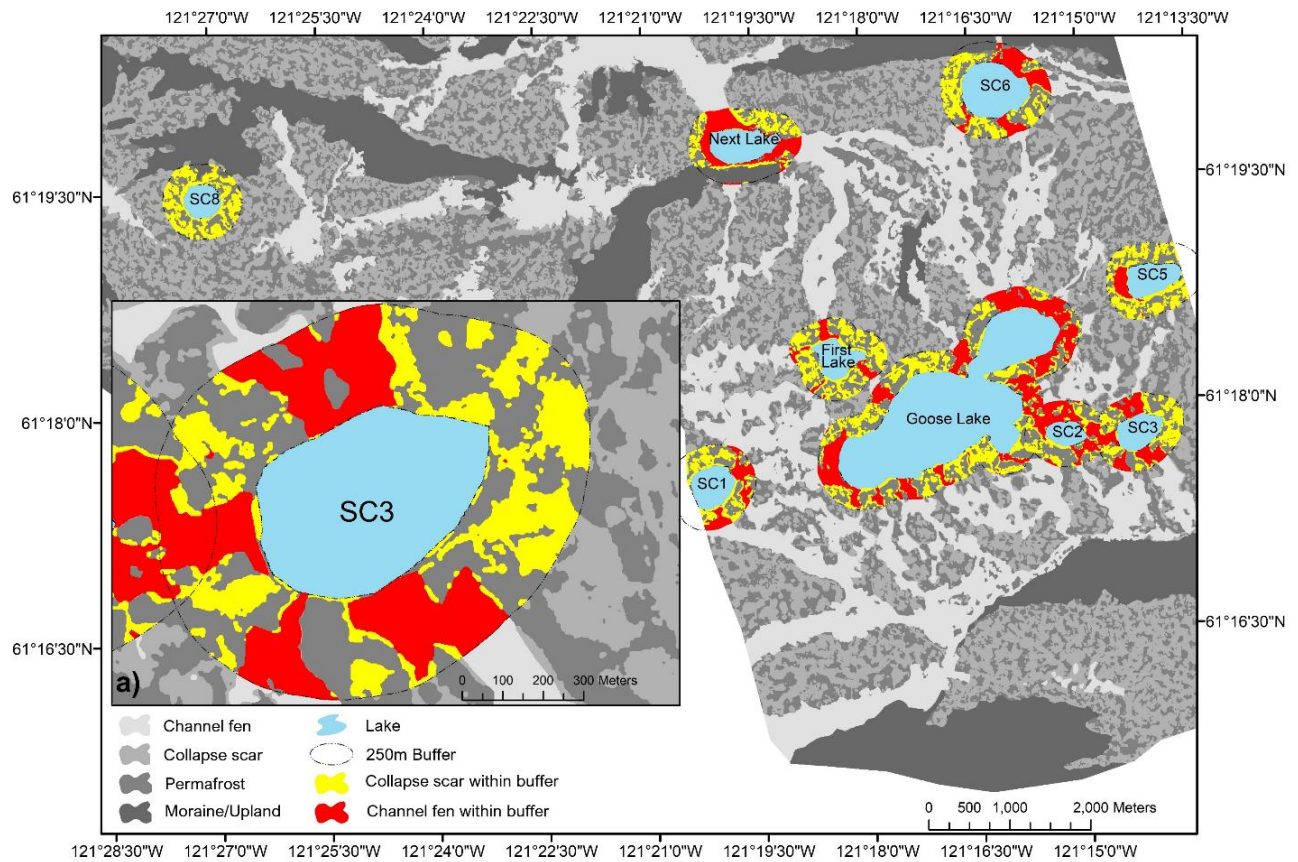


Figure 2.2: Lake depth, temperature, dissolved oxygen and light absorption recorded every 30 minutes from June 7th to August 22nd 2019 from Goose Lake's north basin (A), Goose Lake's main basin (B) and First Lake (C). Precipitation data was recorded from Pluvio totalizing station located near Goose Lake.



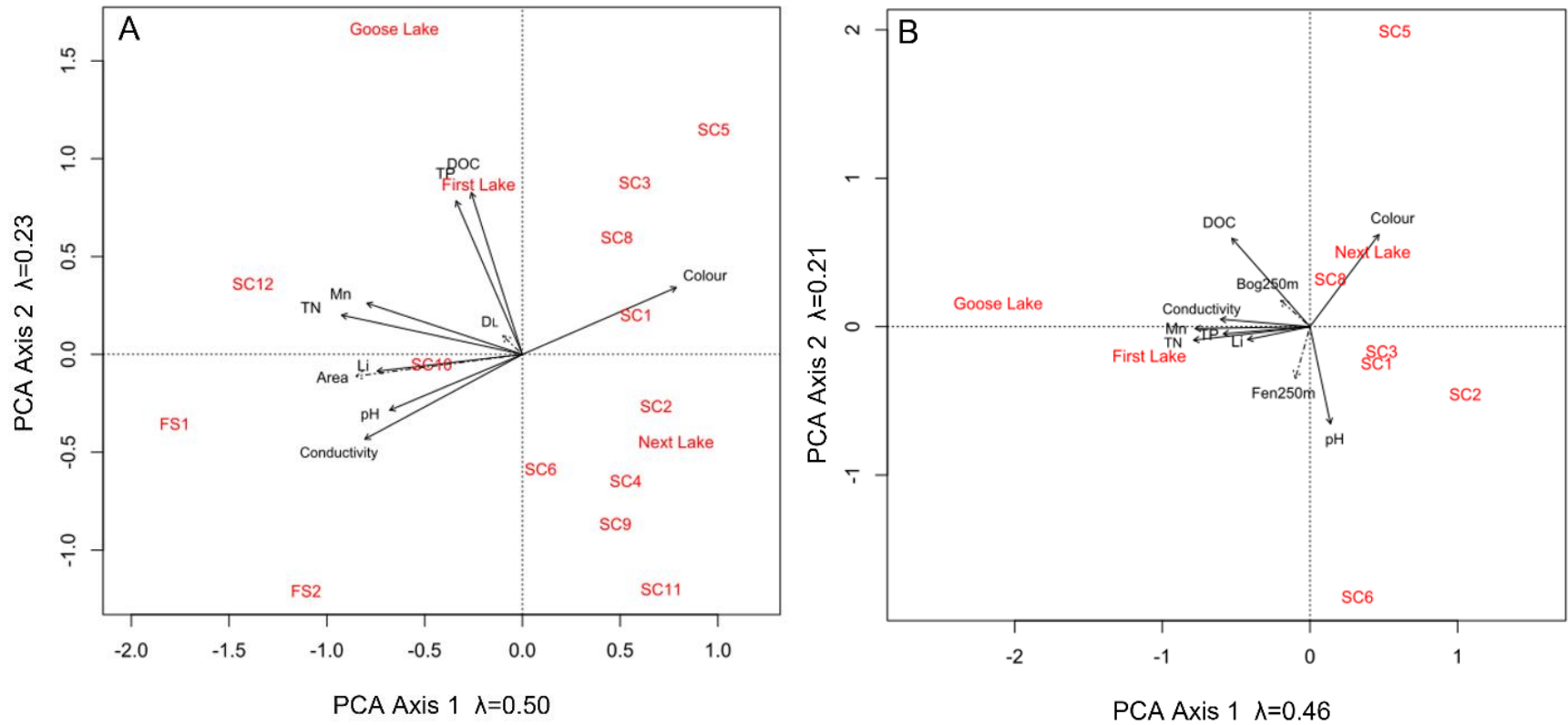


Figure 2.4: Principal components analysis (PCA) of select water chemistry variables and physical characteristics of 16 shallow lakes in the Scotty Creek basin (A) and select water chemistry variables and areal proportion of collapse scar environment (Bog250m) and fen environment (Fen250m) within 250 m of lakes shorelines for 9 lakes included in landscape classification analyses (B). Dashed lines represent variables plotted passively. Area = lake area, D_L = shoreline development index.

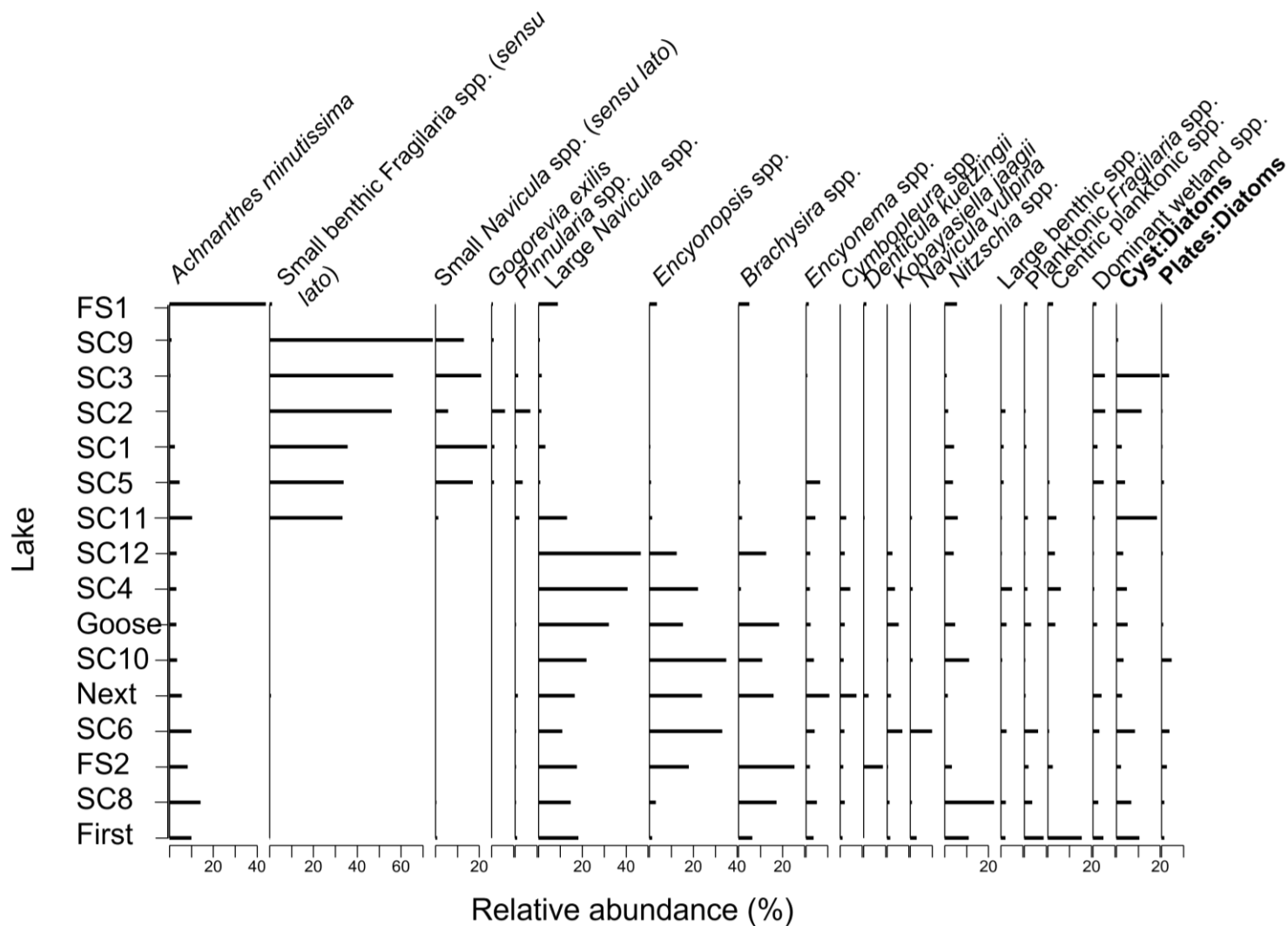


Figure 2.5: Relative abundance diagram displaying the most common diatom taxa in the modern sediments retrieved from 16 shallow lakes in the Scotty creek and neighbouring basins. Species were grouped based on similar ecology. Species or ecological groups present at less than 2% relative abundance were removed. Lakes were ordered using diatom PCA axes scores. Ratio of chrysophyte cysts to diatom valves and protozoan plates to diatom valves are also displayed.

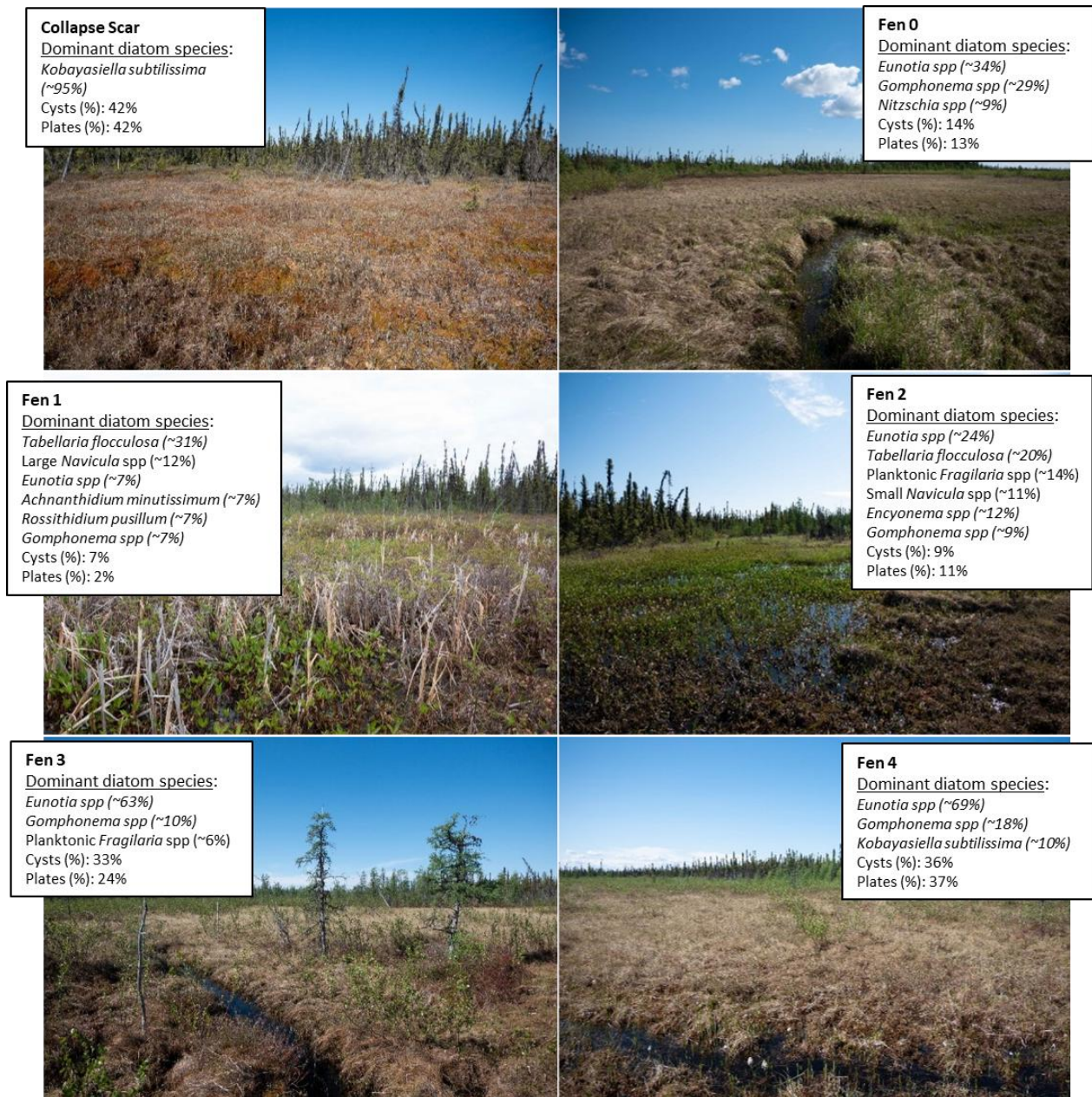


Figure 2.7: Ground-level photographs of wetland sites and corresponding list of dominant diatom species identified in a sample retrieved from the site. Percentage of chrysophyte cysts and protozoan plates, in relation to diatom valves, are also listed.

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Chapter 3: Divergent trajectories of ecological change in shallow thermokarst lakes of a rapidly thawing discontinuous permafrost peatland

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Author's Contributions

KAC, JBK, and WLQ conceived of research ideas and acquired funding, KAC and JRT conducted field work and acquired all samples for analysis. KAC conducted all other analyses and led the writing of the manuscript. This manuscript was integrated with another manuscript and published in Canadian Journal of Fisheries and Aquatic Sciences as:

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Abstract

The southern permafrost peatlands of the Taiga Plains Ecozone (Northwest Territories, Canada) are on the front lines of climate change, sensitive to even small increases in mean annual air temperatures. As permafrost is a major driver of water quantity and quality, studies examining the impacts of thaw on waterbodies of discontinuous permafrost peatlands are necessary for mitigating and adapting to climate change. Here, we use a diatom-based paleolimnological analysis of 15 small, shallow lakes in the Scotty Creek basin (Dehcho region) to provide a regional assessment of trajectories in lake ecosystem change in response to climate warming and permafrost thaw. Diatom assemblages in our study lakes implicate water colour and lake depth as critical, interacting drivers that control the availability of benthic epiphytic habitat. The drastic species turnover recorded in a few lakes indicates there may be an ecological threshold that controls benthic production; however, the ways in which water colour and lake depth interact to drive these threshold shifts is unclear and an area for future research. Finally, we provide evidence that lakes are following divergent trajectories with respect to lake colour, with diatoms indicating increases in water colour (brownification) in some lakes, and increases in water clarity in others, indicating that lake browning is not a unidirectional phenomenon across thawing permafrost landscapes.

Introduction

The accelerated rate of permafrost thaw with climate warming is rapidly transforming landscapes across the circumpolar North (Quinton et al., 2019; Spence et al., 2020; Wright et al., 2022). In discontinuous permafrost peatlands, rapid loss of permafrost is converting forest into wetlands, with implications for hydrological connectivity and biogeochemical cycling in watersheds (Vonk et al., 2015; Wright et al., 2022). Located at the southern limit of permafrost, these ecosystems are on the front lines of change, sensitive to even small increases in mean annual air temperatures (Devoie et al., 2019; Spence et al., 2020) and projected to transition to a permafrost-free landscape in as little as a few decades (Chasmer & Hopkinson, 2017). Given that permafrost is a driver of water quantity and quality (Wright et al., 2022), studies into the impacts of thaw on waterbodies of discontinuous permafrost peatlands are of critical importance for mitigating and adapting to climate change.

In the discontinuous permafrost zone of the Taiga Plains Ecozone, permafrost is typically restricted to forested plateaus, surrounded by a wetland complex made up of collapsed scar wetlands (i.e. bogs and poor fens), linear channel fens, and small thermokarst lakes (Wright et al. 2022). The landscape of the Taiga Plains has low topography, and here channel fens act as the main pathways for water to move through watersheds to the drainage outlet. As permafrost is lost and peat plateaus collapse, bogs and fens become more hydrologically-interconnected, which can impact the flow of materials (e.g. nutrients, organic matter, and sediments) from land to water (Rydberg et al. 2010; Vonk et al., 2015; Wright et al., 2022)

In discontinuous permafrost peatlands, alterations to the biogeochemical cycling of terrestrial organic matter are of primary concern because of the implications for the global carbon cycle

(Cole et al. 2007; Grasset et al. 2018). Permafrost thaw can increase the availability of terrestrial organic matter (t-OM) previously stored in frozen soils (Rydberg et al. 2010), potentially resulting in increased export of dissolved organic carbon (DOC) to ponds, lakes, and streams, with implications for aquatic ecosystem function (Vonk et al. 2015; Wright et al. 2022). For example, increases in DOC concentrations can lead to “lake browning”, a phenomenon that reduces the amount of light that penetrates the water column, limiting primary productivity and increasing carbon subsidies available for heterotrophic respiration, which in turn has implications for lake oxygen dynamics (Vonk et al. 2015; Wright et al. 2022). High concentrations of coloured, or aromatic, DOC have been observed in lakes in permafrost thaw-affected catchments across the circumpolar north, indicating a potential link between permafrost degradation and lake browning (Wauthy et al. 2018). Temporal dynamics of lake DOC are complex, however, and influenced by lake ontogeny (Bouchard et al. 2011). Furthermore, as channel fens and collapse scars process terrestrial organic carbon differently, post-thaw vegetation succession and the position of a lake within the broader watershed hydrological cascade may also influence the trajectory of lake DOC (Gordon et al. 2016). Collectively, these studies indicate considerable gaps of knowledge regarding the prevalence and magnitude of potential thaw-mediated lake browning.

The Scotty Creek basin, located within Taiga Plains ecozone and underlain by sporadic discontinuous permafrost, offers an ideal field location to study lake ecosystem changes resulting from thawing permafrost peatlands. Intensive research examining permafrost hydrology, vegetation changes, and climatological conditions has been conducted at Scotty Creek since the mid-1990s, providing a unique long-term perspective on watershed changes rarely available for remote subarctic regions (Quinton et al. 2019). Despite its well-studied watershed, limited

research has been conducted to date on the many small lakes located within the Scotty Creek basin. Although there are no long-term monitoring records available for the lakes, the field of paleolimnology offers an indirect method for reconstructing past environmental conditions by using chemical, biological, and physical proxy data preserved in lake sediments, in lieu of direct observational records. Numerous paleolimnological proxies have been used to reconstruct changes in thermokarst lakes, including inferences of DOC and other water chemistry parameters (Bouchard et al. 2016). Diatoms, a group of unicellular algae with siliceous cell walls, are especially useful paleolimnological proxies for tracking changes in lake habitat, water depth, and water quality (e.g. Pienitz & Smol 1999; Michelutti et al. 2003; Coleman et al. 2015; Hargan et al. 2015).

We conducted a diatom-based paleolimnological assessment at a coarse temporal scale for 15 lakes in the Scotty Creek and neighboring basins (Figure 1), to provide a snapshot of lake ecosystem change in this region. Three sediment intervals were selected from each sediment core: 1850, 1950, and present-day (surface sediments). The current warming trend in the region began in the 1970s and permafrost was relatively stable until this point (Quinton et al. 2019), so we selected ~1950 as our midpoint interval to capture the period prior to the current period of rapid warming and permafrost thaw. This study provides a regional perspective of the variability in lake ecosystem change trajectories in response to thawing permafrost and potential increased export of t-OM, in a region representative of broader subarctic peatland environments.

Methods

Study site description

The Scotty Creek basin is located in the lower Liard River Valley in the southwestern Northwest Territories of Canada, in the Taiga Plains ecozone (Quinton et al. 2019). It is characterized by low-relief and extensive peatlands, and is underlain by sporadic discontinuous permafrost (Quinton et al. 2019). Air temperatures have been increasing in this region since ~1970, and it is predicted that the area will be permafrost free by mid-century (Chasmer & Hopkinson 2017). Currently, permafrost exists beneath treed plateaus, surrounded by predominately treeless fens and collapse scar wetlands that are expanding with continued permafrost degradation. It has been theorized that current observations of forest loss and wetland expansion in discontinuous permafrost peatlands is a transitional state, and does not represent the end successional stage (Carpino et al. 2021). The continued degradation of permafrost will produce more pathways for water flow, which may ultimately result in the drainage of these wetlands, and the reestablishment of forests on a permafrost free landscape. This is supported by analysis of remotely-sensed imagery from the Scotty Creek basin, which shows evidence of “greening” along the margins of collapsed permafrost thaw scars and evidence of “treed bogs” which appear to be an indication of forest regrowth on drying bogs (Chasmer & Hopkinson 2017; Disher et al. 2020). Similarly, recent research examining the response of the Scotty Creek basin to an El Nino event in 1997/1998 demonstrated a threshold response that resulted in the acceleration of permafrost thaw, and increased drainage efficiency of the landscape (Chasmer & Hopkinson 2017).

The 15 study lakes (Figure 3.1) are small (11 to 244 ha), shallow (~0.9 to 2.1 m;), and circumneutral to slightly alkaline (pH = 7.85-8.75; Table 3.1). At the time of collection, water

colour ranged from 18 to 463 TCU, and DOC ranged from 12.96 to 23.74 mg/L. DOC and water colour were not correlated in this region, suggesting differences in DOC sources or processing between lakes (Chapter 2). Total phosphorus ranged from 8 to 38 $\mu\text{g/L}$, and total nitrogen ranged 0.54 to 1.54 mg/L (Table 3.1).

Core collection and dating

The 15 lakes were accessed by helicopter between July 11-13 of 2018. Sediment cores were collected from the centre of lakes using a Uwitech gravity corer with an internal diameter of 8.6 cm and sectioned into 0.5 cm intervals using a modified Glew (1988) extruder. Sediment core chronologies were established using ^{210}Pb dating and the constant rate of supply model (Appleby, 2001; Appleby and Oldfield, 1978). Samples were analyzed at Queen's University using an Ortec High Purity Germanium Gamma Spectrometer (Oak Ridge, TN, USA) and chronologies were established using ScienTissiME (Barry's Bay, ON, Canada). Certified reference materials were obtained from the International Atomic Energy Association (Vienna, Austria) for efficiency corrections. ^{137}Cs was also used as independent verification as this radioisotope is associated with nuclear fallout which reached peak activity in 1963, before a moratorium was placed on nuclear testing (Appleby 2001). The uppermost 0.5 cm interval (2018), as well as intervals dating to ~ 1850 and ~ 1950 , were selected for analysis. Polynomial regression ($k=2$) was used to interpolate dates and select the interval closest to these time periods.

Diatom preparation and analysis

Diatom slides were prepared following Battarbee et al. (2001) using the hydrogen peroxide method, and mounted using Naphrax®. Diatom valves were identified using an Amscope B690C-PL microscope and multiple reference texts (Krammer and Lange-Bertalot 1997;

Krammer and Lange-Bertalot 1999; Krammer and Lange-Bertalot 2000; Fallu et al. 2000) and online databases (Guiry and Guiry, 2021; Spaulding et al. 2022). Between 350 and 600 valves were counted per interval, except for the bottom sample of SC3 (29-29.5cm; ~1891), where 240 valves were counted as diatom valves were broken and hard to identify. Diatom species were grouped together based on similar ecologies (as discussed in Chapter 2) and were displayed as relative abundances on a relative frequency diagram.

Diatom species data analyses

A principal components analysis (PCA) was used to summarize shifts in diatom species composition between ~1850 to ~1950 and between ~1950 to 2018 using the Vegan package (Oksanen et al. 2019) in R (R Core team). Species data were Hellinger transformed prior to analysis. The samples from both ~1850 and ~1950 were plotted passively, while samples from 2018 were plotted actively. As the primary purpose of running a PCA was to compare the magnitude and direction of change between lakes through time, species data is not displayed on the ordination.

To determine if there were trends in select species across all lakes, a comparison was made of the percent relative abundances between ~1850 and ~1950, and ~1950 and 2018. Species were selected for analysis based on importance in driving variation in the data set (i.e. PCA scores), and habitat preferences identified in Chapter 2 including planktonic species and species groups found in lakes with high (non-chromophoric) DOC versus high colour.

Results and Discussion

Core chronologies

Radioactive decay of ^{210}Pb reached and stabilized at background (i.e. ^{214}Pb) levels in 10 of 15 lake sediment cores (First, Next, SC1, SC4, SC5, SC8, SC9, SC10, SC11, and SC12). A clear ^{137}Cs peak is evident in 6 of these cores (First, Next, SC4, SC5, SC10, and SC12), and support the established core chronologies based on ^{210}Pb dating (Appendices B-P). The sediment core retrieved from Goose Lake shows a steady decline in ^{210}Pb activity; however only two intervals approach or reach background levels. A clear ^{137}Cs peak is evident and supports the chronology established using ^{210}Pb . The sediment core collected from SC2 does not reach background levels, but a clear decline in ^{210}Pb activity occurred that approached and stabilized near background levels, and therefore we feel confident in the established chronology. In the sediment core collected from SC6, only two samples approached or reached background levels. However, a peak in ^{137}Cs at 18cm supports the established ^{210}Pb chronology, so we remain confident in the selection of our sediment intervals for analysis. Radioactive decay in cores collected from SC3 and FS2 did not reach background levels, and the large ^{137}Cs peak identified in SC3 and the small ^{137}Cs peak in FS2 did not support established chronologies for these cores. We interpret data for these cores with caution but based on ^{137}Cs peaks we feel confident that the samples selected at ~1950 for these cores are older than 1970, where warming is believed to have begun in this region.

Diatom-inferred lake change

Across all 15 lakes, 140 diatom species were identified. Principal components analysis (PCA) axis 1 explained 23% of the variation in the dataset. Lakes on the right (positive PCA1 values) of the ordination have high abundances of diatom species that include but are not limited to

Navicula minima, *Sellaphora seminulum*, *Staurosira construens*, and *S. venter*, which are species that have been identified in waters that are more highly coloured (Figure 3.2; Chapter 2; Pienitz et al., 1999). Lakes on the left (negative PCA1 values) of the ordination had high abundances of *Navicula cryptocephala*, *N. cryptotenella*, which are large benthic species, and *Encyonopsis descripta*, and *E. cesatii* (Figure 3.2), which are epiphytic species. All of these species have been identified in lakes with high dissolved organic carbon (DOC) with high water clarity (Chapter 2). PCA axis 2 explained 11% of the variation of the data set, driven by diatom species that include but were not limited to *Discostella pseudostelligera*, a planktonic species, and *Eunotia praerupta* and *E. bilunaris*, which are species commonly found in wetlands (positive axis 2 values).

Lake sites at all time periods (~1850, ~1950, and 2018) are spread primarily along axis 1, with the exception of SC9, which plots negatively on axis 2, and First Lake, which plots positively along axis 2. We suggested in Chapter 2 that lake separation along diatom PCA axis 1 may be due to differences in benthic production. Lakes that plot positively along PCA axis 1 (SC1, SC2, SC3, SC5, and SC9) prevent the development of a benthic moss mat owing to their highly coloured water, while those that plot negatively along PCA axis 1 (Next, Goose, SC4, SC6, SC10, and SC12) allow for moss mat development (high autochthonous DOC) and support a higher abundance of epiphytic diatom species owing to their relatively clear water.

Many factors associated with a warming climate can affect the composition of diatoms, including changes to lake physical properties (e.g. thermal stability) and availability of resources (e.g. nutrients and light). These factors can interact and lead to variability in diatom responses to climate change (Rühland et al 2015). Although no consistent, straightforward trend in the direction and magnitude of diatom-inferred lake change across all lakes is evident in the PCA ordination, some general patterns are observed. For example, shifts in species composition were

greater between 1950 and 2018 compared to 1850 and 1950 for most lakes. Such an accelerated rate of change in the lakes aligns with the accelerated rates of permafrost thaw (Chasmer & Hopkinson, 2017) and resulting landcover (Beilman and Robinson, 2003; Carpino et al., 2021) and hydrological (Connon et al., 2018; St. Jacques & Sauchyn, 2009) change in their catchments and throughout the study region in recent decades. Other patterns are discussed in more detail below.

Highly coloured lakes

Lakes that fall to the right (positive PCA1 values) of the PCA ordination (SC1, SC2, SC3, SC5, and SC9; Figure 3.2) have high abundances of *N. minima*, *S. seminulum*, *S. construens*, and *S. venter*, (Figure 3.3) and are lakes with high colour (Table 3.2). SC9, which plots negatively along axis 2, had markedly lower diversity compared to SC1, SC2, SC3, and SC5 (Figure 3.3). As the deepest lake in the data set (2.1m), the low diversity might be explained by low light penetration in the benthic zone due to deeper waters and dark water colour. Small-celled diatoms are better able to compete for limiting resources, including light (Finkel et al., 2009) and therefore dominate the abundance in this deeper lake.

Diatom assemblages in lakes SC1, SC2, SC3, and SC5 shift further to the right (increase in PCA1 values) in the ordination (Figure 3.2), which is associated with species that are prevalent in lakes with higher colour. However, although increases in small *Navicula* species *sensu lato* (mostly *N. minima* and *Sellaphora seminulum*) are observed (Figure 3.3; 3.4), decreases in the abundances of small benthic *Fragilaria* species *sensu lato* (i.e. *S. construens* and *S. venter*), were also observed (Figure 3.3; Figure 3.4). As both species groups are associated with higher colour, the increase in one and the decrease in the other may be a result of other ecological changes associated with a warming environment, such as an increase in the length of the ice-free season

or increases in nutrients exported from thawing permafrost. Alternatively, changes in colour may confer an advantage for the small *Navicula* species (*sensu lato*) over the small *Fragilaria* species (*sensu lato*); although both are competitive under low light, one might out-compete the other.

There remains confusion over the taxonomic identity of small *Naviculoid* species, including the species we have identified here as *N. minima* and *S. seminulum*. *N. minima* has been misidentified in the literature as many species including *Eolimna minima*, *Sellaphora atomoides*, *S. seminulum* and *S. saugerresii*. Wetzel et al. (2015) attempts to improve clarity over identification of small *Naviculoid* species, and based on this analysis the species identified in these lakes as *N. minima* is synonymous with *S. saugerresii*. The confusion and frequent misidentification of these small species in the literature creates a challenge in determining habitat preferences, so determining the significance of the shift identified here is challenging and remains speculative. Small benthic *Fragilaria* species, however, are commonly found in harsh, low light conditions, and decrease in abundance with warming as new habitats emerge (Bouchard et al., 2013; Rühland et al., 2008), which supports the speculation that the shift to higher proportions of small *Navicula* species (*sensu lato*) is a result of climate warming. Future investigations of diatom biogeography in small lakes of the Taiga Plains are required to identify the drivers of a shift between small *Navicula* and small *Fragilaria*.

While the diatom assemblage shifts in SC1, SC2, SC3, SC5, and SC9 are more muted, the shift in SC11 is more pronounced. The diatom composition in SC11 shifted from *Pinnularia* species (*P. gibba*, *P. interrupta*, *P. legumen*, *P. maior*, *P. microstauron*, *P. nodosa*, *P. streptoraphe*, and *P. viridis*), *Denticula kuetzingii*, and large benthic species, to small benthic *Fragilaria* species, and large *Navicula* species. The decrease in epiphytic *Pinnularia* species and increase in small-celled *Fragilaria* species is consistent with a decline in benthic vegetation and greater

competition for resources that favour small-celled species, such as what would occur with increasing water colour. A shift towards these small diatom species was also identified in a thermokarst lake further east, near Kakisa (southern NT), and was attributed to the acceleration of permafrost thaw identified in aerial imagery and a subsequent increase in coloured DOC (Coleman et al. 2015). Therefore, we suggest diatom changes in SC11 are likely tracking pronounced brownification.

Tracking benthic moss mat development

Lakes that fall to the left (negative PCA1 values) of the PCA ordination (Next, Goose, SC4, SC6, SC10, and SC12) have high abundances of *Navicula cryptocephala*, *N. cryptotenella*, *Encyonopsis descripta*, and *E. cesatii*. Many of these species are epiphytic and all have been found to be associated with benthic moss mats (Chapter 2). These lakes generally have higher DOC despite having lower than average colour (Table 3.2), which suggests the DOC in these lakes may be from aquatic sources (Pagano et al., 2014). Reduced colour in lakes can also be the result of photobleaching, which would be expected in lakes that have high residence times; however, as these lakes are all connected to the channel fen network, there is nothing to suggest that high residence time and photobleaching would impact them and not the other lakes of this study.

The trajectories of diatom changes in these lakes are variable, with no clear, consistent pattern observed from the PCA biplot (Figure 3.2), though closer examination at the species-level reveals some trends. For example, abundances of *Encyonopsis* species (*E. cesatii* and *E. descripta*) increased in most of these lakes between ~1950 and present (2018) (Figure 3.3; Figure 3.4), but were fairly stable between ~1850 and ~1950. The increase in *Encyonopsis* species is likely the result of moss mat development, as these are epiphytic species. Warming air

temperatures and increased length of the open water season would promote the development of benthic vegetation, and therefore this increase is likely a result of regional warming that accelerated after ~1970 (Quinton et al 2019). Abundances of large *Navicula* species (*N. cryptocephala*, *N. cprtotenella*, and *N. radiosa*) were more variable through time (Figure 3.3; Figure 3.4). The presence of these large benthic species, as well as *Encyonopsis* species, suggests that conditions were favourable for benthic primary production (i.e. high water clarity) in most of these lakes for at least the past ~170 years, with FS2 as a notable exception.

FS2 underwent an almost complete turnover in species between 1850 and present (Figure 3.3), transitioning from an assemblage dominated by small benthic *Fragilaria* species to an assemblage dominated by epiphytic *Encyonopsis* species and *Brachysira* species, which are common in lakes with higher pH (Spaulding et al., 2021). This shift is indicative of moss mat growth and expansion. A similar diatom shift was identified in a thermokarst lake in the Old Crow Flats, Alaska, US and was also attributed to an increase in water clarity that allowed for macrophyte development (MacDonald et al., 2012). We suggest two possible mechanisms that might explain this dramatic shift. First, we postulated (Chapter 2) that an increase in fen development due to continued permafrost thaw might have a flushing affect on lakes and decrease the high concentration of chromophoric DOC as more water moves through the system. Olefeldt et al. (2012) found that while fens export more DOC annually than other landscape features, DOC concentrations are lower due to increased water availability for transport. The diatom shift recorded in FS2 may be a result of decreasing colour, which would support the development of a benthic moss mat. Alternatively, it has been hypothesized that as permafrost continues to degrade, the development of new hydrological pathways may begin to drain these permafrost wetlands (Chasmer & Hopkinson 2017; Carpino et al., 2021), and therefore we might

be seeing evidence of this through decreased lake depth, which would also support moss mat development. Archived aerial images may be key to determining what may have caused this marked diatom shift and might provide key insights in the future trajectory of other lakes in this region.

Increases in planktonic production

First Lake is compositionally different than the other lakes in this study and became more dissimilar from the other lakes through time (Figure 3.2). This lake is unique in that it has a high abundance of planktonic species, including small centric species (mostly *Lindavia michiganiana* and *Discostella pseudostelligera*) and planktonic *Fragilaria* species (mostly *F. tenera*) that drive lake changes along PCA axis 2 (Figure 3.3; Figure 3.4). Although the increase in planktonic species is most striking in First Lake, increases in planktonic species were observed in most lakes in the Scotty Creek basin (Figure 3.3; Figure 3.4). A key competitive advantage of these planktonic species is the ability to stay in the water column in a thermally stratified lake, especially if light resources are limiting (Rühland et al., 2015); however, evidence suggests that these shallow lakes do not thermally stratify (Chapter 2), at least based on one year (2019) of instrumental data. A shift to increased planktonic production at the expense of benthic production could also occur in response to increased highly coloured DOC (Rosén et al., 2009). Further evidence that this may be the mechanism underlying the increase in planktonic diatoms in First Lake comes from the concomitant species shifts to smaller-sized diatom species (Figure 3.3), which are generally more competitive for resources including nutrients and light (Rühland et al. 2015). Remotely sensed data quantifying permafrost loss around First Lake confirms that permafrost has been degrading here since at least the mid 20th century and most notably during

the last two decades (Quinton et al., 2011) providing further evidence that diatom-inferred changes in this lake are linked to thawing permafrost.

In First Lake, we also see an increase in epiphytic species, such as *Achnantheidium minutissimum*, and an increase in large *Navicula* species, which we have observed primarily in the clearer lakes. First Lake is shallow (~0.9m) compared to the average (~1.3m) of the lakes examined in this study. The shallow nature of this lake may support benthic moss mat development, despite darkening water colour. This highlights the importance of understanding context when interpreting species changes in the sediment record (Rühland et al. 2015). The interacting factors of lake depth and water colour in the shallow lakes of the discontinuous permafrost peatlands should be carefully considered when interpreting shifts in diatom assemblages, as even small changes in lake depth may alter the delicate light-DOC balance.

The unique diatom assemblage of a hydrologically disconnected lake

Although the water chemistry of SC8 is unremarkable compared to the other lakes in this study (Table 3.2), it stands out as having an assemblage that is dominated by some species groups that are only found in low abundances in most of the other lakes. *Nitzschia* species (mostly *N. perminuta*) and *Achnantheidium minutissimum* increase in this lake through time and are found in high abundances in the modern assemblage. *N. perminuta* and *A. minutissimum* are common across the circumpolar north, and have been found to be associated with periphyton (Michelutti et al., 2002, 2007). These generalist species are found across a large gradient of water chemistry variables (Duda et al., 2019; Michelutti et al., 2002, 2007), and therefore changes in the relative abundance of these species in SC8 are likely not tracking any changes in water chemistry. As these species are often found to be associated with periphyton the increase in relative abundance of these species may be tracking moss mat development. Based on landscape classification using

remotely sensed images, SC8 was determined to be hydrologically isolated (Chapter 2), which might explain why the diatom assemblage in this lake differs from other lakes, but the underlying mechanism behind this is unknown.

Conclusions and Future Directions

This research sought to determine the impact of permafrost thaw on small, shallow lakes in a rapidly thawing discontinuous permafrost peatland. It has been hypothesized that permafrost thaw may lead to lake browning (Coleman et al. 2015; Wauthy et al. 2018), but our results suggested that while water colour in some lakes may be increasing (e.g. SC11), water colour may be decreasing in others (e.g. FS2). Lake DOC dynamics are complex, particularly in lakes in the discontinuous permafrost peatlands, which are subject to multiple stressors related to climate change including warming air temperatures, changing ice dynamics, and permafrost thaw.

We suggest that diatom assemblage changes recorded in our study lakes are the result of an interaction between water colour and lake depth that control the availability of benthic epiphytic habitat. Our results also suggest the existence of ecological thresholds that trigger the shift from benthic to planktonic primary production (e.g. First Lake) or a shift to primarily benthic primary production (e.g. FS2); however, how water colour and lake depth interact to create these thresholds is unclear at present and an area for future research. Additionally, gaps in our understanding of the ecology of some common species in this region create challenges for interpreting complex changes. Further studies should seek to better understand the regional species preferences of diatoms identified in these lakes. Pairing paleolimnological studies using multiple proxies with studies using remotely sensed data that track landscape changes may also

be useful for confirming that the changes in lake ecology inferred from lake sediment cores are tracking changes in landscape.

Tables

Table 3.1: Physical characteristics and modern water chemistry statistics for 15 lakes in the Scotty Creek and surrounding basins, collected July 2018. Shoreline development index is the ratio of the length of a shoreline, to the circumference of a circle with same area, where an index of 1 would represent a perfect circle.

	Mean	SD	Min	Max	Median
Depth (m)	1.3	0.4	0.9	2.1	1.2
Area (km ²)	1.06	1.69	0.11	7.13	0.32
Shoreline Development Index	1.18	0.21	1.02	1.75	1.09
pH	8.23	0.27	7.85	8.75	8.20
DOC (mg/L)	18.79	3.13	12.96	23.74	18.35
True Colour (TCU)	176	124	18	463	174
TP (µg/L)(unfiltered)	18.3	7.9	8.0	38.0	17.0
TN (mg/L)(filtered)	0.90	0.28	0.54	1.54	0.79
Conductivity (uS/cm)	106.9	58.5	55.5	244.2	83.1
Alkalinity (CaCO ₃)(mg/L)	54	29	28	124	43
Calcium (mg/L)	15.4	6.5	7.9	29.8	13.3
Potassium (mg/L)	0.61	0.65	0.19	2.49	0.34
Lithium (µg/L)	1.4	0.8	0.7	3.2	1.2
Magnesium (mg/L)	4.67	3.08	2.24	12.70	3.51
Manganese (µg/L)	17.3	8.3	4.9	35.1	15.5
Sodium (mg/L)	2.35	1.93	0.74	7.25	1.62
Silicon (mg/L)	1.52	0.98	0.27	4.33	1.21
Strontium (µg/L)	61.1	36.0	28.5	149.0	45.3

Table 3.2: Lake depth, lake area, dissolved organic carbon (DOC) concentrations, and true colour of 15 lakes in the Scotty Creek and surrounding basins, collected July 2018.

Lake	Depth (m)	Area (km ²)	DOC (mg/L)	True Colour (TCU)
Goose Lake	1.1	2.44	23.74	53.42
First Lake	0.9	0.17	21.93	249.3
Next Lake	1.5	0.24	18.25	258.2
FS1	1	7.13	19.3	26.71
FS2	1.5	1.68	14.98	17.81
SC1	1.3	0.21	16.93	222.6
SC2	1.7	0.11	18.04	311.6
SC3	1.8	0.18	18.44	276
SC4	1.1	0.22	17.2	142.5
SC5	1	0.21	23.64	463
SC6	1.1	0.4	15.84	53.42
SC8	0.9	0.15	19.94	284.9
SC9	2.1	0.82	12.96	151.4
SC10	1.2	0.73	20.01	89.03
SC11	2	1.14	15.85	195.9
SC12	0.9	1.16	23.57	26.71

Figures

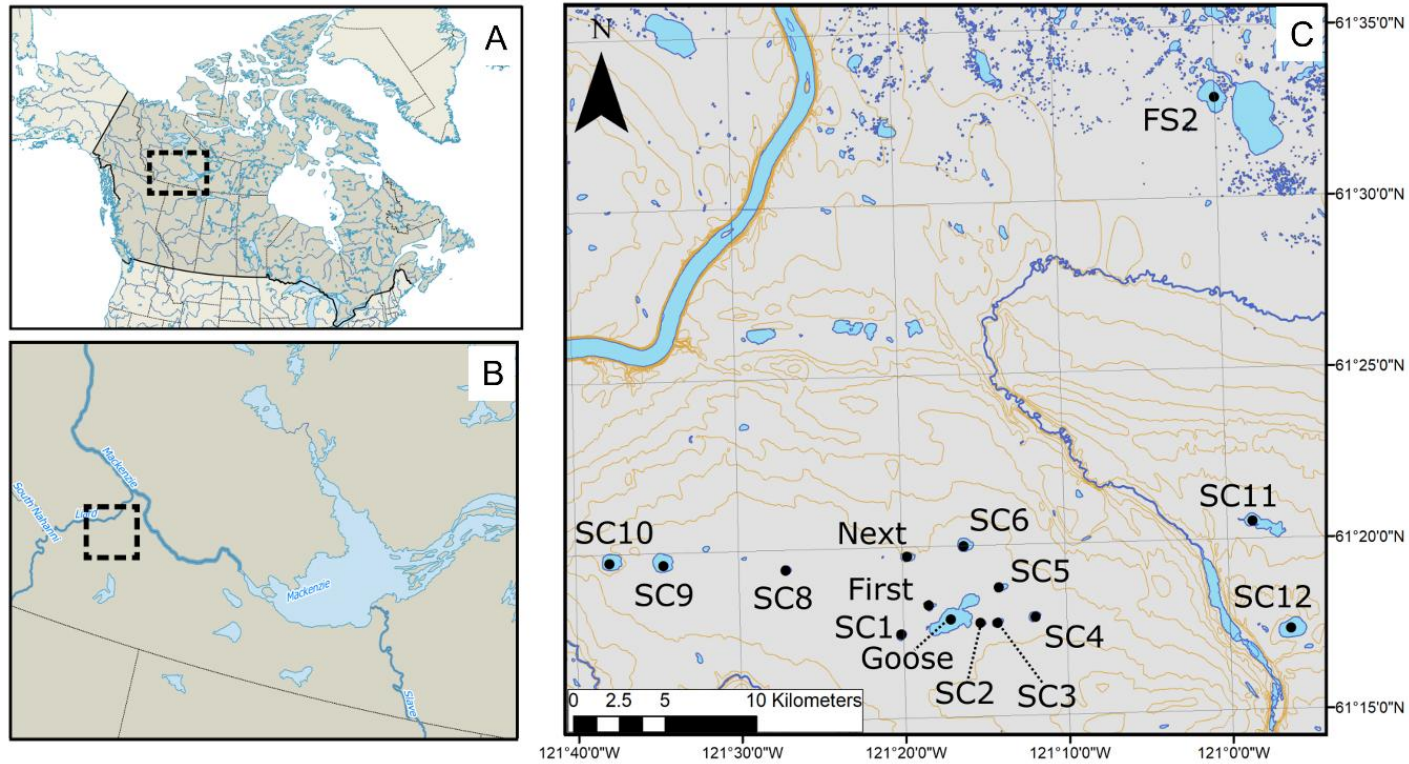


Figure 3.1: Map of study area. (A) Approximate location of site within Canada, (B) approximate location of site within Taiga Plains ecozone, (C) location of all study sites.

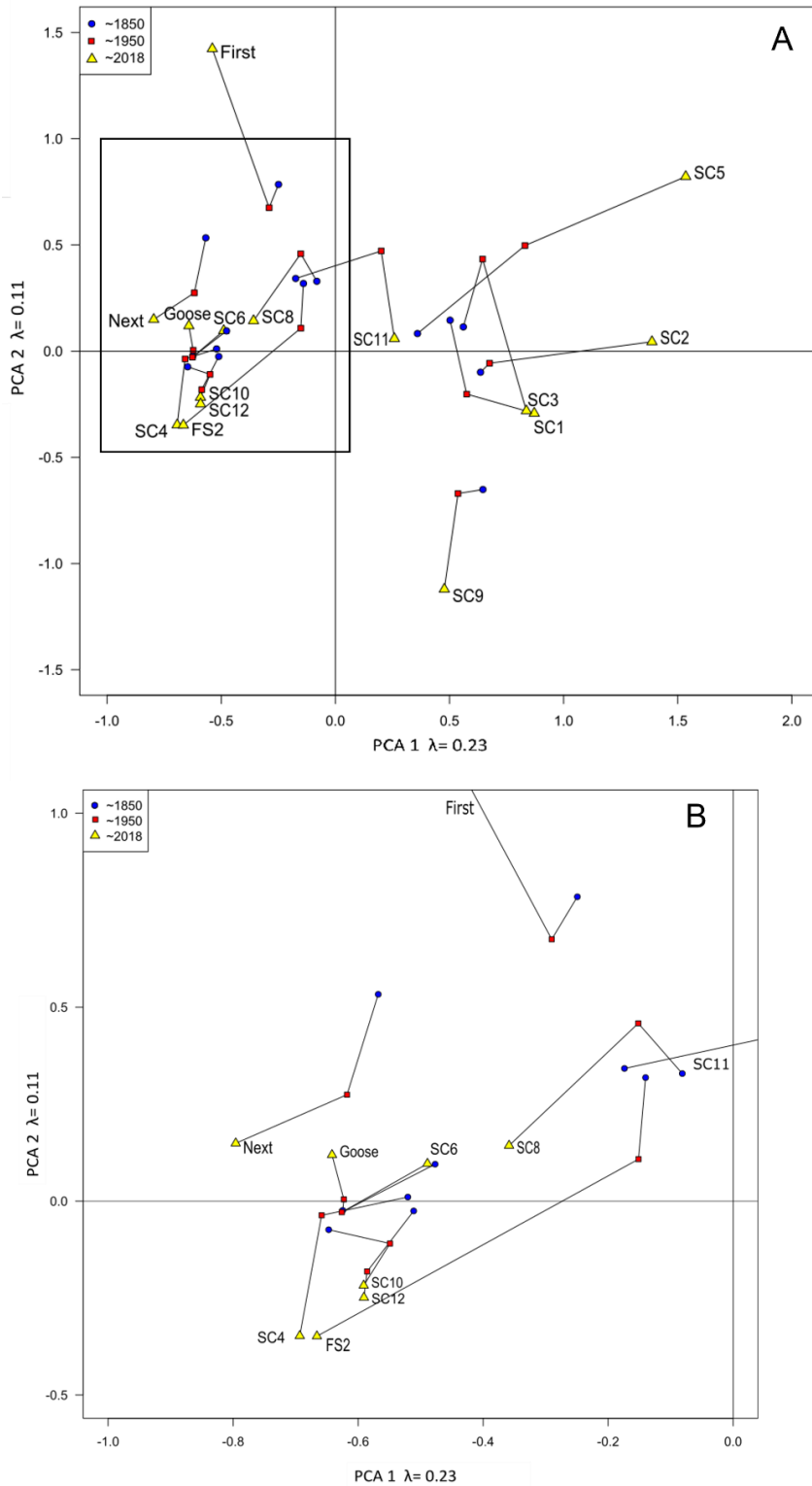


Figure 3.2: (A) Principal components analysis (PCA) biplot of diatom species in 15 shallow lakes in the Scotty Creek basin across three different time periods (~1850, ~1950, ~2018). Species names and vectors were removed the ordination to highlight the degree and direction of change in species composition between ~1850-1950 and ~1950-2018 for each lake. (B) Enlarged section of the ordination highlighted in (A).

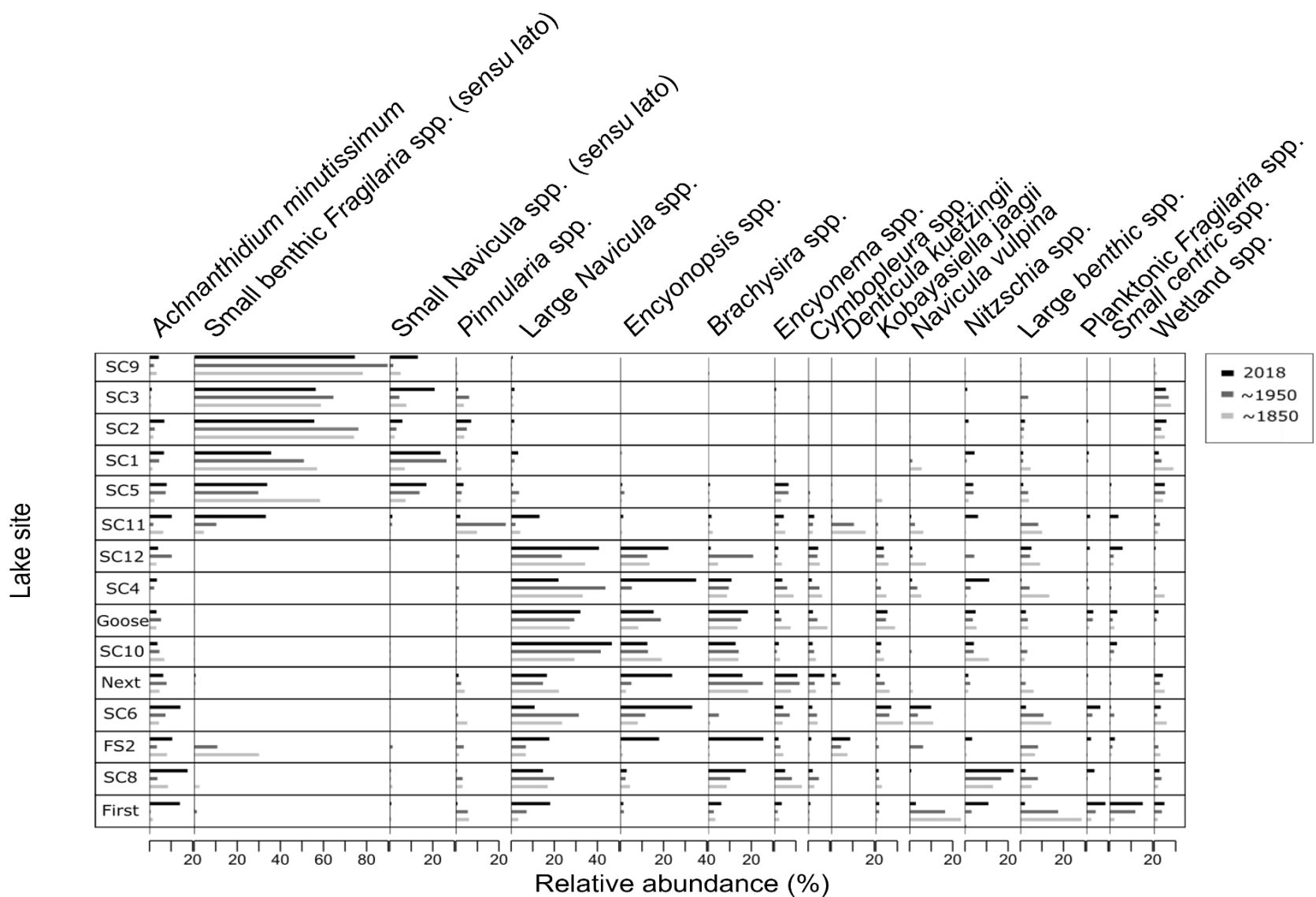


Figure 3.3: Relative abundance diagram displaying the most common diatom taxa in three time periods (~1850, ~1950, and 2018) from 15 shallow lakes in the Scotty creek and neighbouring basins. Species were grouped based on similar ecology. Species or ecological groups present at less than 2% relative abundance were removed.

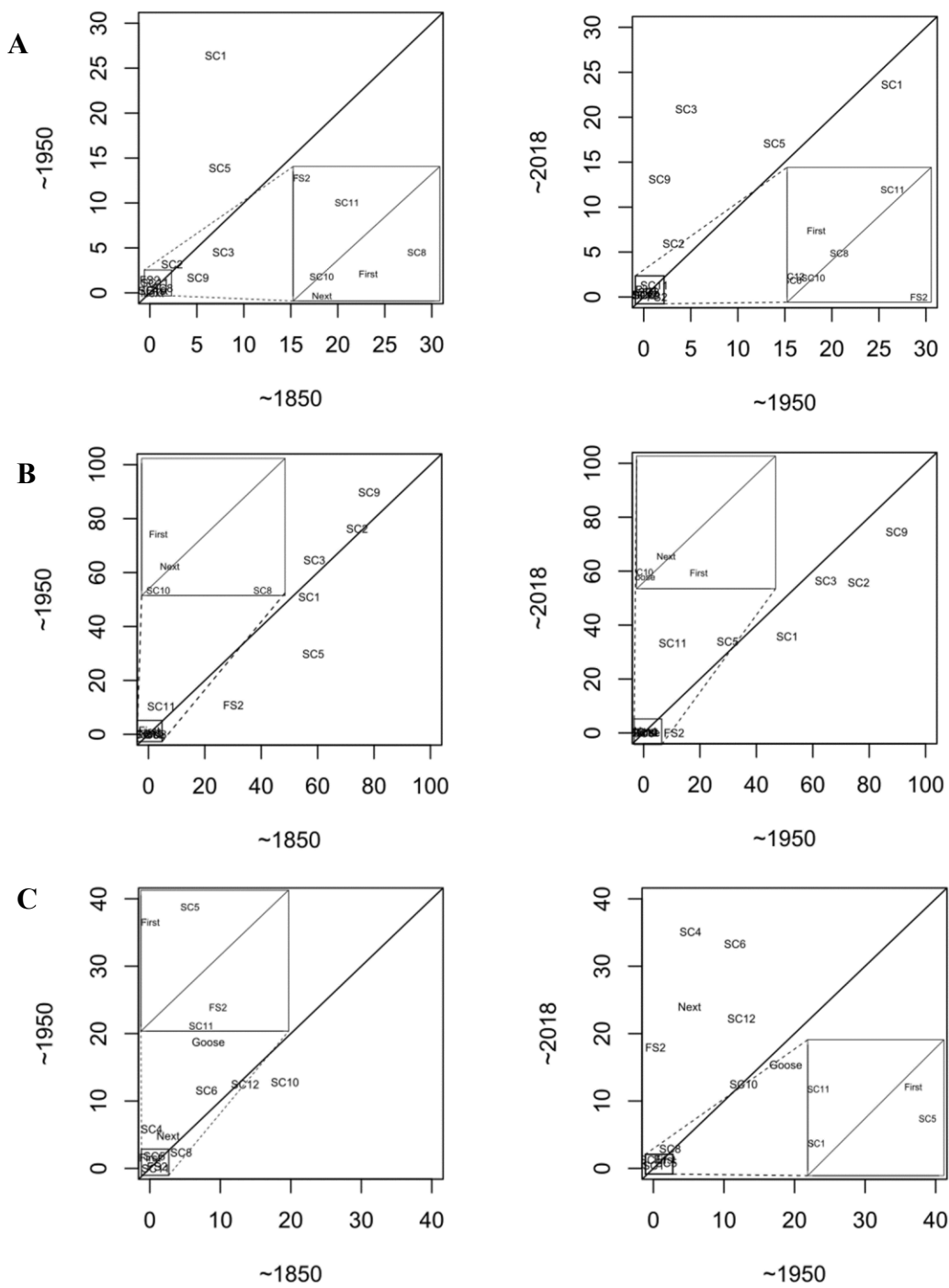


Figure 3.4: Scatterplots with 1:1 line showing changes in A) Small *Navicula* species (*sensu lato*); B) Small benthic *Fragilaria* species (*sensu lato*); C) *Encyonopsis* species; D) Large *Navicula* species; and E) Planktonic species, between ~1850 and ~1950 (left), and ~1950 and 2018 (right).

Chapter 4: Examining trajectories of ecological change in five small lakes along a gradient of hydrological connectivity in a rapidly thawing discontinuous permafrost peatland

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Author's Contributions

KAC, JBK, and WLQ conceived of research ideas and acquired funding, KAC and JRT conducted field work and acquired all samples for analysis. KAC conducted all other analyses and led the writing of the manuscript. All authors contributed to research ideas, field planning, and research guidance. This manuscript is in preparation for submission to the Journal of Paleolimnology.

Abstract

Small shallow lakes are abundant features of high latitude landscapes and play a critical role in the biogeochemical cycling of carbon. The rapid loss of permafrost is mobilizing vast stores of carbon and bound mercury into the surrounding wetlands and lakes, yet these ecosystems remain understudied. Long-term records are needed to understand the environmental trajectories of small lakes in rapidly changing landscape, and how trajectories of lake change are influenced by their hydrological and biogeochemical connections to the terrestrial landscape. Here we use paleolimnological methods to track long-term changes ecology and sources of organic matter to five small lakes along a gradient of hydrological connectivity using diatoms, mercury, stable isotopes of carbon and nitrogen, and elemental ratios of organic carbon to nitrogen. We aim to understand the differences in response between connected and isolated lakes, and the role that position in a hydrological cascade may play in the magnitude of response. Understanding the impact to aquatic ecosystems and biogeochemical cycling at the rapidly changing permafrost boundary will aid our ability to predict and model changes that will occur as the permafrost boundary continues to move northward.

Introduction

Small, shallow lakes play a critical role in the global biogeochemical cycling of carbon, and alterations to these understudied ecosystems have important implications for the global carbon budget (Downing, 2010; Tranvik et al., 2018). These ecosystems are abundant features across the circumpolar North (Olefeldt, et al., 2021b) where climate warming is enhancing biogeochemical activity and hydrological connectivity in watersheds (Connon et al., 2014; Olefeldt, et al., 2021a). Of particular concern are the impacts of thawing permafrost in highly organic terrain, where permafrost is rapidly being lost in response to anthropogenic climate change (Karlsson et al., 2012; Payette, 2004; Wright et al., 2022). Permafrost peatlands store vast quantities of organic carbon and mercury that can be mobilized upon thaw (Ryberg et al. 2010; Korosi et al. 2015; Vonk et al. 2015; Olefeldt et al 2021b). As small, shallow lakes are connected to the surrounding wetland complex along hydrologic cascades, carbon, mercury, and other chemical constituents released from thawing permafrost will traverse through these waterbodies along the path to the drainage outlet. Consequently, our understanding of the implications of permafrost thaw on biogeochemical cycling in peatlands is incomplete without accounting for limnological dynamics in small, shallow lakes.

The southern Taiga Plains ecozone (Northwest Territories, Canada) is a peatland-dominated landscape that is predicted to be permafrost-free by 2050 (Chasmer & Hopkinson 2017).

Documented increases in stream discharge independent of changes in precipitation indicate a landscape in a period of rapid transition because of thawing permafrost (Connon et al., 2014; Quinton et al., 2019; Quinton & Baltzer, 2013). The landscape is a mosaic of permafrost free wetlands (primarily channel fens and collapse scars) and permafrost plateaus, interspersed by shallow water bodies. As permafrost thaws, the forested peat plateaus become waterlogged and

transition into wetlands (Carpino et al., 2021). The primary hydrological function of collapse scars on the landscape is water storage, while channel fens act as corridors that convey water to the main drainage outlet. An increase in the proportion of channel fens therefore increases the hydrological connectedness of the landscape (Connon et al., 2014; Olefeldt et al., 2021b). The increased movement of water across the landscape can also increase the flow of materials (e.g. sediments, organic matter, nutrients, and contaminants) from land to aquatic ecosystems, including that which was previously stored in frozen soils (Rydberg et al., 2010; Vonk et al., 2015). Widespread “lake brownification” [the darkening of water colour because of increased terrestrial organic matter (t-OM)] has been projected in areas impacted by permafrost thaw (Wauthy et al., 2018).

While several studies provide evidence of lake brownification across the North (Coleman et al., 2015; Wauthy et al., 2018; Chapter 2), this trend is not universal, with individual lakes following different ecological trajectories (Rosén et al., 2009; Bouchard et al., 2013; Coleman et al., 2015; Korosi et al., 2015; Chapter 3). Similarly, ecohydrological trajectories in northern peatland landscapes exhibit considerable spatial heterogeneity that complicates efforts to model their carbon sink capacity under future climate warming scenarios (Zhang et al., 2022). The limnology of small, shallow lakes, including patterns and trajectories in lake water quality, is expected to be tightly coupled to the terrestrial landscape. The proportion of nearshore collapse scars or channel fens may be an important driver of lake water chemistry, given the distinct differences in water chemistry between the two wetland types (Mzobe et al., 2018; Olefeldt & Roulet, 2012; Chapter 2). Collapse scars tend to export DOC with higher C/N ratios, higher aromaticity and higher colour than fens, while fens overall export more DOC due to high water transport (Olefeldt & Roulet, 2014). Therefore, a lake’s response to permafrost thaw may be driven by changes in the

local geography that leads to the formation of either fens or collapse scars. However, this relationship is not straight forward (Chapter 2), and while the presence and degree of landscape coverage of wetlands contributes to lake water chemistry, the nature of the connections may also be important (Rosen et al., 2009). For example, Gordon et al. (2016) found that carbon aromaticity increased along a cascade of connected collapse scars and fens, likely due to the enrichment of recalcitrant, aromatic compounds through microbial degradation as water moved along the cascade. Similarly, Olefeldt and Roulet (2014) also found that fens are biogeochemical hotspots and carbon aromaticity increased from fen inflow to fen outflow. Groundwater fluxes to small, shallow lakes is likely also an important contributor to water quality, and groundwater fluxes are projected to increase with permafrost thaw (Olefeldt et al., 2021b). Very little is currently known about the role of groundwater in driving spatial and temporal variations in subarctic lake water quality.

Increasing export of DOC from permafrost peatlands can act as a vector for the release and transport of contaminants bound within the organic matrix. Mercury is of particular concern, as it binds to organic matter and can enter lakes along with terrestrial organic matter run-off (Korosi et al., 2015). Accumulating in permafrost soils over millennia (Obrist et al., 2017; Schuster et al., 2018), the leaching of mercury from thawing permafrost soils will delay the recovery of northern ecosystems from mercury pollution (Fahnestock et al., 2019; Gordon et al., 2016; Rydberg et al., 2010). Thermokarst wetlands, particularly the channel fens, are hotspots for the microbial transformation of mercury to its highly toxic organic form, methylmercury (Wright et al., 2022). If thawing permafrost increases the export of methyl mercury from northern peatlands into drainage outlets, it could pose a health risk to northern communities (Gordon et al., 2016).

Despite evidence that small lakes are functionally different than large lakes (Manasypov et al., 2015) and play an important role hydrological and biogeochemical cycling at landscape and global scales (Cole et al., 2007; Grasset et al., 2018), data on small lakes is scarce. The paucity of long-term monitoring data on small lakes in northern peatland regions means we are missing critical context needed to understand the future of permafrost peatland landscapes under a warming climate. Long-term records are needed to understand the environmental trajectories of small lakes, and how trajectories of lake change are influenced by their hydrological and biogeochemical connections to the terrestrial landscape. In the absence of direct monitoring data, paleolimnological methods can be used to reconstruct past environments and provide the missing long-term context. Paleolimnology is a multidisciplinary science that uses biological, physical, and chemical proxy data stored in lake sediment cores to study environmental change.

Here, we apply a multi-proxy paleolimnological approach to document trajectories of ecological and biogeochemical change in five small lakes in the Scotty Creek basin (Taiga Plains, Northwest Territories) in different hydrological settings. Three of the study lakes are connected along a hydrological cascade, and two lakes are isolated from the main channel fen network. We analyzed diatoms (unicellular siliceous algae) as paleoecological indicators, which have been shown to be useful for tracking changes related to dissolved organic carbon, light, water depth, and aquatic plant growth (Bouchard et al., 2017; Coleman et al., 2015; Korosi et al., 2022; Michelutti et al., 2003; Pienitz et al., 1999; Pienitz & Smol, 1993; Chapter 2). We also analyzed mercury, stable isotopes of carbon and nitrogen, and elemental ratios of organic carbon to nitrogen to track potential changes in biogeochemical cycling and sources of organic matter to the lakes. The overall aim of this study was to derive new insights into the role that hydrological connectivity may play in influencing trajectories of lake biogeochemical and ecological change

in thawing permafrost peatlands. Are responses to permafrost thaw muted in lakes that have more hydrological connections? Does position in hydrological cascade impact response? Answering these questions will aid in projections of future change as the permafrost boundary continues to move northward.

Methods

Site Description

The Scotty Creek basin is in the Dehcho region of the Northwest Territories (NT), in the lower Liard River Valley ~50km south of Fort Simpson. The lower Liard River valley is an open-water and peatland rich area characterized by highly organic flat terrain (Quinton et al., 2019). Over 3 decades of intensive research in the Scotty Creek basin has documented rapid landscape changes associated with thawing permafrost as air temperatures increased (Chasmer & Hopkinson, 2017; Quinton et al., 2019). Recent observations of landscape drying indicates that the opening of hydrological pathways is ultimately leading to wetland drainage, which will eventually support the re-establishment of forests on permafrost-free land (Chasmer & Hopkinson, 2017; Disher et al., 2020; Carpino et al., 2021).

We selected study five lakes within the Scotty Creek basin (Figure 4.1): three lakes that are connected by channel fens along a hydrological cascade (Goose Lake to First Lake to Next Lake), and two lakes that are hydrologically isolated from the channel fen network (SC5, SC8), based on results from Chapter 2. The original Scotty Creek Research Station (SCRS) was located on the northeast shoreline of First Lake but was moved to its current location near the northwest margin of Goose Lake because of ground subsidence from thawing permafrost at the original

site. While SC5 and SC8 are not connected to the channel fen network based on land classification analyses, an unconnected fen environment is present on the shoreline of SC5 (Chapter 2). Alkalinity in these lakes ranged from 28 to 50 mg/L CaCO_3 , while pH was circumneutral to slightly alkaline and ranged from 7.9 to 8.3 mg/L CaCO_3 (Table 1). TN (total nitrogen, filtered) ranged from 0.8 to 1.2 mg/L and TP (total phosphorus, unfiltered) ranged from 9 to 38 $\mu\text{g/L}$ (Table 1). DOC ranged from 18.3 mg/L in Next Lake to 23.7 mg/L in Goose Lake, while colour ranged from 53 TCU in Goose Lake to 463 TCU in SC5 (Table 1). We note here, however, that equipment deficiencies detected after analyses were complete suggest that there numbers may not be accurate. We remain confident that while the value may not be correct, comparison between lakes is still valid as observations in the field and examination of pictures of water samples confirmed that lakes with visibly high colour had the highest values and lakes with lower values had lower colour. We do however need to exercise a high degree of caution when comparing the colour of these lakes to lakes from other data sets.

Core collection and chronology establishment

Sediment cores were collected from the centre of the lakes between July 11 and 13 of 2018, using a Uwitech™ gravity corer with an internal diameter of 8.6 cm. For Goose Lake, which consists of two basins, the sediment core collected from the centre of the smaller, northwestern basin. Cores were sectioned into 0.5 cm intervals on the same day using a modified Glew (1988) extruder. Select intervals were freeze dried and sent to Queen's University for ^{210}Pb dating (Appleby, 2001) using an Ortec High Purity Germanium Gamma Spectrometer (Oak Ridge, TN, USA). Certified reference materials were obtained from the International Atomic Energy Association (Vienna, Austria) for efficiency corrections. The ^{214}Pb was used to establish background (supported) ^{210}Pb (Appleby, 2001; Appleby and Oldfield, 1978). Chronologies were

established using the constant rate of supply model (Appleby and Oldfield, 1978), while ^{137}Cs was used as an independent age-marker. The ^{137}Cs radioisotope is associated with nuclear fallout, which reached peak activity in 1963 before an international moratorium was placed on atmospheric nuclear bomb testing (Appleby 2001).

Sedimentary analyses

Diatom preparation, identification, and analyses

For Goose Lake, First Lake, Next Lake, and SC5, every interval between 0cm and 10cm was selected for analysis, and temporal resolution was decreased past 10cm. Due to a higher clastic content in SC8, every other interval was selected for analysis up until 18cm and additional intervals at 23 and 28cm were also selected for analyses. Diatom samples were prepared using the hydrogen peroxide method (Battarbee et al. 2001) and Naphrax® was used as a mounting medium. Diatom valves were identified using an Amscope B690C-PL microscope and multiple reference texts (Krammer and Lange-Bertalot 1997; Krammer and Lange-Bertalot 1999; Krammer and Lange-Bertalot 2000; Fallu et al. 2002) and online databases (Guiry and Guiry, 2021; Spaulding et al. 2022). Between 300-700 diatoms were counted for most intervals for all 5 lakes, except for First Lake intervals 12.5 and 16.5cm, where diversity was low, and diatoms were scarce. Here a minimum of 200 valves were counted. Protozoan plates and chrysophyte cysts, where encountered, were also enumerated.

Diatoms were grouped together based on similar ecologies according to Chapter 2, and groups or taxa recorded at less than 2% abundance were removed. The remaining groups/taxa were displayed as relative abundances along with proportion of plates and cysts. Hills N2 diversity (Hill 1973) was calculated using the full rarefied diatom set. Stratigraphic zones for all lake cores were defined using a constrained incremental sum of squares (CONISS) cluster analysis (Grimm,

1987) and a broken stick model (Legendre & Legendre, 2012), based on the entire diatom assemblage. A principal components analysis (PCA) was performed on Hellinger-transformed diatom species data, to summarize changes in diatom composition through time and compare against changes in geochemical proxies. All analyses and graphing were done using the R statistical computing environment (R Core Team 2020) and the rioja (Juggins 2023) and vegan (Oksanen et al. 2019) and ggplot2 (Wickham 2019) packages.

Elemental and isotope analyses

Select sediment intervals were freeze dried and sent to the Water Quality Centre at Trent University (Peterborough, ON) for analysis of total mercury (THg), organic carbon (C), nitrogen (N), and stable isotopes of carbon and nitrogen ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$). THg was analyzed using a Milestone Direct Mercury Analyzer. C and N were analyzed using a Eurovector Elemental Analyser, on freeze-dried sediments that were retreated using acid fumigation to remove inorganic carbon following Harris et al., 2001. Untreated freeze-dried sediments were used for $\delta^{13}\text{C}/\delta^{15}\text{N}$ analysis, on a Eurovector Elemental Analyser coupled to a Nu Horizon CF-IRMS. Carbon to nitrogen ratios (C/N) were calculated by first calculating the ratio of C/N by weight, and then multiplying by 1.167, which is the ratio of atomic weights of carbon and nitrogen. Sedimentary THg, %OC, %N, C/N ratio, $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$ were plotted with diatom PCA axes 1 and 2 using ggplot in R (Wickham 2019).

Results

Sediment core chronologies

The sediment core retrieved from Goose Lake showed a steady decline in ^{210}Pb activity, however only one reached background levels (Appendix B). A clear ^{137}Cs peak is evident and

supports the chronology established using ^{210}Pb . For the sediment cores retrieved from the remaining four lakes (First Lake, Next Lake, SC5, and SC8), radioactive decay of ^{210}Pb reached and stabilized at background (i.e. ^{214}Pb) levels (Appendices C, D, I, and K). A clear ^{137}Cs peak is evident in First Lake, Next Lake and SC5 and support the established core chronologies (Appendices C, D, and I). Based on the CRS model, the oldest date established for Goose Lake was 1927 ± 11 years (core depth 14-14.5 cm); the oldest date established for First Lake was 1971 ± 16 years (core depth 2-2.5 cm); the oldest date established for Next Lake was 1916 ± 13 years (core depth 10.5-11 cm); the oldest date established for SC5 was 1893 ± 24 years (core depth 14-14.5 cm); and the oldest date established for SC8 was 1855 ± 24 years (core depth 16-16.5 cm).

Diatom and elemental/isotopic analyses

Goose Lake

Three biostratigraphic zones were identified for diatoms in Goose Lake. In Zone 1 (32-32.5cm), the most abundant diatom taxa were large *Navicula* species (*N. cryptocephala*, *N. crytotenella*, and *N. radiosa*), *Kobayasiella jaagii*, and *Encyonema* species (*E. silesiacum* and *E. hebridica*) (Figure 4.2). The shift from Zone 1 to Zone 2 (28.5-17 cm) was marked by an increase in *Fragilaria tenera*, centric planktonic species (*Lindavia michiganiana* and *Discotella pseudostelligera*), *Encyonopsis* species (*E. cesatii* and *E. dscripta*), *Brachysira* species (mostly *B. vitrea*), large *Navicula* species, *Achnantheidium minutissimum*, *Nitzschia* species (mostly *N. palea* and *N. perminuta*), *Sellaphora* species (*S. pupula* and *S. laevissima*) and *Cymbopleura incerta*, and a concomitant decrease in *Kobayasiella jaagii*, *Encyonema* species and several large benthic species including *Neidium ampliatus*, *Navicula vulpina*, and *Stauroneis phoenicenteron* (Figure 4.2). The shift from Zone 2 to Zone 3 (16.5-0 cm, ~1900 to present-day) was marked by

more subtle changes in relative abundance between species/species groups (Figure 4.2). Relative abundances of *Fragilaria tenera*, centric species, *Encyonopsis* species, *Brachysira* species, large *Navicula* species and *Achnanthes* species continued to increase, while *Kobayasiella jaagii* and *Encyonema* species continued to decrease. While *Nitzschia* species, *Sellaphora* species and *Cymboppleura* species increased between Zone 1 and Zone 2, they decreased between Zone 2 and Zone 3 (Figure 4.2). The relative abundance of chrysophyte cysts also decreased during the diatom species transition between Zone 2 and Zone 3, while the relative abundance of protozoan plates increased. Hills N2 species diversity was lower in Zone 3 than Zone 2 (Figure 4.2) and was generally lower in Goose Lake than the other lakes in this study.

Atomic C/N values were consistently between 12.8-13.8 throughout the core, with no unidirectional trend evident (Figure 4.3). $\delta^{13}\text{C}$ values increased from -20.1 to -18.8 ‰ after ~1990 while $\delta^{15}\text{N}$ varied between -1.1 and -0.6 ‰, with the highest (least negative) value recorded in the surface sediment interval (Figure 4.3). Concentrations of THg ranged from 90 – 200 ng/g OC throughout most of the sediment core, except for a notable peak of ~440 ng/g OC identified at 14.25cm (~1927 $\pm$ 11 years).

First Lake

Three biostratigraphic zones were identified using in the First Lake sediment core. Zone 1 spanned most of the core (16-3.5 cm) (Figure 4.4). The dominant diatom species in Zone 1 were *Sellaphora* species (*S. pupula* and *S. laevissima*), *Pinnularia* species (mostly *P. gibba* and *P. microstauron*), *Neidum ampliatus*, *Stauroneis phoenicenteron* and *Navicula vulpina* (Figure 4.4). Zone 2 (3.5-2.0 cm) is a zone of transition, which marks the shift in diatom assemblage from the dominant taxa of Zone 1 to the diatom assemblage of Zone 3 (2.0-0 cm, ~1970 to present), which was characterized by centric planktonic species (*Lindavia michiganiana*, and

Discotella pseudostelligera), large *Navicula* species (*N. cryptocephala*, *N. cryptotenella*, and *N. radiosa*), *Nitzschia* species (mostly *N. perminuta* and *N. palea*), *Achnanthes minutissimum*, *Fragilaria tenera*, and *Brachysira* species (mostly *B. vitrea*) (Figure 4.4). The relative abundance of chrystophyte cysts began to decrease in Zone 2, and almost disappeared by Zone 1, while the presence of protozoan plates was more variable, although generally higher towards the top of the core. Species diversity increased throughout the core and was highest in Zone 3 (Figure 4.4).

Throughout most of the core, %OC and %N remained relatively stable (46.5 % to 48.6%, and 3.6% to 3.9%, respectively), except for a notable peak at the 6-6.5cm interval with %OC and %N content reaching 54 % and 4.4% respectively (Figure 4.5). The atomic C/N ratio peaked just prior to this at the 7-7.5 cm interval, at 15.4 compared to ~14.5 for the remainder of the core. $\delta^{13}\text{C}$ generally decreased throughout most of the core and ranged from 25.4 to -24.3 ‰ (Figure 4.5). The $\delta^{15}\text{N}$ also remained relatively stable through most of the core, ranging between -1.3 and -0.8 ‰, but increased markedly from -0.52 ‰ at 25 cm to 1.1 ‰ in the most recent sediments (2018). The $\delta^{15}\text{N}$ increase coincided with more marked shifts in diatom assemblages, particularly along PCA axis 1. THg increased throughout most of the sediment record from ~ 80 to 150 ng/g OC (Figure 4.5).

Next Lake

Four biostratigraphic zones were identified in the Next Lake sediment core, though the diatom assemblage was generally stable and the transitions between zones marked by only subtle shifts in species relative abundance (Figure 4.6). Large *Navicula* species (*N. cryptocephala*, *N. cryptotenella*, and *N. radiosa*) and *Brachysira* species (*B. vitrea*, *B. styriaca*, and *B. zellensis*)

were the dominant diatom taxa throughout the core (Figure 4.6). The transition from Zone 1 (19.5-12 cm) to Zone 2 (11.5-3.5 cm) occurred ~1915, and was marked by a slight increase in centric planktonic taxa (*Lindavia michiganiana* and *Discotella pseudostelligera*), *Encyonopsis* species (*E. cesatii* and *E. descripta*), *Cymbella delicatula*, *Cymbopleura incerta*, and *Encyonema* species (*E. silesiacum* and *E. hebridicum*), and a decrease in *Pinnularia* species (*P. microstauron* and *P. gibba*), *Denticula kuetzingii*, *Kobayasiella jaagii*, *Sellaphora* species (*S. pupula* and *S. laevissima*) and large benthic species (mostly *Neidium ampliatus* and *Stauroneis phoenicenteron*) (Figure 4.6). The transition from Zone 2 to Zone 3 (3.5-0.5 cm) occurred at ~2005, marked by a decrease in Hills N2 diversity (Figure 4.6). Zone 4 encompasses only the surface interval, marked by a large increase in *Encyonopsis* species. Relative abundances of chrysophyte cysts were low throughout the sediment record, although higher abundances are present from 16 to 9cm, which also coincided with higher abundances of large benthic species (Figure 4.6). Relative abundances of protozoan plates were also fairly low and were slightly higher in the bottom of the core when chrysophyte cysts and large benthic diatom species were more abundant (Figure 4.6).

The Next Lake sediment core had the lowest organic carbon content of all cores, ranging from 22.5 to 29%. The %N ranged from 2.0 to 3.1%, and generally increased through time (Figure 4.7). C/N ratios decreased from 14.6 to 11.1 from 30-18 cm core depth and were relative stable above 18cm (Figure 4.7). The $\delta^{13}\text{C}$ values decreased from -24.5‰ to values between -25.1 and -26.1‰ in the top 10cm of the core, which spans the early 1900s to present (Figure 4.7). The $\delta^{15}\text{N}$ varied between -1.9 to 0.8 ‰ for most of the core, increasing to 0.46 ‰ in the top 1cm (Figure 4.7). THg exhibited a sharp increase from ~200 ng/g OC to ~630 ng/g OC at 12.5 cm (pre-

1900s), consistent with the timing of increase in diatom PCA axis 1 scores (Figure 4.7). THg concentrations declined from 12 cm towards the surface of the sediment core (Figure 4.7).

SC5

Four biostratigraphic zones were identified from CONISS and the broken stick model. Small *Navicula* species *sensu lato* (mostly *N. seminulum* and *N. minima*) and small benthic *Fragilaria* species *sensu lato* (mostly *Staurosira construens* and *S. construens* var. *venter*) were the dominant diatom taxa throughout the sediment core (Figure 4.8). The transition from Zone 1 (32.5-28 cm) to Zone 2 (26.5-17 cm) was marked by an increase in small benthic *Fragilaria* and a decrease in small *Navicula* (Figure 4.8). The transition from Zone 2 to Zone 3 (16.5-11 cm) just prior to ~1890 was marked by the reverse trend, a decrease in small benthic *Fragilaria* and an increase in small *Navicula*, along with the appearance of *Frustulia rhomboides* var. *saxonica*, an increase in *Kobayasiella jaagii*, and a decrease in *Denticula kuetzingii* (Figure 4.8). Hills N2 diversity also increased at the transition from Zone 2 to Zone 3. The transition from Zone 3 to Zone 4 (10.5-0 cm) at ~1950 was marked by an increase in *Diploneis* (*D. finnica* and *D. oblongella*), a slight increase in small benthic *Fragilaria*, and a decrease in *Kobayasiella jaagii* (Figure 4.8).

Both %OC and %N experienced a sharp, temporary decrease at 14.5 cm (~35% to ~25% and ~3.4% to ~2.5%, respectively), but were generally stable over time otherwise. This corresponded to a sharp, temporary decrease in C/N from ~13.4 to ~11.1 (Figure 4.9). The sharp decrease in %OC, %N, and C/N corresponded to the start of a shift in diatom assemblages, based on shifts in PCA axis 1 and PCA axis 2 (Figure 4.9). The $\delta^{13}\text{C}$ also decreased from ~-27.0 to -29.0‰ and THg increased from a range between ~110 and ~130 ng/g OC to a range between ~240 and ~460

above a core depth 14.5 cm (Figure 4.9). The $\delta^{15}\text{N}$ values were generally positive, ranging from ~1-2, except for a sharp, temporary decrease to -2.43‰ at 22 cm (Figure 4.9).

SC8

Four biostratigraphic zones were identified in the SC8 sediment, although the most notable changes occur at ~1960 during the transition from Zone 2 (18.5-10 cm) to Zone 3 (9.5-6 cm)(Figure 4.10). At this time, *Fragilaria tenera* appears and increases, along with increases in *Brachysira* (*B. styriaca* and *B. vitrea*) and *Nitzschia* species (*N. palea* and *N. perminuta*), and decreases in *Neidium ampliatus*, *Sellaphora* species (*S. pupula* and *S. laevissima*), *Pinnularia* species (mostly *P. microstauron*), *Kobayasiella jaagii*, and *Stauroneis phoenicenteron*. *Achnantheidium minutissimum* exhibited slight increases in relative abundances at the transition from Zone 3 to Zone 4 (6-0 cm) in ~1995 (Figure 4.10). Small benthic *Fragilaria* species (*sensu lato*) were recorded in small relative abundances in Zones 1 and 2 but were almost entirely absent from Zones 3 and 4 (Figure 4.10). Relative abundances of chrysophyte cysts were highest in Zones 2 and 4, and protozoan plates were almost entirely absent in Zones 1 and 2 (Figure 4.10). Zone 2 had the highest diversity measured using Hills N2 diversity index (Figure 4.10).

The %OC remained relatively stable at ~40%, and the %N increased slightly from 2.8-3.6% between 20-25 cm. C/N exhibited a subsurface peak of ~18.7 at 25 cm, but otherwise ranged from ~12.8-14, with a slight decrease towards the surface of the sediment core (Figure 4.11). The $\delta^{13}\text{C}$ decreased from -21.3‰ at 18cm to -22.7‰ at the top of the core, except for a value of -20.5‰ at 8cm (Figure 4.11). The $\delta^{15}\text{N}$ decreased throughout the core from a value of 0.58‰ at

the bottom to -0.98‰ at the surface (Figure 4.11). THg generally increased from ~90 ng/g OC at the bottom of the core to ~180 ng/g OC at the top of the core (2018), except for a sharp, temporary decrease in THg to 20 ng/g OC at 6cm (~1995) (Figure 4.11).

Discussion

Goose Lake (hydrologically well-connected, headwater lake)

The diatom species in Goose Lake were largely benthic species, representing both epiphytic and non-attached species that are typical of circumneutral to slightly alkaline lakes along a wide gradient of lake trophic (Coleman et al., 2015; Hargan et al., 2015; Rühland et al., 2003; Chapter 2). Goose Lake has comparatively high water clarity and a benthic moss mat that was noted at the time of sampling, that would provide habitat for the epiphytic diatom taxa reported in Goose Lake (Chapter 2). Atomic C/N values range between 12.8-13.8 throughout the core, indicating a mixture of organic matter deriving from algal and vascular plant sources (Meyers & Teranes, 2002). The shifts in diatom relative abundance recorded in Goose Lake were subtle, but indicated a slight shift from epiphytic species (e.g. *Encyonema* species) to epipelagic species (e.g. *Encyonopsis* species, *Brachysira* species, and large *Navicula* species), and a decrease in overall species diversity. The decrease in species diversity is likely attributable to the increased dominance of a few species groups (i.e. *Encyonopsis* species, *Brachysira* species, and large *Navicula* species). Although many of the species present prefer oligotrophic waters (e.g. *Encyonopsis* and *Brachysira* species), many large *Navicula* species are often found in waters with higher nutrients (Rühland et al., 2003). Therefore, the increase in this species group in Goose Lake may indicate increasing nutrient export to the lake resulting from permafrost thaw and/or general warming. The observed increase in planktonic centric species at 16.5 cm (likely

dating to the late 1800s or early 1900s) fits a broader circumpolar trend of increasing planktonic diatom taxa in post-industrial sediments attributed to an increase in the length of the open-water season and/or increasing nutrients as a result of climate warming, which can support higher planktonic diatom production (Rühland et al., 2015; Rosén et al., 2009).

Coincident with an increase in planktonic diatom species was a decrease in the proportion of chrysophyte cysts relative to diatoms, and slight increase in protozoan plates. In high-latitude lakes, the highest percentages of chrysophyte cysts relative to diatoms were found on semi-aquatic mosses (Douglas & Smol, 1987). The ratio of chrysophyte cysts to fossil diatoms has also been used as an index for lake trophy, where chrysophyte cysts are thought to be more abundant relative to diatoms under oligotrophic conditions because chrysophytes can switch to heterotrophy (Smol, 1985). The decrease in chrysophyte cyst prevalence, therefore, may be mirroring the relative increase in planktonic to benthic diatom production and/or increasing nutrients. The slight increase in the relative abundance of protozoan plates might be indicative of increased wetland influence, as they were most prevalent in collapse scar and fen habitats in the Scotty Creek basin compared to lakes (Chapter 2), and are known more generally to prefer very shallow, acidic waters (Siver et al., 2020).

The diatom assemblage changes (particularly assemblage changes reflected by PCA axis 1 scores) corresponded to modest decreases in %OC and %N, a spike in THg $\sim 1927 \pm 11$ years (corrected for organic carbon), and modest enrichment in $\delta^{13}\text{C}$. Long-term increases in mercury export in subarctic peatlands can occur as a result of peat subsidence (Klaminder et al., 2008; Korosi et al., 2015; Rydberg et al., 2010), but a pulse increase, such as we observed here, is likely more indicative of a single event like lake expansion or a forest fire. Lake expansion floods terrestrial soils and can lead to short-term increases in mercury flux to the lake sediments,

similar to the phenomenon that occurs with reservoir formation (Bodaly & Fudge, 1999; Hall et al., 1998, 2005; Thienpont et al., 2019). Goose Lake currently consists of two distinct basins, a large main basin, and a smaller basin to the northeast. It is possible that these two basins were separate lakes in the past that merged to form one lake. This has not been confirmed, and if it is the case, the timing of the expansion and connection of the two basins is unknown. Next Lake exhibited a similar downcore trend in THg to Goose Lake, with a notable subsurface spike, which supports a regional disturbance as a likely explanation for the changes observed in sediment cores of these lakes. Forest fires release mercury to the atmosphere through biomass combustion (Friedli et al., 2001; Wang et al., 2010) and can also cause a temporary increase in the flux of organic matter, which contains mercury (Schuster et al., 2018), from the watershed to aquatic ecosystems (Biswas et al., 2007; Korosi et al., 2015). A macroscopic charcoal peak was recorded ~100 years ago in a peat core collected from a thermokarst bog near First Lake, indicating a local fire event (Pelletier et al., 2017) and Łíídlı́ Kúé First Nation elders have spoken of a large fire that burned through the area in the 1920s, consistent with the timing of the spike in THg.

Forest fires are known to accelerate permafrost thaw, leading to more gradual hydrological and biogeochemical alterations in the watershed (Gibson et al., 2018; Korosi et al., 2015; Pelletier et al., 2017). The observed gradual decreases in %OC and %N, enrichment in $\delta^{13}\text{C}$, and biological changes may be reflecting fire-induced (or, alternatively, general warming-induced) changes in the landscape. $\delta^{13}\text{C}$ depletion is known to occur with increases in terrestrial carbon in subarctic peatlands (Korosi et al., 2015; Rosén et al., 2009), suggesting that the slight enrichment of $\delta^{13}\text{C}$ in Goose Lake could reflect an increase in the relative proportion of autochthonous organic matter sources in lake sediments, for example because of increases in lake primary production.

We caution, however, that the magnitude of the changes in the organic matter proxies is small and occurring at sediment depths where diagenesis is likely still occurring (Meyers & Teranes, 2002; Sobek et al. 2014).

First Lake (hydrologically well-connected, second lake in the cascade)

First Lake exhibited pronounced changes in diatom assemblages, in contrast to the muted diatom assemblage changes observed in Goose Lake. The initial assemblage consisted mostly of large benthic epipelagic species such as *Sellaphora pupula* and *S. laevissima* (length range 32-53 μm), *Neidium ampliatum* (40-100 μm), and *Navicula vulpina* (length range: 85-110 μm). Post-1970 (5cm) these species are present in low abundance and have been replaced by another group of benthic epipelagic species (*Navicula cryptocephala*: 21-34 μm ; *N. cryptotenella* 14-40 μm ; and *N. radiosa*: 52-105 μm), epiphytic *Achnanthes minutissimum* (5.6-20.8 μm), epiphytic *Nitzschia* species (8-20 μm), planktonic centric species (3.7-14 μm) and *Fragilaria tenera* (50-75 μm), which has been found in both planktonic and moss habitats (Michelutti et al. 2003). The general trend is therefore toward an increase in epiphytic and planktonic species, and a decrease in the average size of diatoms. This diatom assemblage change co-occurs with an increase in Hills N2 diversity and, like Goose Lake, a decrease in the relative proportion of chrysophyte cysts to diatoms.

The increase in planktonic centric diatoms in First Lake is more pronounced than in Goose Lake, appearing and increasing to ~20% relative abundance in First Lake compared to more subtle increases from 1-2% to 8-10% in Goose Lake. Based on decades of field observations at the Scotty Creek Research Station, water depth in First Lake has decreased since the 1990s (unpublished data), but no detectable corresponding decreases in planktonic diatoms (or other

biological proxy changes) occurred. Decreases in valve size has been identified as a response to greater competition over resources, including light (Rühland et al., 2015). This may also explain the increase in planktonic species that would be more competitive in low light conditions over benthic species due to their ability to stay higher in the water column (Rühland et al., 2015). C/N values in the sediments were higher in First Lake than Goose Lake (14.5-15.4 in First Lake versus 12.8-13.8 in Goose Lake), likely indicating a comparatively greater proportion of allochthonous carbon (which is typically chromophoric). Substantial permafrost thaw and ground subsidence of the nearshore landscape has been documented at First Lake using aerial imagery dating back to at least 1947 (Quinton et al., 2011). This may have increased terrestrial organic matter contributions to First Lake, resulting in browner/darker waters and altering nutrient cycling, and driving floristic changes in the diatom assemblage (Rühland et al., 2015). Complicating this, however, is the increase in relative abundance of epiphytic species which are indicative of an increase in benthic moss habitats, which would be unexpected if light penetration has been reduced through lake browning caused by increases in allochthonous carbon. Additionally, light penetration in Goose Lake and First Lake was similar based on continuous logger data collected over the summer months in 2019 (Chapter 2). First Lake is unique among 15 lakes in or near the Scotty Creek basin in terms of the magnitude of increase in planktonic species (Chapter 3).

Enrichment in $\delta^{15}\text{N}$ was observed post-1970, corresponding to diatom assemblage shifts along PCA axis 2. Interpreting trends in $\delta^{15}\text{N}$ can be difficult (Meyers & Teranes, 2002), because ^{15}N can become enriched or depleted because of changes in nitrogen sources (Bragazza et al., 2005, Cheng et al., 2016; Meyers & Ishiwatar, 1993; Savard et al., 2017), temperature (Savard et al., 2017) or changes in biogeochemical processing (Chapin, 1996; Gälman et al., 2009).

Additionally, post-depositional processing can alter values as much as 3.25‰ (Chapin, 1996), which is greater than the range of values in the First Lake core, and so interpretation of the increase in $\delta^{15}\text{N}$ should be made with caution. However, permafrost thaw is known to be occurring along the nearshore of First Lake (Quinton et al., 2011), and thaw is known to alter nutrient cycling (Olefeldt et al., 2021b), which would be predicted to impact $\delta^{15}\text{N}$. Consideration of this, and the concomitant changes in diatom assemblages as a paleoecological proxy, support the inference that there has been a change in nitrogen sources and/or cycling in First Lake.

A subtle depletion in $\delta^{13}\text{C}$ was observed from the bottom of the core to the surface, along with a gradual increasing trend in THg. The timing, however, did not directly correspond to the observed diatom assemblage changes. In a small, subarctic peatland lake (informally named TAH-7) located ~250 km southeast of Scotty Creek, diatom assemblage changes indicated a transition from a clearwater lake to a highly coloured lake (Coleman et al., 2015) that paralleled a depletion in $\delta^{13}\text{C}$ of 8 ‰ and increases in terrestrial organic matter biomarker concentrations (Korosi et al., 2015). First Lake has relatively high benthic moss production when compared within a broader spatial assessment of small, shallow lakes in the Scotty Creek and neighboring basins (Chapter 2), and our inferred responses to thaw in First Lake are likely of a smaller magnitude than what was observed in TAH-7 that did not involve crossing critical ecological thresholds for light. We did, however, observe small subsurface peaks in C/N (from 14.5 to 15.4 at 7 cm) and %OC and %N (from ~45 to 55% and ~3.6-4.2%, respectively, at 6 cm) prior to changes in the biological fossil data. The increase in %OC, %N, and C/N could indicate a pulse input of terrestrial organic matter, as allochthonous organic matter has higher C/N than autochthonous organic matter (Meyers & Teranes, 2002). In the absence of corresponding changes in other paleolimnological indicators, and considering that the magnitude of change is

low, this remains speculative. No corresponding peak in THg was observed, though mercury is often associated with terrestrial organic matter sources (Korosi et al., 2015; Rosén et al., 2009).

Next Lake (hydrologically well-connected, last lake in cascade)

Next Lake exhibited similar diatom assemblage changes to First Lake and Goose Lake, but like Goose Lake, changes in Next Lake diatoms were subtle. Atomic C/N values in the surface sediments of Next Lake were lower than First Lake and Goose Lake (~11 in Next Lake compared to ~13-15 in Goose Lake and First Lake); however, they were higher in the past, declining from 14.5 to ~11 in the pre-industrial period. A decrease in C/N ratios is indicative of an increased proportion of autochthonous organic matter, which is typically richer in nitrogen. Therefore this may be a warming signal resulting from increased lake productivity. However, as described above for Goose Lake, Next Lake exhibited a similar subsurface peak in THg that may reflect a local forest fire event. Depletion in $\delta^{13}\text{C}$ of ~2‰ corresponded to the higher influx of THg, indicating a greater relative contribution of allochthonous carbon to the lake sediments, contradicting the increase in autochthonous carbon suggested by the decrease in C/N ratios.

SC5 (hydrologically isolated)

The dominant diatom taxa in SC5 are small benthic *Fragilaria* and small *Navicula* species (*sensu lato*), which are common in highly coloured lakes in the Taiga Plains, including neighboring lakes at Scotty Creek that are well connected to the channel fen network (Coleman et al., 2015; Chapter 2). That these species are present in high abundances throughout the sediment record of SC5 suggests that this lake may have always been light-limited.

The most notable diatom assemblage change occurred pre-1900s (16cm), marked by an increase in small *Navicula* species and a decrease in small benthic *Fragilaria* species. It is challenging to infer an environmental change that might be responsible for this species shift, particularly due to the taxonomic confusion and frequent misidentification of small Naviculoid species, including the species we have identified here as *N. minima* and *S. seminulum* (Wetzel et al., 2015). It is therefore prudent to examine other metrics and proxies to elucidate a possible mechanism behind this shift. For example, while the small *Navicula* species were increasing, the diversity of the assemblage also increased markedly. This is commonly seen with climate warming, as the growing season increases, and new habitats open (Rühland et al., 2015). Additionally, the thawing of organic material may increase the nutrient load to lakes. Therefore, while SC5 may have always had relatively dark waters, which would reduce the ability of larger benthic flora to flourish, the increased growing season and possibly increased nutrient concentrations may confer an advantage to the more diverse group of small *Navicula* species, but additional research on diatom species ecologies in the region is needed. Further possible evidence of an increased terrestrial signature comes from the observed depletion in $\delta^{13}\text{C}$ (albeit of small magnitude), and an increase in THg that is often associated with terrestrial organic matter run-off (Korosi et al., 2015; Rosén et al., 2009; Rydberg et al., 2010).

Around the time of the onset of the diatom assemblage shift, there occurred a sharp, temporary decrease in %OC and %N, and a corresponding decrease in the C/N ratio, indicating a reduction in terrestrial organic matter inputs into the lake. This is a similar, but opposite, pattern to the hydrologically connected lakes, where short-term subsurface peaks in organic matter biomarkers (OC, N, THg) commonly preceded the onset of long-term diatom assemblage shifts. The subsurface peak in THg in Next Lake and Goose Lake occurred in ~ 1900 and $\sim 1927 \pm 11$ years,

respectively. First Lake, the CRS dating record only extended back to ~1970, not far back enough to capture the timing of the subsurface peak in %OC, %N, and C/N. Given that the uncertainties in the ^{210}Pb dating record increase towards ~1900, it is reasonable to postulate that the subsurface peaks (Goose, First, Next) and troughs (SC5) are temporally coherent and related to a common driver, although we can only speculate as to the mechanism behind the opposing patterns. The hydrological isolation of SC5 from the channel fen network may offer a clue as to why the opposite pattern was observed in SC5, as the changes will more closely reflect the local setting. A temporary decrease in C/N was also observed in Lake TAH-7 (~250 km southeast) in the same sediment interval where a macroscopic charcoal peak indicated a local fire event (Korosi et al., 2015). This is somewhat counterintuitive, as recent field studies at Scotty Creek observed that wildfire on permafrost peat plateaus at Scotty Creek was associated with increased C/N and higher DOC aromaticity in soil porewaters (Burd et al., 2018). Lake sediments are reflecting the net effect of simultaneous changes occurring in its catchment and within-lake processes, which can complicate interpretation of biogeochemical trends. Macroscopic charcoal analysis would be key to determining if wildfire is a common driver behind these changes.

SC8 (hydrologically isolated)

The diatom assemblage in SC8 is presently dominated by *Brachysira* species, which are indicators of oligotrophic, alkaline waters with high pH, and *Nitzschia* species and *Achnanthes minutissimum*, which are found across a large gradient of water chemistry variables (Michelutti et al., 2003). The water chemistry of SC8 does not differ in any meaningful way in comparison to other lakes studied in the region (Coleman and Korosi 2023) and therefore water chemistry is an unlikely explanation for the diatom assemblage present in

this lake. The main shift in diatom species assemblage occurred ~mid 20th century. It was marked by a slight increase in planktonic *Fragilaria* spp., *Brachysira* species, *Nitzschia* species and *Achnantheidium minutissimum*, and a decrease in *Sellaphora pupula/laevissima*, and other epiphytic diatoms. These changes are consistent to those seen the hydrologically connected lakes (Goose, First, and Next), of a magnitude similar to Goose and Next Lake. Atomic C/N values in SC8 were within the range of ~12.5-14, except for one sediment interval near the bottom of the core that had a C/N of 18.7, the highest C/N value recorded in the sediments of all five study lakes. Temporal resolution of diatom analysis was lower towards the bottom of the core, and we only have two intervals that coincide with the higher C/N. Those two intervals, however, had slightly higher abundances of *Nitzschia* species and small benthic *Fragilaria*. While the low temporal resolution for diatoms at the bottom of the core prevents us from definitively linking a decrease in C/N to a decrease in the abundances of *Nitzschia* and small benthic *Fragilaria*, we can confidently say that it was not associated with pronounced diatom species turnover, only modest changes in relative abundances within the existing assemblage.

SC8 was the only one of the five study lakes to show a temporal trend of depletion of $\delta^{15}\text{N}$, with the other lakes generally exhibiting enrichment. It is also the only study lake to show a sharp, temporary decrease in THg, occurring at ~1995, interrupting what had been a general, modest increasing trend. There is no evidence of an event occurring around ~1900 causing temporary biogeochemical changes in SC8 as there was in the other four study lakes. As SC8 is further away from the other lakes, it's possible that it was not impacted by the suspected wildfire.

Conclusion

We sought to understand the role that hydrological connectivity plays in influencing trajectories of lake biogeochemical and ecological change in thawing permafrost peatlands. In four out of five study lakes (three hydrologically connected lakes, and one isolated lake) the diatom assemblages were dominated by benthic taxa, including a high proportion of epiphytes that indicate clear water with sufficient light penetration to the benthic zone to support moss and other aquatic plant growth. Two of the hydrologically connected lakes (Goose Lake and Next Lake), exhibited similar present-day diatom assemblages and a similar muted shift in diatom assemblage changes through time, as well as similar subsurface peaks in THg. The other hydrologically connected lake, First Lake, exhibited the most marked shift in diatom assemblage out of all five lakes, from predominately large benthic species to a high proportion of small planktonic species, which we interpret to be a result of increased export of allochthonous carbon from the catchment, resulting in the darkening of lake water colour. It has been speculated that higher catchment hydrological connectivity may mute a lake's response to changes in export of organic material coming in from the catchment (Bertolet et al. 2018), but our data do not support this, particularly as one of the isolated study lakes (SC8) exhibited the most muted response.

Carbon aromaticity has been observed to increase along cascades of connected collapse scars and fens (Olefeldt and Roulet 2014; Gordon et al. 2016). We do not see this pattern reflected in lake sediment C/N along the Goose-First-Next hydrological cascade, as First Lake has the highest C/N values of the three lakes, indicating the greatest relative contribution from more allochthonous, recalcitrant sources. The C/N values in First Lake were also higher than observed in the hydrologically isolated lakes (SC5, SC8). We did, however, observe a pattern of decreasing $\delta^{13}\text{C}$ along the Goose-First-Next cascade. The hydrologically isolated lakes showed

opposing patterns, with SC8 sediments exhibiting $\delta^{13}\text{C}$ values similar to Goose Lake, while SC5 had the lowest $\delta^{13}\text{C}$ values of all lakes and a diatom assemblage indicating a low-light environment with high chromophoric DOC. A trend of $\delta^{13}\text{C}$ depletion was observed in Next Lake, First Lake, SC5, and SC8, while a trend towards $\delta^{13}\text{C}$ enrichment was observed in Goose Lake. Several interacting factors such as hydrological connections to other landscape features, local geology, water table depth, and proportion of organic content may play a larger role than the larger connections between lakes.

The timing of diatom changes appeared to be synchronous between Goose Lake, Next Lake, and SC5, with the onset of diatom changes occurring after what appears to be biogeochemical indicators of a pulse disturbance event, manifested as sharp peaks (Goose, Next) or troughs (SC5) in THg, %OC, and(or) C/N. First Lake also showed biogeochemical evidence of a pulse disturbance (peak in %OC, %N, and C/N) that may be synchronous with Goose, Next, and SC5, but diatom assemblage changes occurred later. Forest fires are a common disturbance in boreal permafrost peatlands that are known to stimulate permafrost thaw, causing changes in the landscape that play out over longer timescales. We speculate that this may be what we are observing in our study lakes. We also speculate that lakes may differ in short-term biogeochemical responses to fire events based on hydrological connectivity (“peaks” in well-connected lakes versus “troughs” in isolated lakes). Future studies could test this by examining paired records of fire reconstructions from macroscopic charcoal and lake biogeochemical reconstructions in isolated and hydrologically connected lakes.

Tables

Table 4.1: Modern water chemistry of 5 lakes in the Scotty Creek basin, collected July 2018. TN: total nitrogen, TP: total phosphorus, DOC: dissolved organic carbon.

Lake site	Alkalinity mg/L CaCO ₃	pH	TN mg/L	TP µg/L	DOC mg/L	Colour (TCU)
Goose Lake	50	8.0	1.2	38	23.7	53
First Lake	43	8.4	1.0	25	21.9	249
Next Lake	43	7.9	0.7	9	18.3	258
SC5	28	7.6	0.8	16	23.6	463
SC8	30	8.1	0.8	19	19.9	285

Figures

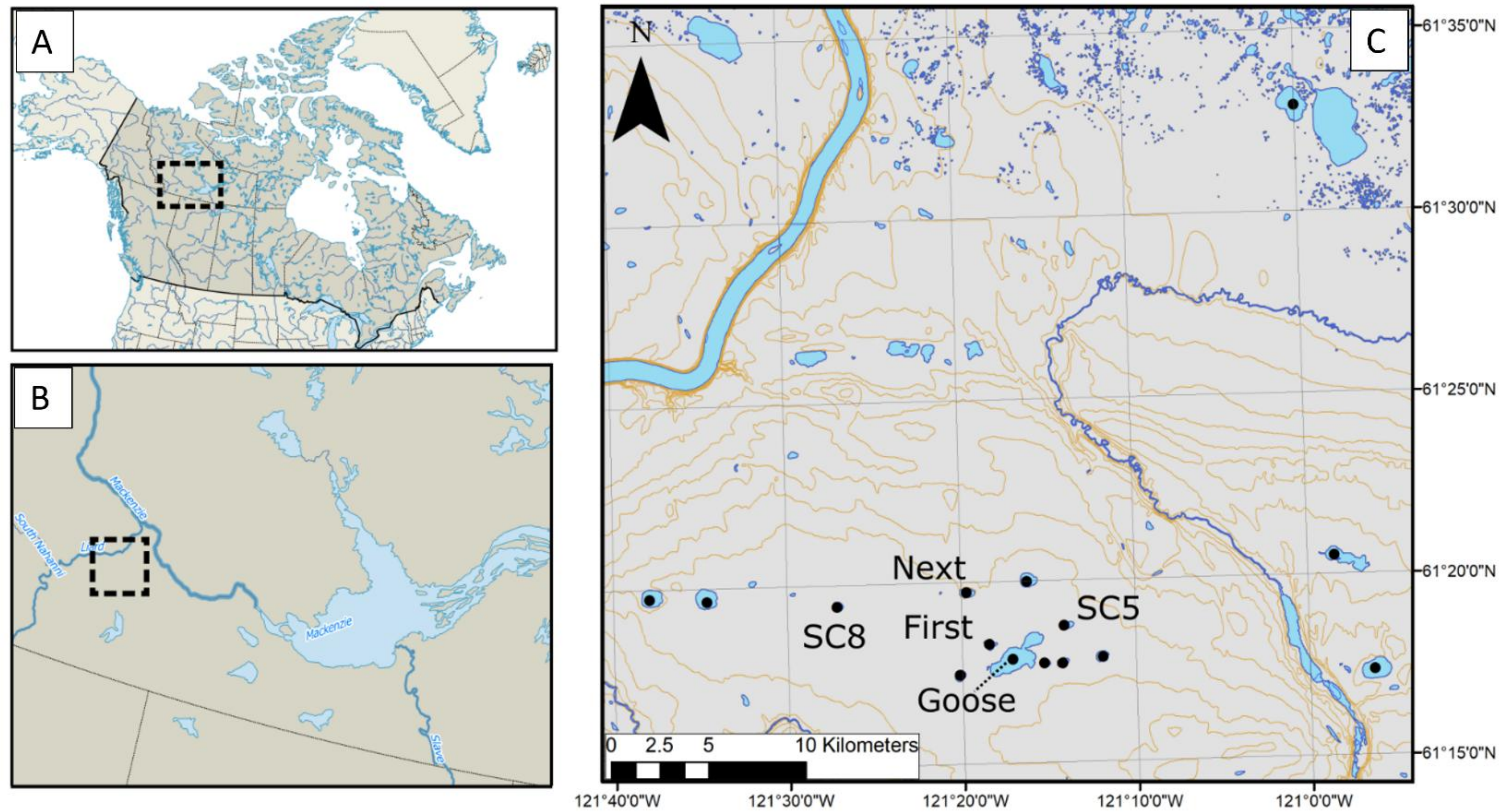


Figure 4.1: Map of study area. (A) Approximate location of site within Canada, (B) approximate location of site within Taiga Plains ecozone, (C) location of all study lakes: Goose Lake, First Lake, Next Lake, SC5, and SC8.

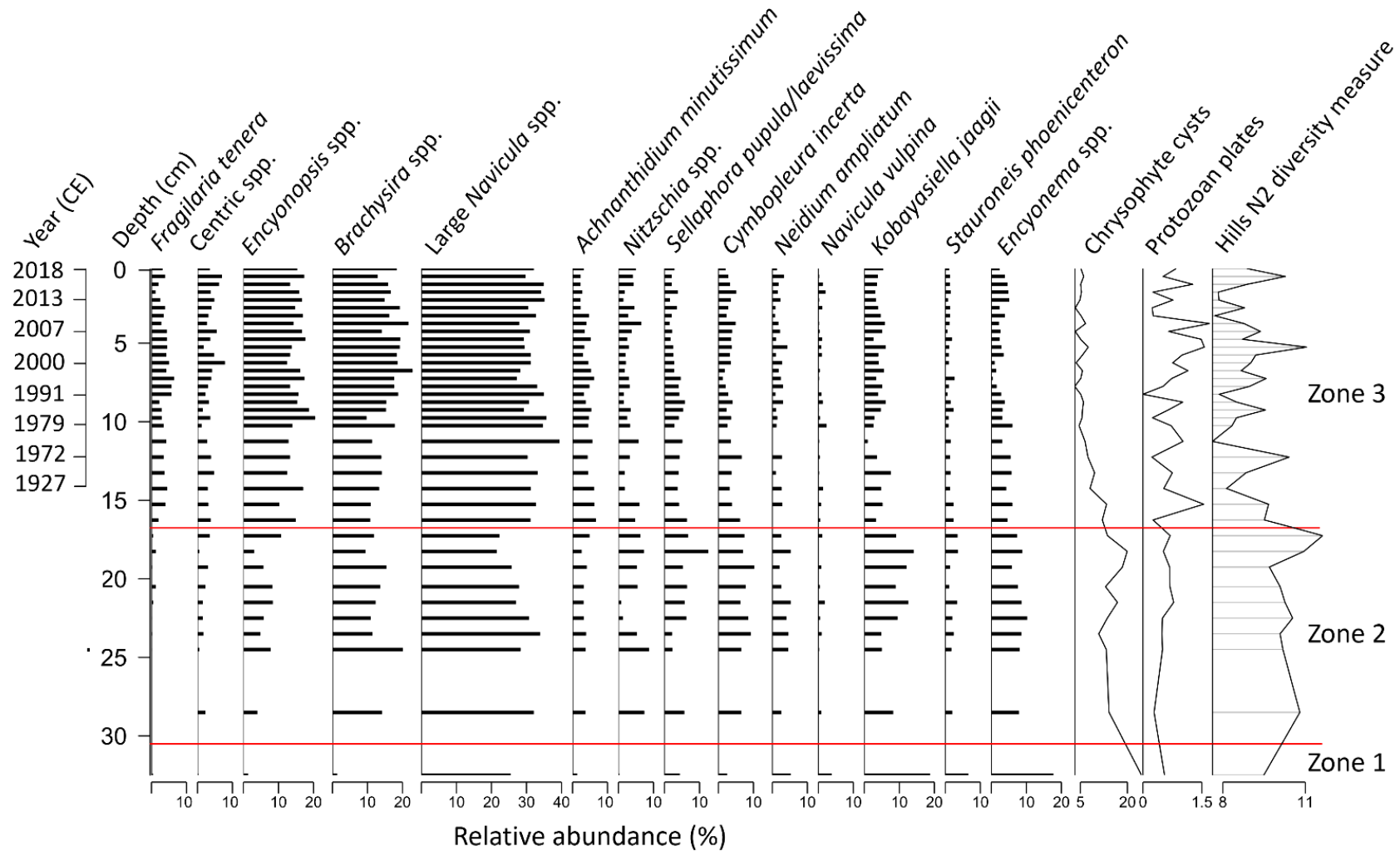


Figure 4.2: Relative abundance diagram for Goose Lake, displaying the most common diatom species. Species were grouped based on similar ecology. Species or ecological groups present at less than 2% relative abundance were removed. Hills N2 diversity scores, ratio of chrysophyte cysts to diatom valves and protozoan plates to diatom valves are also displayed. Horizontal red lines delineate diatom biostratigraphic zones.

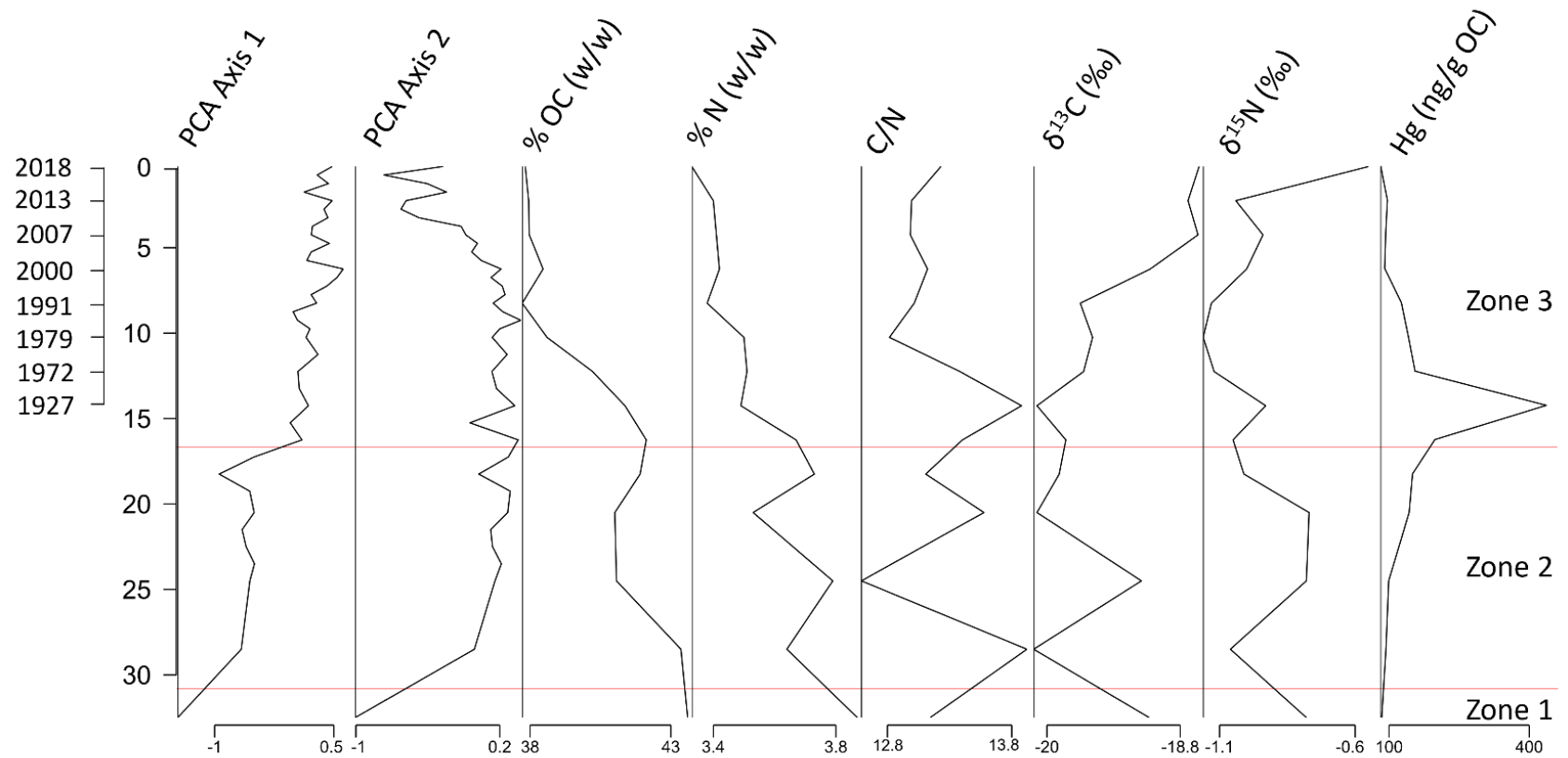


Figure 4.3: Relative abundance diagrams of total mercury (Hg), stable isotopes of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$), and elemental ratios of organic carbon to nitrogen (C/N) for Goose Lake. PCA values are were calculated from diatom species assemblages displayed in Figure 4.2. Horizontal red lines delineate diatom biostratigraphic zones.

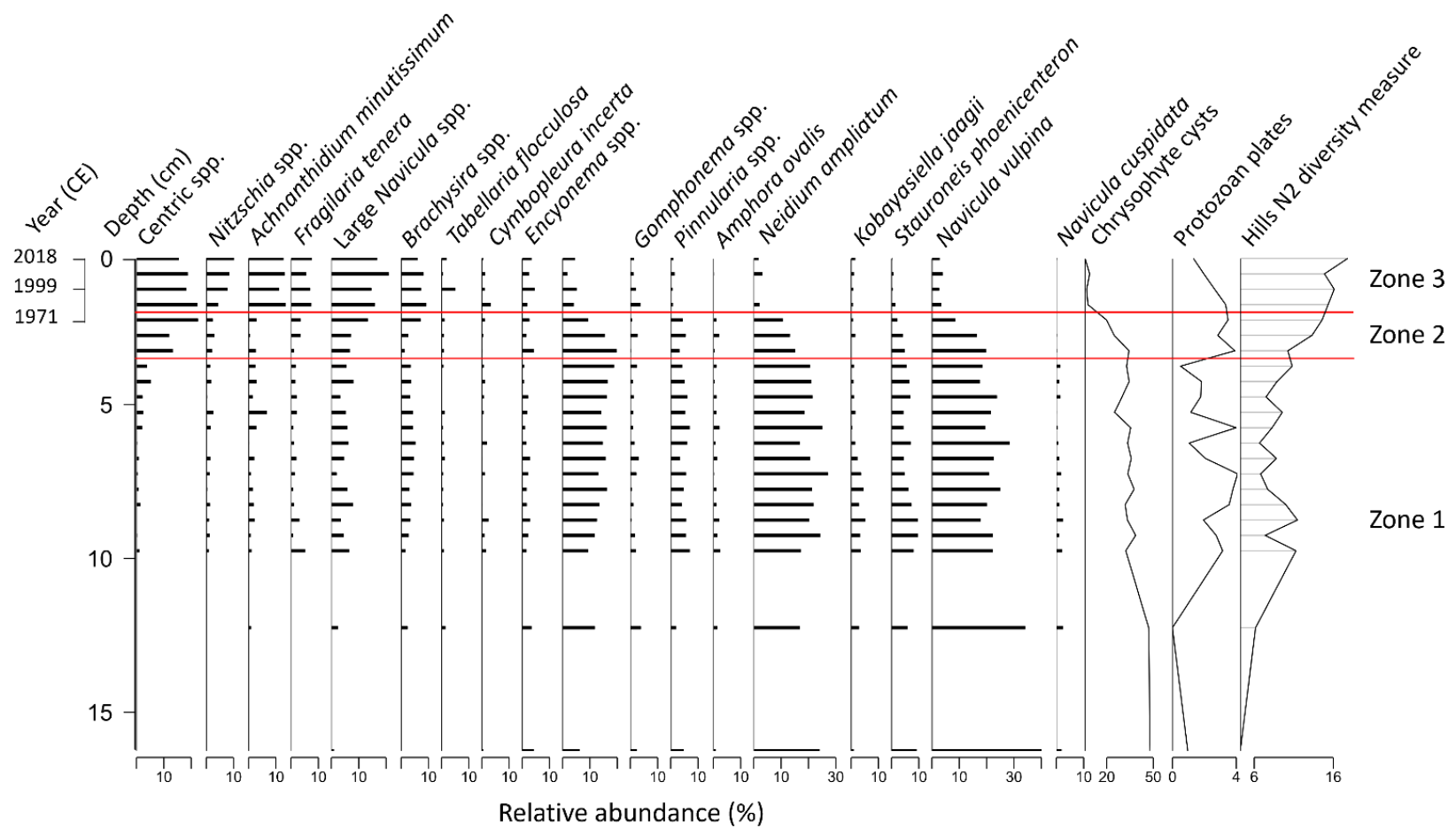


Figure 4.4: Relative abundance diagram for First Lake, displaying the most common diatom species. Species were grouped based on similar ecology. Species or ecological groups present at less than 2% relative abundance were removed. Hills N2 diversity scores, ratio of chrysophyte cysts to diatom valves and protozoan plates to diatom valves are also displayed. Horizontal red lines delineate diatom biostratigraphic zones.

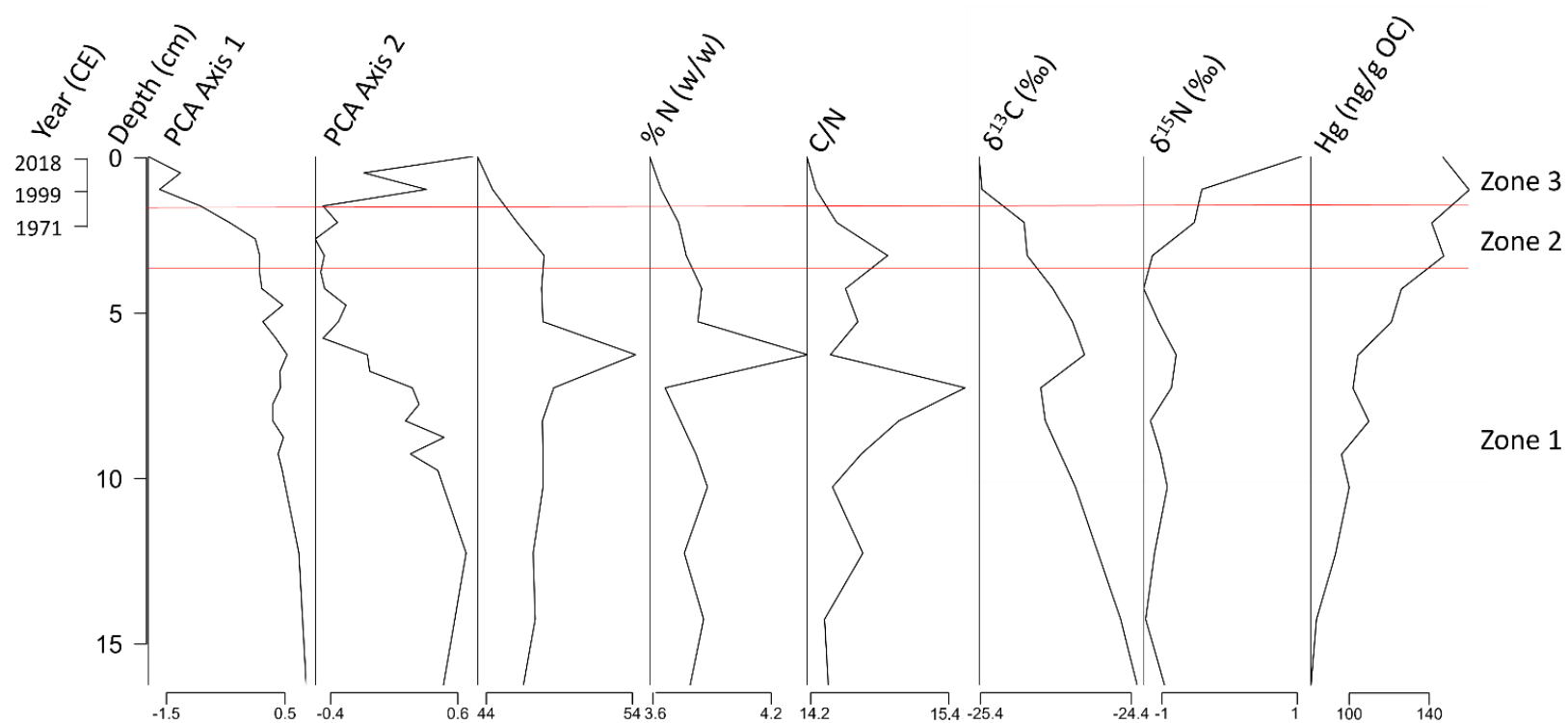


Figure 4.5: Relative abundance diagrams of total mercury (Hg), stable isotopes of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$), and elemental ratios of organic carbon to nitrogen (C/N) for First Lake. PCA values were calculated from diatom species assemblages displayed in Figure 4.4. Horizontal red lines delineate diatom biostratigraphic zones.

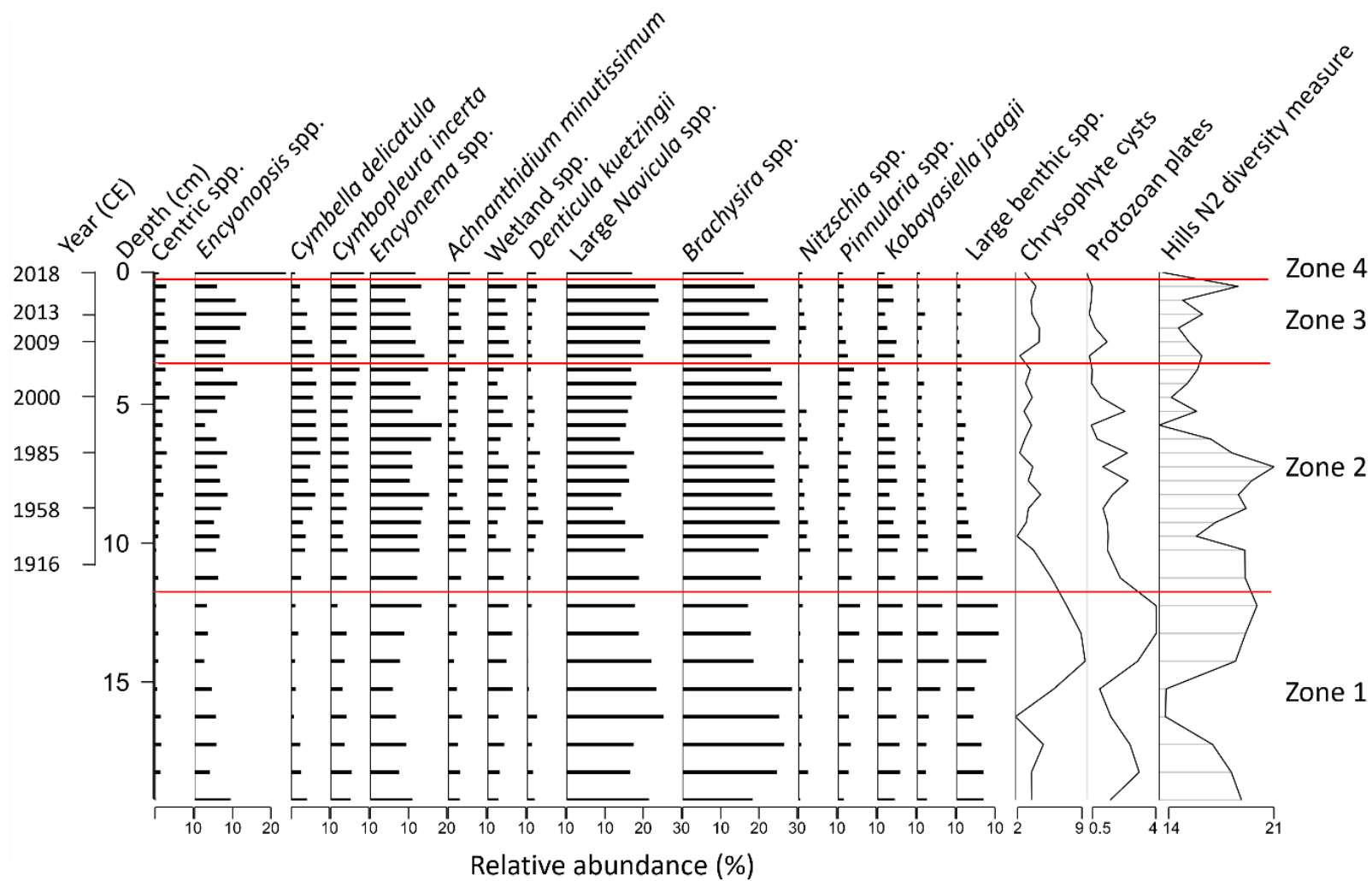


Figure 4.6: Relative abundance diagram for Next Lake, displaying the most common diatom species. Species were grouped based on similar ecology. Species or ecological groups present at less than 2% relative abundance were removed. Hills N2 diversity scores, ratio of chrysophyte cysts to diatom valves and protozoan plates to diatom valves are also displayed. Horizontal red lines delineate diatom biostratigraphic zones.

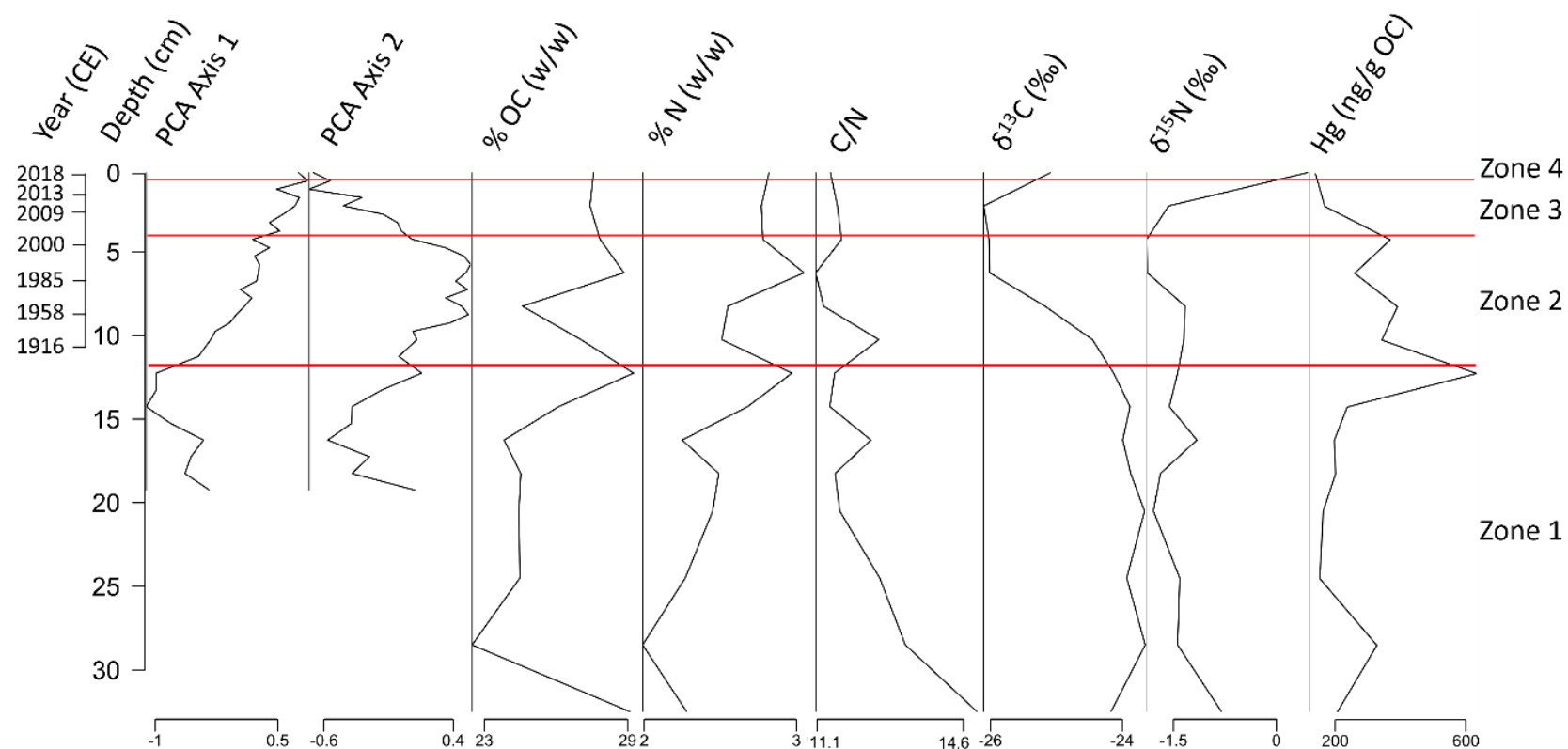


Figure 4.7: Relative abundance diagrams of total mercury (Hg), stable isotopes of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$), and elemental ratios of organic carbon to nitrogen (C/N) for Next Lake. PCA values were calculated from diatom species assemblages displayed in Figure 4.6. Horizontal red lines delineate diatom biostratigraphic zones.

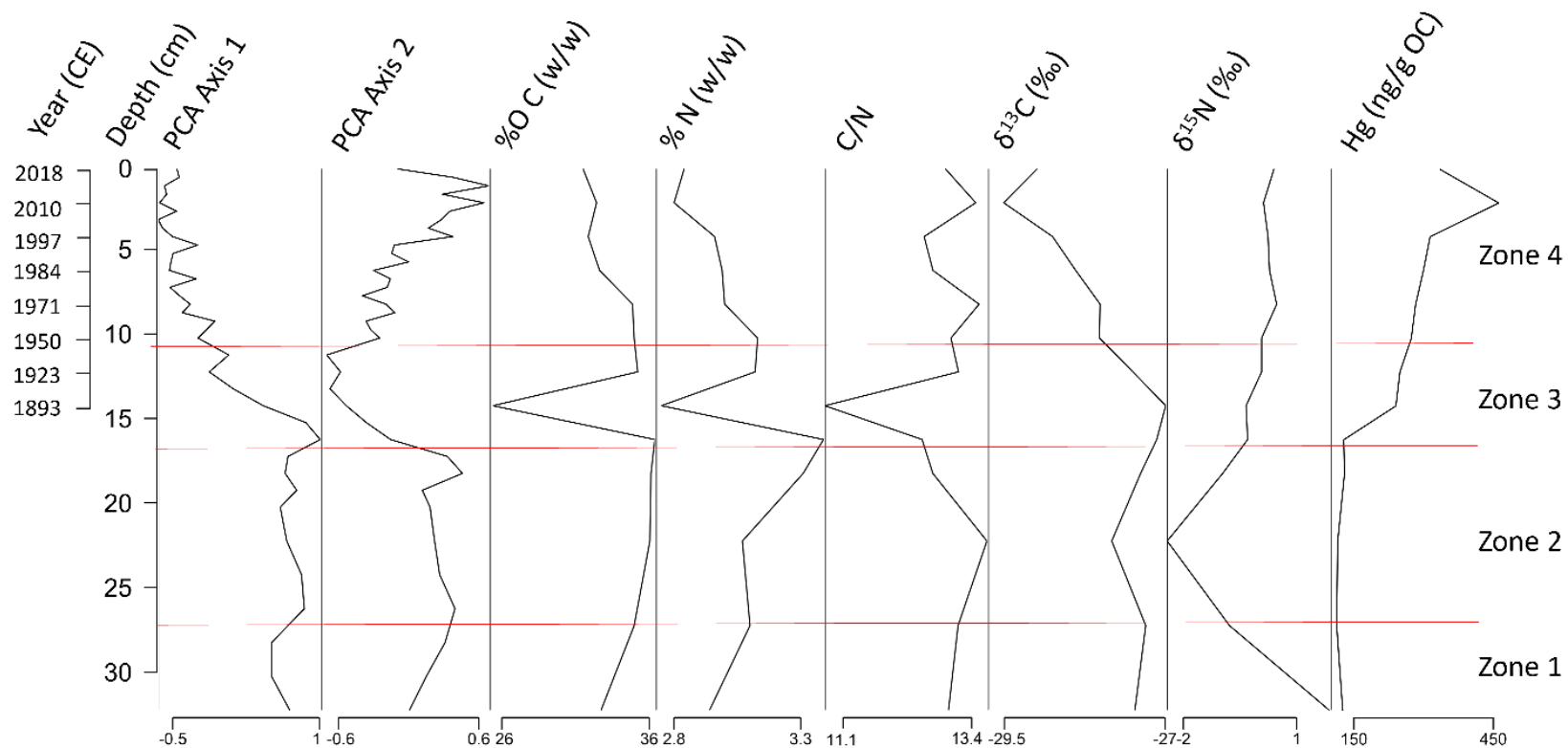


Figure 4.9: Relative abundance diagrams of total mercury (Hg), stable isotopes of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$), and elemental ratios of organic carbon to nitrogen (C/N) for study lake SC5. PCA values were calculated from diatom species assemblages displayed in Figure 4.8. Horizontal red lines delineate diatom biostratigraphic zones.

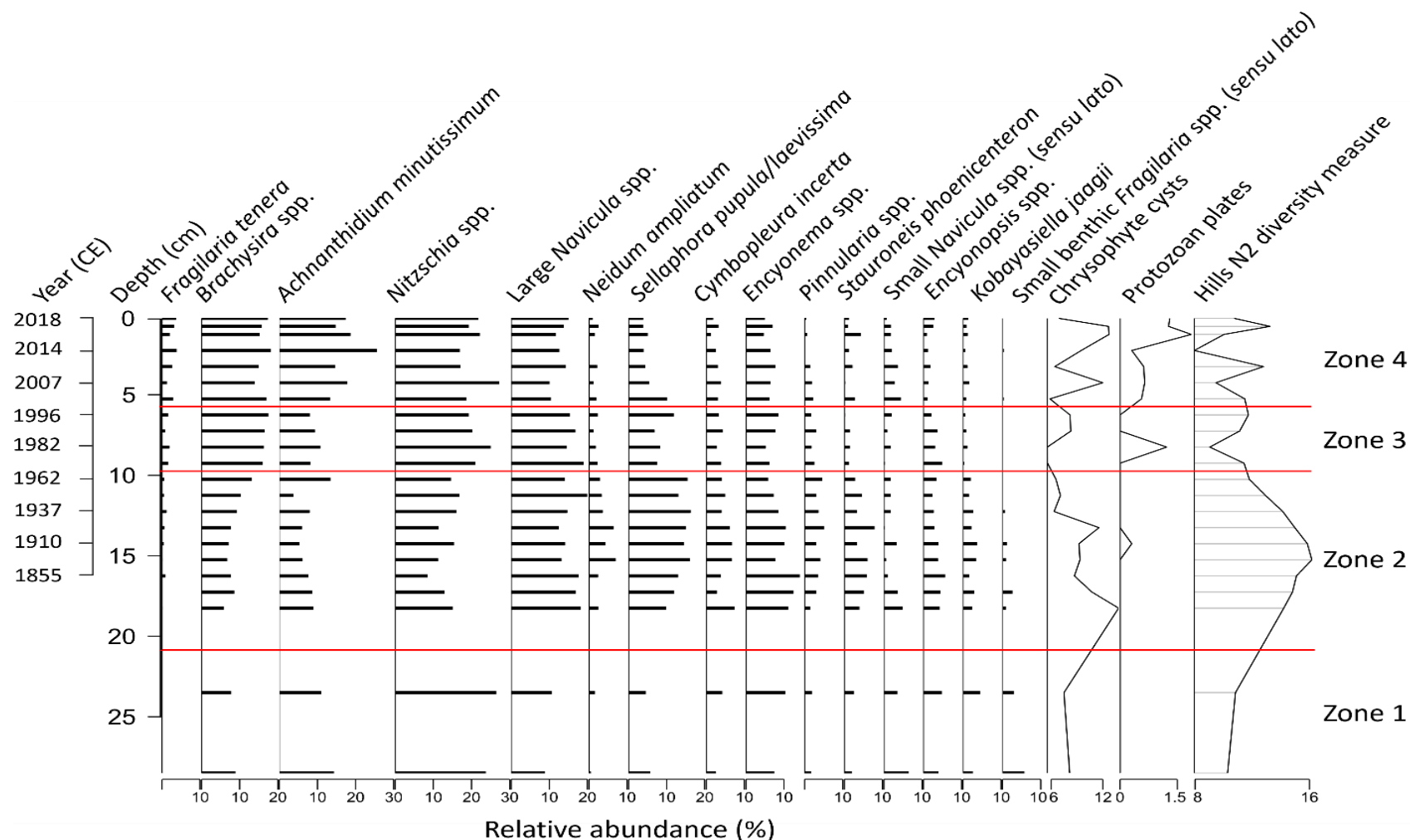


Figure 4.10: Relative abundance diagram for study lake SC8, displaying the most common diatom species. Species were grouped based on similar ecology. Species or ecological groups present at less than 2% relative abundance were removed. Hills N2 diversity scores, ratio of chrysophyte cysts to diatom valves and protozoan plates to diatom valves are also displayed. Horizontal red lines delineate diatom biostratigraphic zones.

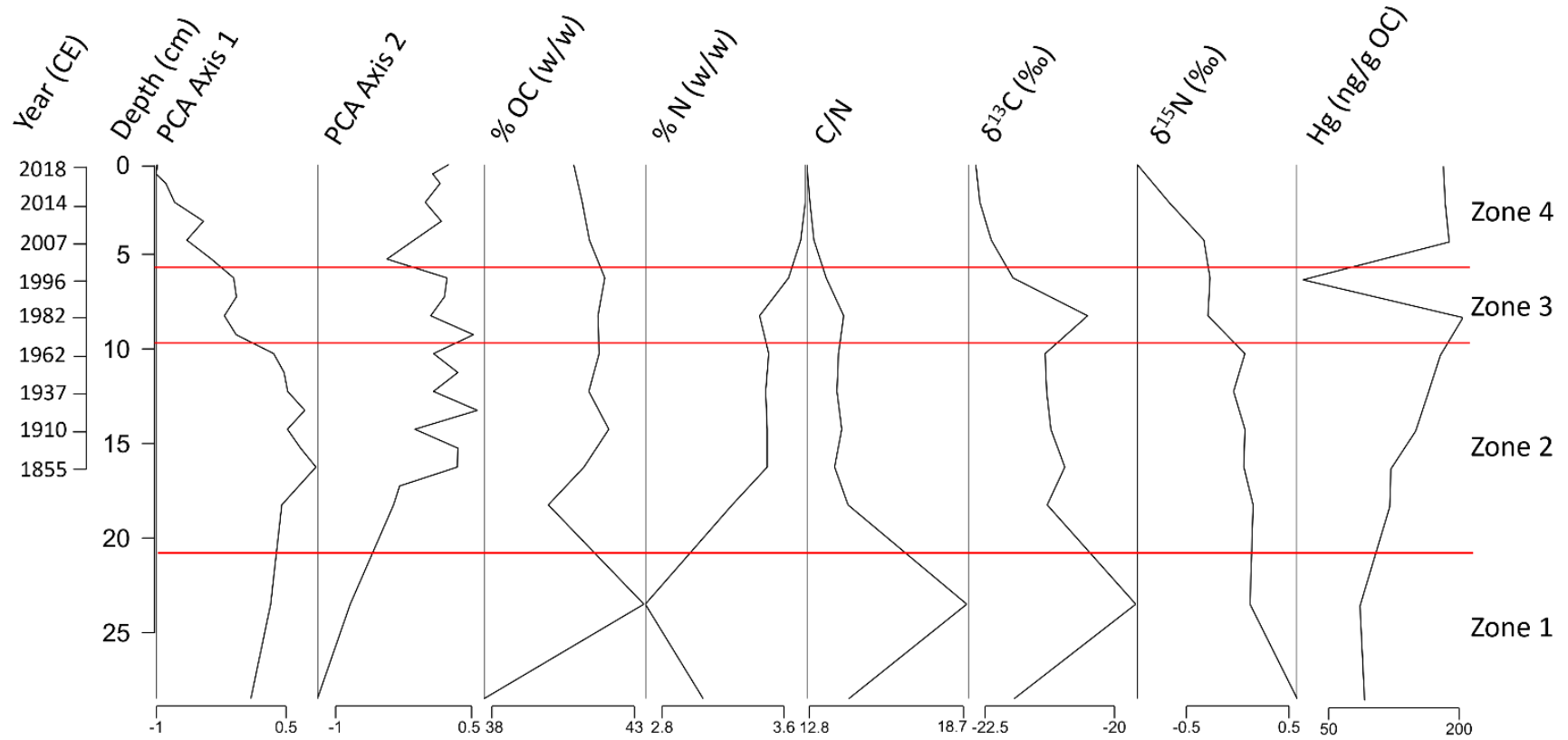


Figure 4.11: Relative abundance diagrams of total mercury (Hg), stable isotopes of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$), and elemental ratios of organic carbon to nitrogen (C/N) for study lake SC8. PCA values were calculated from diatom species assemblages displayed in Figure 4.8. Horizontal red lines delineate diatom biostratigraphic zones.

Chapter 5: General Conclusions

The overall goal of this research was to characterize spatial patterns in small, shallow permafrost peatland lakes, assess temporal trends in lake response to a rapidly thawing permafrost landscape, and evaluate potential drivers of ecological change in these lakes. This dissertation also presents the first limnological characterization of small lakes at or near the Scotty Creek Research Station, addressing an important gap in the ecohydrological field research that has been ongoing for several decades. Two key findings emerged from the research: (1) DOC quality, rather than DOC quantity, is a key driver of variability in lakes of the Scotty Creek basin; (2) Most lakes are experiencing only modest changes based on paleolimnological proxy data despite the widespread prevalence of permafrost degradation. There was a lack of correlation between DOC and lake colour in the study lakes, a notable deviation from most boreal lake regions. This highlighted the need to characterize DOC quality, in addition to DOC quantity. Lake colour was a primary driver of diatom community structure, further highlighting the importance of DOC quality for lake ecology. Small benthic *Fragilariaceae* and small *Navicula* species (*sensu lato*) was associated with higher lake color, while *Encyonopsis* and large *Navicula* species were found in higher-clarity waters. Small benthic *Fragilariaceae* are tolerant of low-light conditions, indicating that light availability and its influence on benthic habitat structure is a major driver of variation in diatom assemblages.

Lakes exhibited divergent trajectories of ecological change based on diatom assemblages in sediment intervals corresponding to 1850, 1950, and present-day. Only one of the 15 lakes (SC11) exhibited a shift in diatom assemblage from predominately large benthic species, to small benthic *Fragilaria* species, and small *Navicula* species between 1950 and present-day, consistent with lake browning. Lake FS2 exhibited the opposite trend, with a decrease in small benthic

Fragilareae taxa. First Lake exhibited an increase in planktonic diatom taxa that was more pronounced than the other study lakes. The mechanism behind the increase in planktonic diatoms in First Lake is unclear. Across the circumpolar Arctic, increases in planktonic diatoms have been a primary diatom response to climate warming across the circumpolar Arctic, linked to declining ice-covered season and greater thermal stability; however, this would not explain why the trend is most pronounced in First Lake and not the other lakes, as climate warming would be a regional stressor. Diatom assemblage changes in the remaining lakes were relatively subtle. For the five lakes where sediment cores were examined at high temporal resolution, diatom assemblage shifts often followed a geochemical anomaly potentially indicating a fire event that could have initiated rapid loss of permafrost. Further study is needed to confirm this (see “Future Directions” below)

I identified lake hydrological connectivity as a potentially significant control on present-day lake water chemistry and ecology, and that the influence of permafrost thaw on trajectories of change in lakes would be related to changes in hydrological connection. However, the mechanism I used to characterize hydrological connections, including the identification of lakes along a hydrological cascade at the Scotty Creek Research Station, and landscape classification (i.e. proportion of bogs and fens surrounding the lake) did not show any clear relationship to present-day conditions or past changes. While the proportion of fens was assumed to be good proxy for the degree of hydrological connectivity of a lake, we did not assess the nature of these connections. For example, if fens were connected to bogs, or receiving water through “bog capture” following permafrost degradation, this would likely have implications for the export of highly aromatic and dark waters to connected lakes. Additionally, with the thawing of permafrost, changing groundwater connections become increasingly important. Groundwater has

not been studied at Scotty Creek, and although studies have since been initiated, the research was not far enough along to guide the methods used in my dissertation research.

Future directions

This research provided the first attempt to characterize the limnology and trajectory of ecosystem change for small lakes in a rapidly thawing discontinuous permafrost peatland and can serve as a guide for future research to provide an understanding of lakes as both sentinels and agents of permafrost landscape change. While this work begins to characterize the connections between land and water, future work should endeavour to better characterize these relationships by characterizing the hydrology and water balance of lakes through analysis of hydrogen and oxygen isotopic analysis. Oxygen and hydrogen isotope analysis could assist in disentangling the influence of groundwater and water residence time on DOC quality (Blais et al., 2015). This would be further enhanced by a more thorough characterization of DOC quality through fluorometric and spectrophotometric methods (Weishaar et al., 2003; McKnight et al., 2001), rather than simply DOC concentration and colour. Had it not been for COVID-19, I would have re-surveyed the 15 lakes to collect water for isotope and DOC quality analysis.

Data Chapter 3 also hinted at the possible importance of fire in stimulating diatom assemblage changes, likely through the role of fire in accelerating permafrost thaw. One of the lakes in this data set, SC11, recorded a near complete species turnover representing a shift from a high-clarity assemblage to one characteristic of highly coloured waters. However, this was based on only 3 sediment intervals (1850, 1950, and present-day). A detailed analysis of organic carbon and mercury in sediment cores from Scotty Creek identified an anomaly in organic

carbon (transient decrease in percent organic carbon, and an anomaly in the atomic carbon to nitrogen ratio) that is roughly consistent with the timing of diatom changes, at least based on the three intervals analyzed (Abulu 2023). A high-temporal resolution paleolimnological analysis of both diatoms and charcoal (to reconstruct fire history), would confirm whether the organic carbon anomaly corresponds to the change in diatoms, and confirm whether the anomaly is related to a forest fire event. If so, this would be a similar trend to one I identified near Kakisa for my MSc research, and would reveal important linkages between fire, permafrost, and lake browning.

While my dissertation research demonstrated the importance of water colour as a primary control on diatom assemblages, we also see shifts over time in other diatom species that cannot be explainable through the dichotomy of high-clarity and low-clarity species. For example, in one lake (SC5) we see a shift from small benthic *Fragilariaceae* species to small *Naviculoid* species, both of which are found more predominately in low clarity lakes. Similarly, the mechanism behind the increase in planktonics in First Lake may not be following the standard interpretation of a response to a longer ice-free season and more stable waters, as we would have expected that trend to be more prevalent across the region. It would be valuable to examine diatom assemblages across a broader water quality and latitudinal gradient in the Taiga Plains ecoregion, to better resolve diatom species-environment relationships, especially considering that these lakes do not exhibit a correlation between DOC concentration and lake colour as is typical for most boreal regions. Past studies aimed at characterizing diatom species-environment relationships in subarctic lakes have emphasized a treeline gradient (Pienitz & Smol, 1993, Pienitz et al., 1999; Rühland et al., 2003) and may not be adequately reflecting diatom assemblage drivers in the Taiga Plains. Through expansion of this data set we may be able to

identify secondary controls over diatom community assemblages, and therefore a clearer understanding of other changes happening in these lakes outside of lake browning.

Finally, due to logistical challenges, both with the COVID-19 pandemic, and difficulties in accessing these sites during spring thaw, data recorded using continuous light, temperature, and oxygen data loggers was limited to 3 months, and only for one year (2019). I was not able to capture spring freshet or autumn cooling. Permafrost thaw is projected to impact temperature, light, and oxygen dynamics, and long-term monitoring using continuous data loggers could offer useful insights. The Scotty Creek Research Station is an ideal location for this, because the infrastructure exists to support such a program. In particular, the observation of periods of oxygen depletion in First Lake should be explored further, first to confirm whether this was tracking oxygen depletion, or if there was an issue with the logger sinking into the mud. First Lake is relatively sheltered, and it is possible for periodic oxygen depletion to occur during warm, calm periods. Oxygen is an important control on internal nutrient loading, mercury methylation, and carbon biogeochemistry, and therefore the frequency of hypoxia or anoxia in shallow lakes has broad significance.

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Appendices

Appendix A

Groupings in relative frequency diagram	Species	Taxon Code
Small benthic <i>Fragilaria</i> spp. (<i>sensu lato</i>)	<i>Pseudostaurosira brevistriata</i>	PSEBREV
	<i>Pseudostaurosira parasitica</i>	PSEPARA
	<i>Staurosira construens</i>	STACONS
	<i>Staurosira construens var venter</i>	STAVENT
Small <i>Navicula</i> spp. (<i>sensu lato</i>)	<i>Navicula minima</i>	NAVMINI
	<i>Sellaphora seminulum</i>	SELSEMI
<i>Encyonopsis</i> spp.	<i>Encyonopsis cesatii</i>	ENCCESA
	<i>Encyonopsis descripta</i>	ENCDESC
<i>Pinnularia</i> spp.	Grouped for RDA	PINSPP
	<i>Pinnularia gibba</i>	<2%
	<i>Pinnularia interrupta</i>	<2%

	<i>Pinnularia legumen</i>	<2%
	<i>Pinnularia maior/viridis</i>	<2%
	<i>Pinnularia microstauron</i>	<2%
	<i>Pinnularia nodosa</i>	<2%
	<i>Pinnularia obscura</i>	<2%
	<i>Pinnularia streptoraphe</i>	<2%
Large <i>Navicula</i> spp.	<i>Navicula cryptocephala</i>	NAVCRC
	<i>Navicula cryptotenella</i>	NAVCRT
	<i>Navicula radiosa</i>	NAVRADI
<i>Brachysira</i> spp.	<i>Brachysira styriaca</i>	BRASTYR
	<i>Brachysira vitrea</i>	BRAVITR
	<i>Brachysira zellensis</i>	BRAZELL
<i>Encyonema</i> spp.	<i>Encyonema gracilis</i>	ENCGRAC
	<i>Encyonema silesiacum</i>	ENCFILE
	<i>Encyonema hebridicum</i>	<2%

	<i>Encyonema perpusillum</i>	<2%
<i>Cymbopleura</i> spp.	<i>Cymbopleura incerta</i>	CYMINCE
	<i>Cymbopleura angustata</i>	<2%
	<i>Cymbopleura lapponica</i>	<2%
<i>Nitzschia</i> spp.	<i>Nitzschia fonticula</i>	NITFONT
	<i>Nitzschia palea</i>	NITPAL
	<i>Nitzschia alpina</i>	<2%
	<i>Nitzschia angustata</i>	<2%
	<i>Nitzschia intermedia</i>	<2%
	<i>Nitzschia recta</i>	<2%
	<i>Nitzschia vermicularis</i>	<2%
Large benthic spp.	<i>Neidium ampliatus</i>	NEIAMPL
	<i>Stauroneis phoenicenteron</i>	STAPHOE
	<i>Staurones javanica</i>	<2%
Planktonic <i>Fragilaria</i> spp.	<i>Fragilaria tenera</i>	FRATENE

	<i>Fragilaria nanana</i>	<2%
	<i>Fragilaria ulna</i>	<2%
Centric planktonic spp.	<i>Cyclotella</i>	CYCPSEU
	<i>comensis/pseudostelligera</i>	
	<i>Cyclotella michiganiana</i>	CYCMICH
	<i>Cyclotella bodanica</i>	<2%
Dominant wetland spp.	<i>Gomphonema acunimatum</i>	<2%
	<i>Gomphonema angustatum</i>	<2%
	<i>Gomphonema gracile</i>	<2%
	<i>Gomphonema parvalum</i>	<2%
	<i>Gomphonema subtile</i>	<2%
	<i>Gomphonema truncatum</i>	<2%
	<i>Kobayasiella subtilissima</i>	KOBSUBT
	<i>Tabellaria flocculosa</i>	TABFLOC
	<i>Eunotia</i> spp. (grouped for RDA)	EUNSPPP

Eunotia bilunaris <2%

Eunotia circumborealis <2%

Eunotia formica <2%

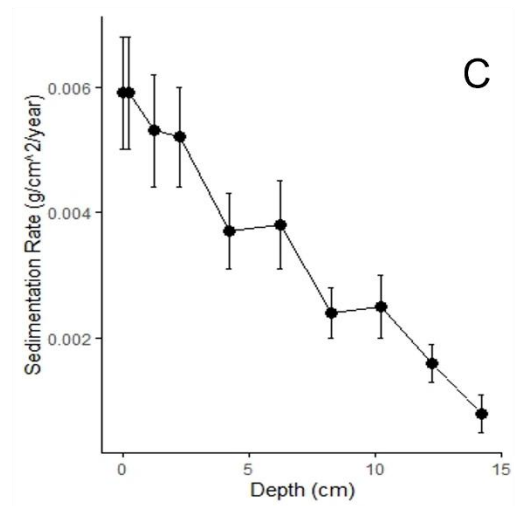
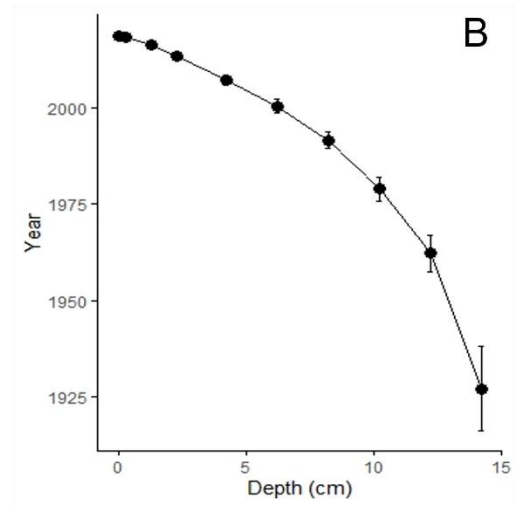
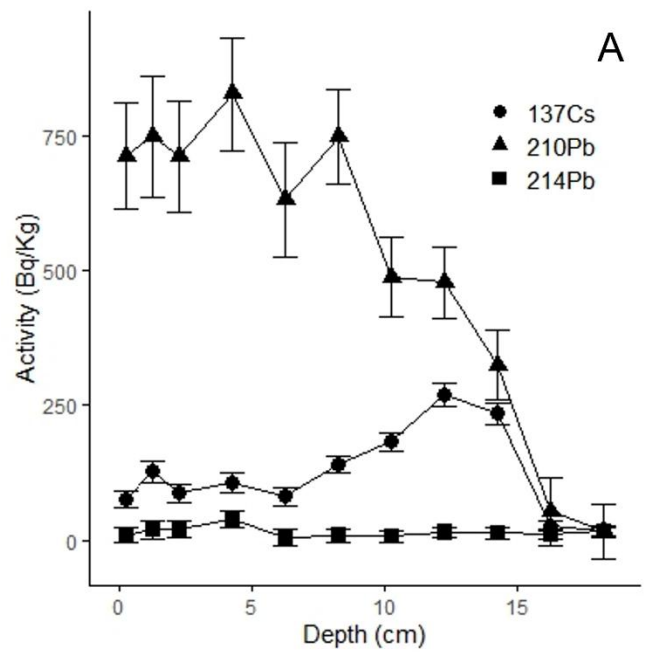
Eunotia incisa <2%

Eunotia praerupta <2%

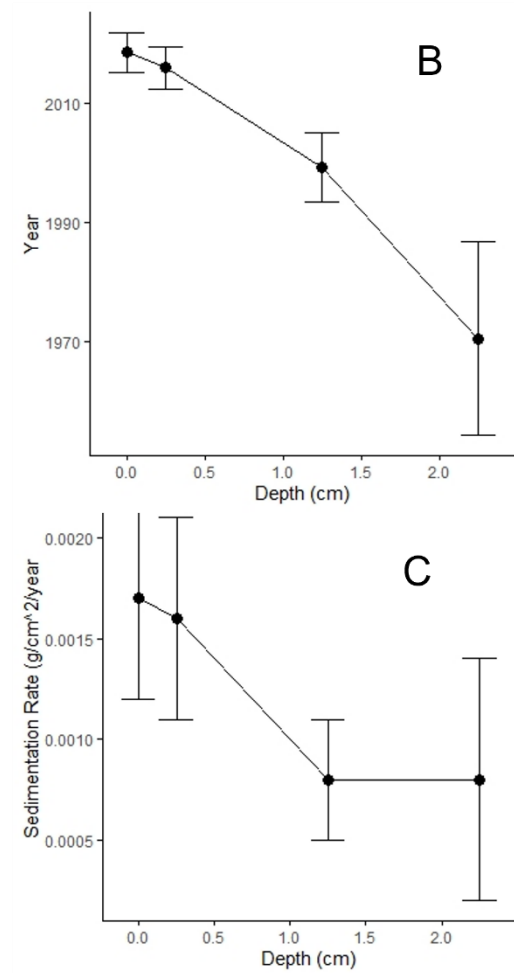
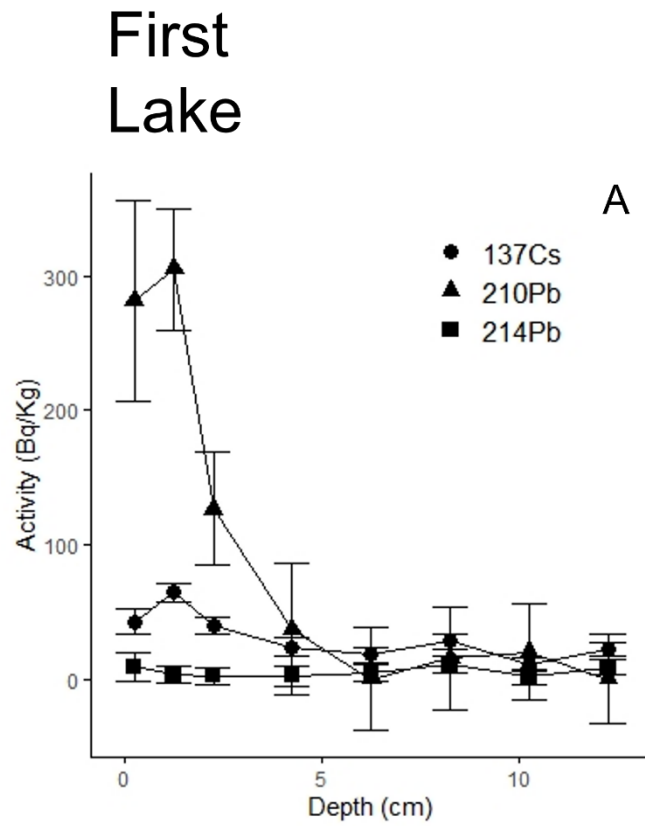
<i>Achnanthes exigua</i>	ACHEXIG
<i>Achnanthes minutissima</i>	ACHMINU
<i>Amphora</i> spp. (grouped for RDA)	AMPSPPP
<i>Amphora pediculus</i>	<2%
<i>Amphora thumensis</i>	<2%
<i>Chamaepinnularia mediocris</i>	CHAMEDI
<i>Cocconeis placentula</i>	COCPLAC
<i>Delicata delicatula</i>	DELDELI
<i>Denticula kuetzingii</i>	DENKUET
<i>Diploneis oblongella</i>	DIPOBLO

<i>Fragilaria capucina</i>	FRACAPU
<i>Kobayasiella jaagii</i>	KOJAAG
<i>Microcostatus kuelbsii</i>	MICKUEL
<i>Navicula leptostriata</i>	NAVLEPT
<i>Navicula rhynchocephala</i>	NAVRHYN
<i>Navicula vulpina</i>	NAVVULP
<i>Nupela vitiosa</i>	NUPVITI
<i>Sellaphora laevissima</i>	SELLAEV
<i>Sellaphora pupula</i>	SELPUPU
<i>Sellaphora vitabunda</i>	SELVITA

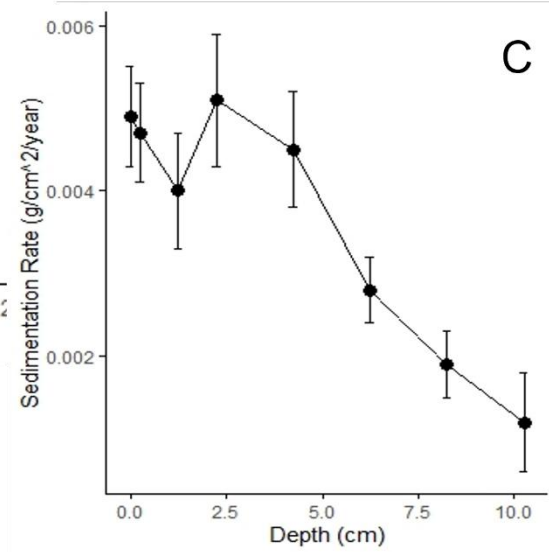
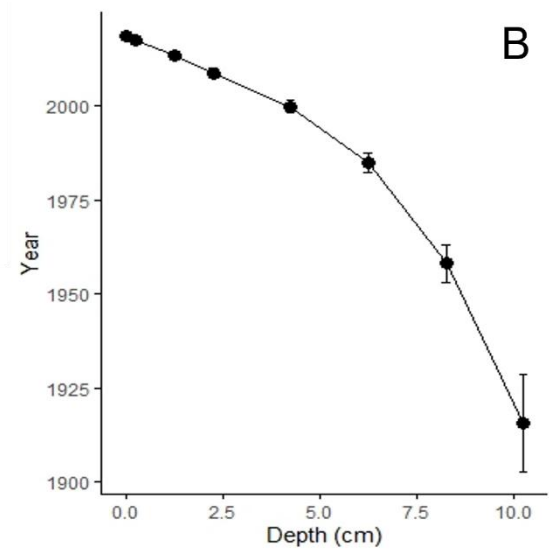
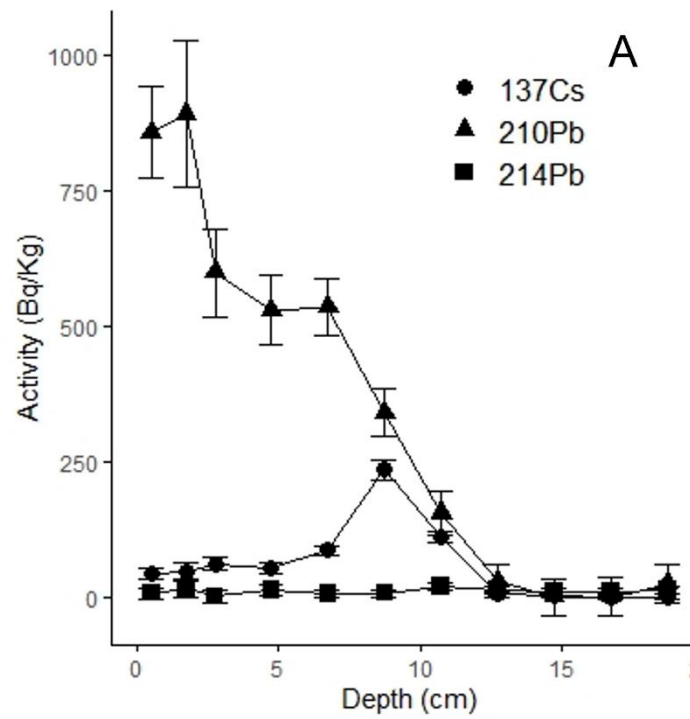
Goose Lake

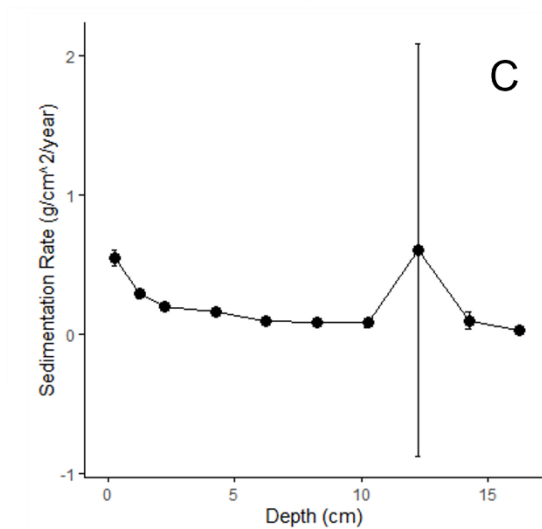
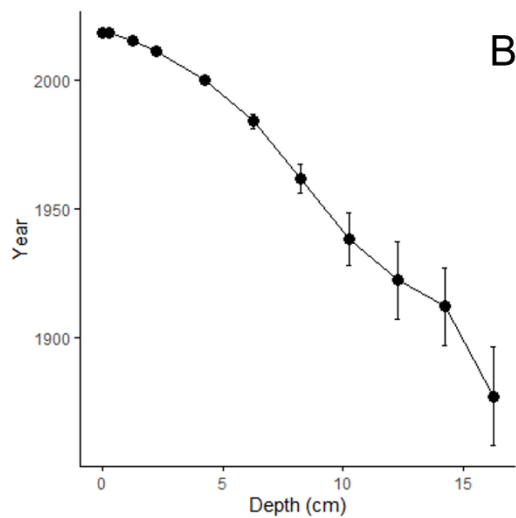
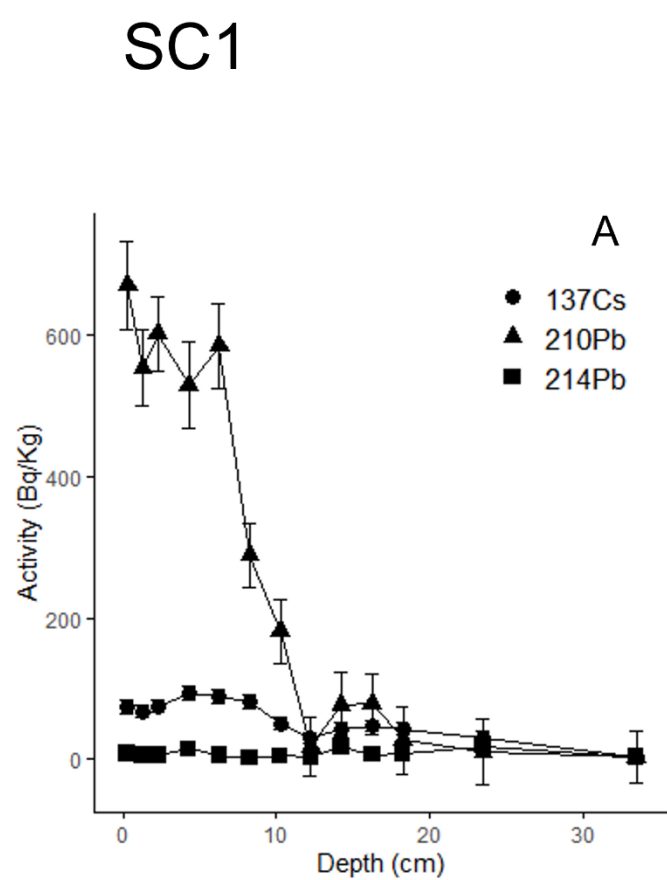


Appendix C

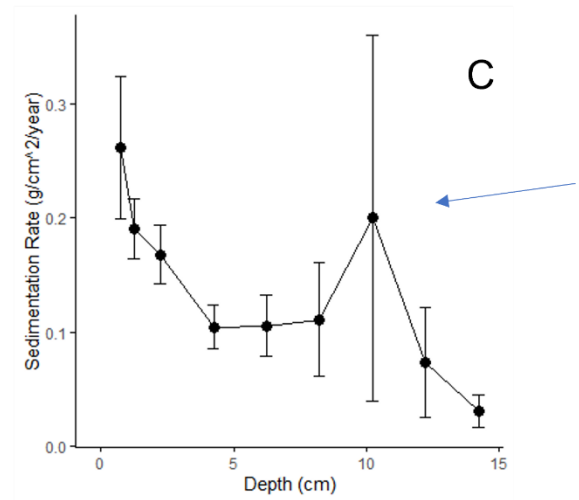
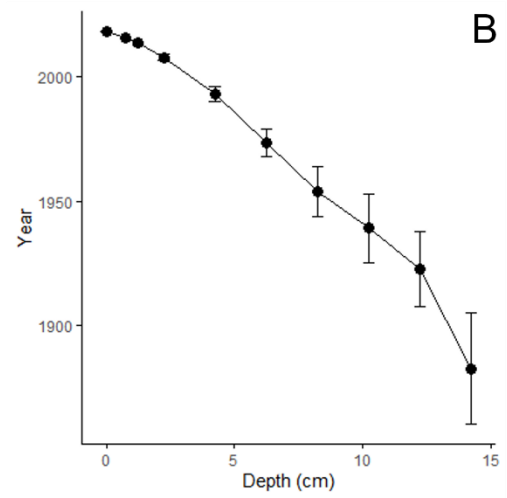
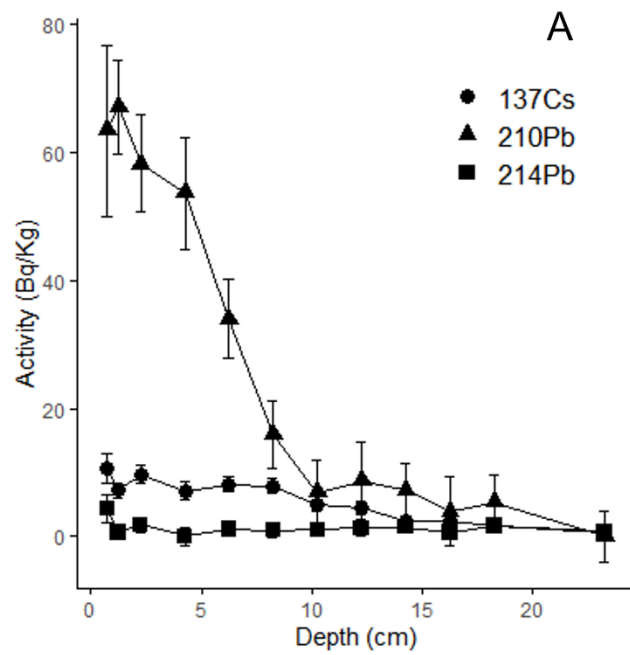


Next Lake

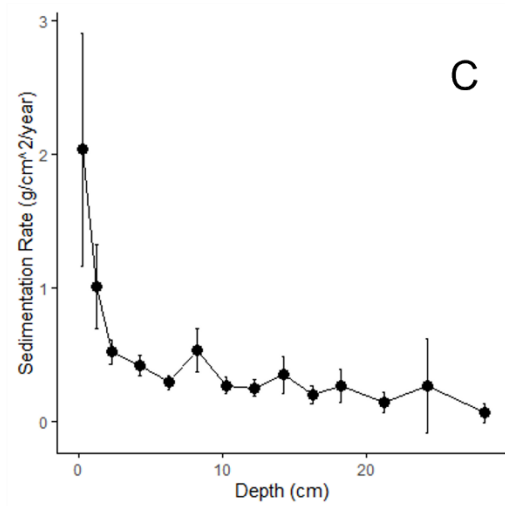
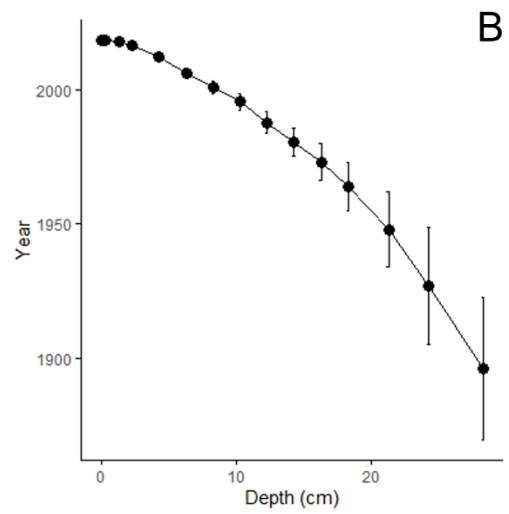
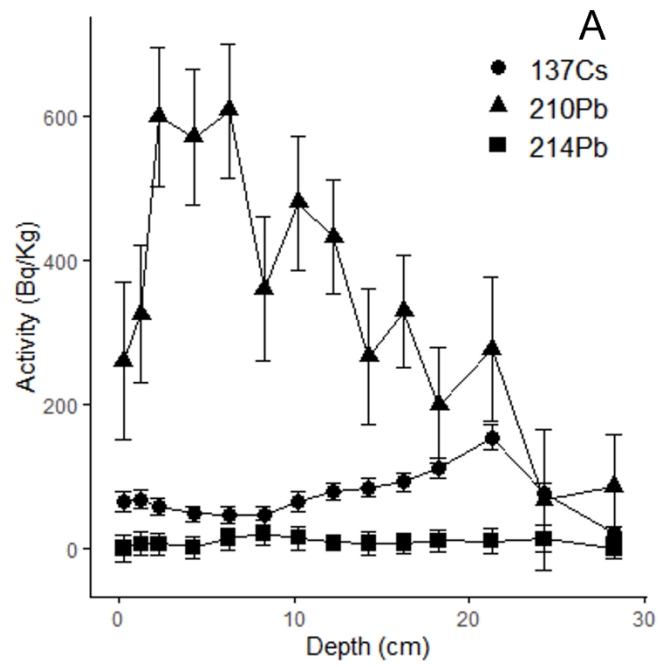




SC2

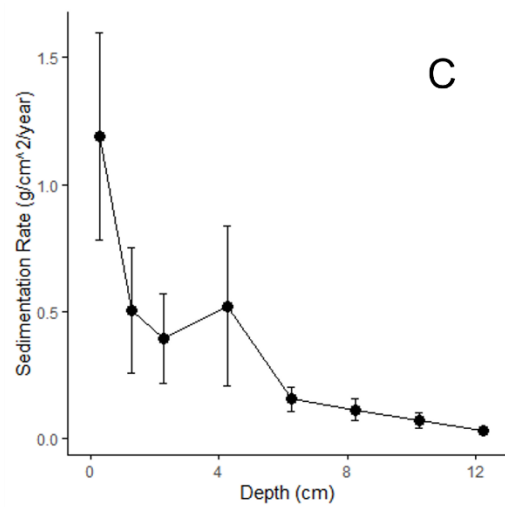
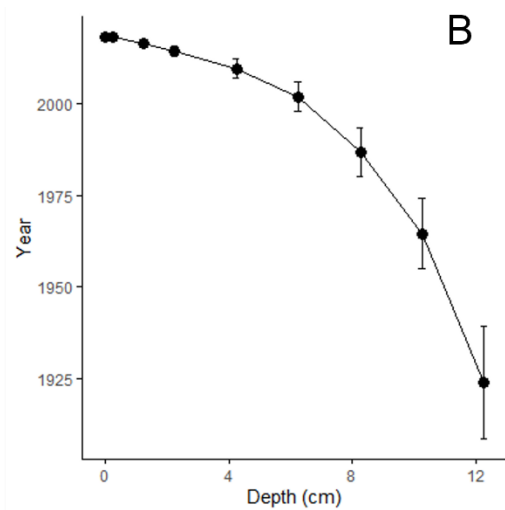
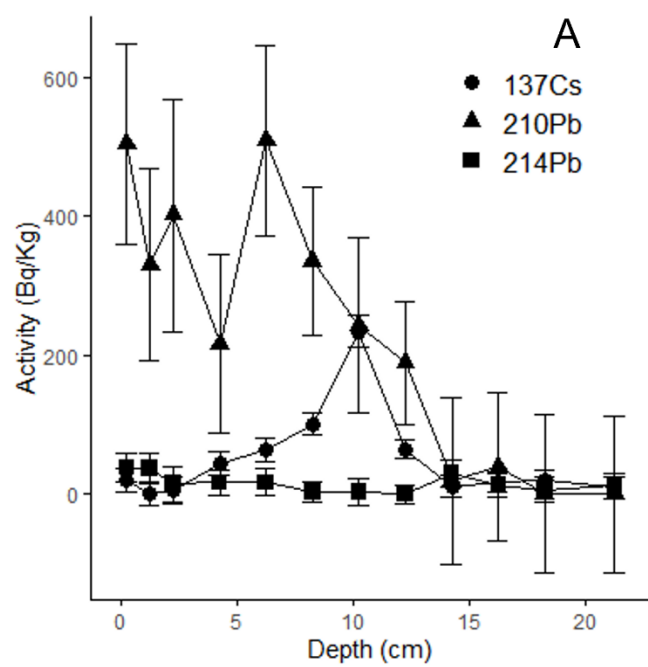


SC3

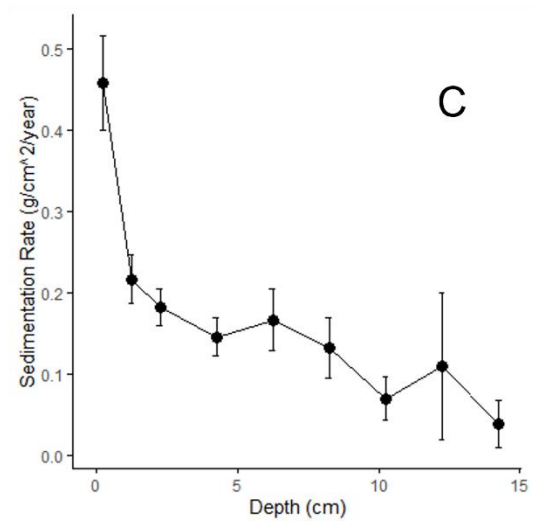
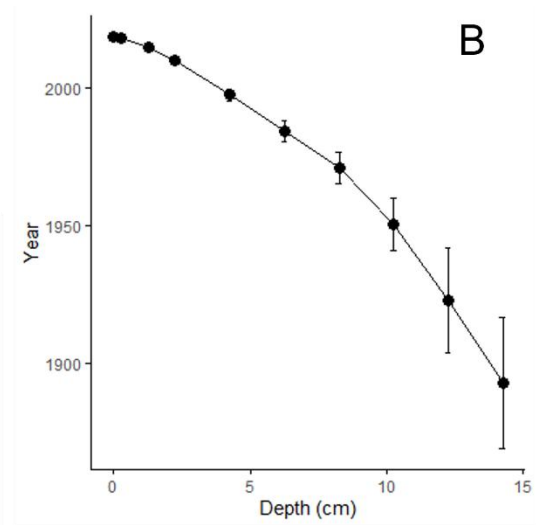
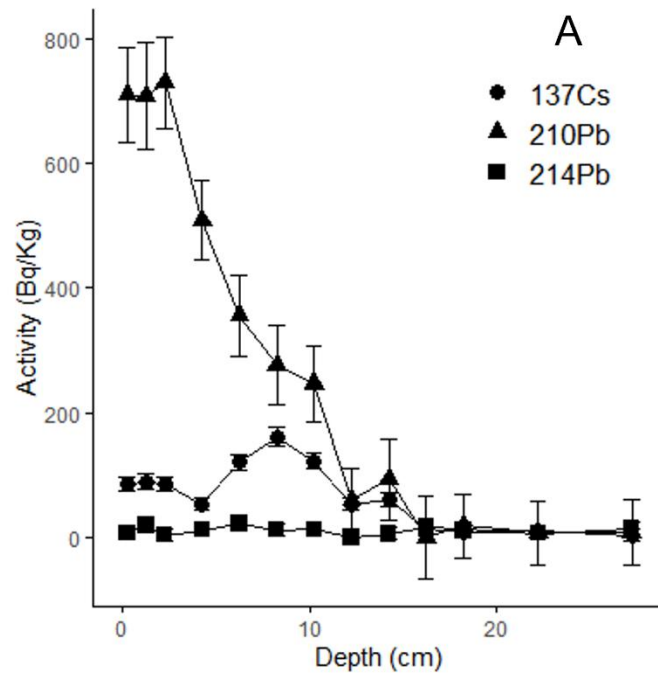


Appendix H

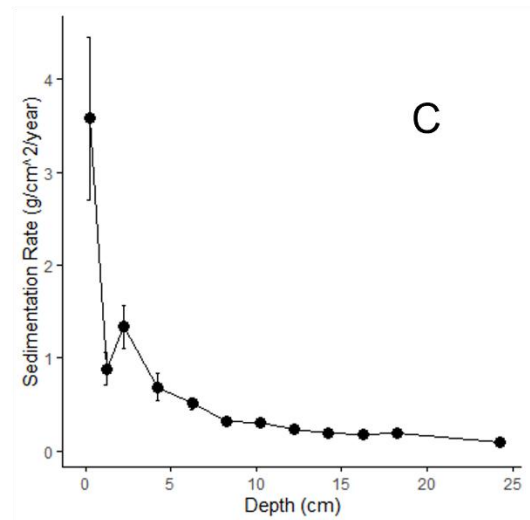
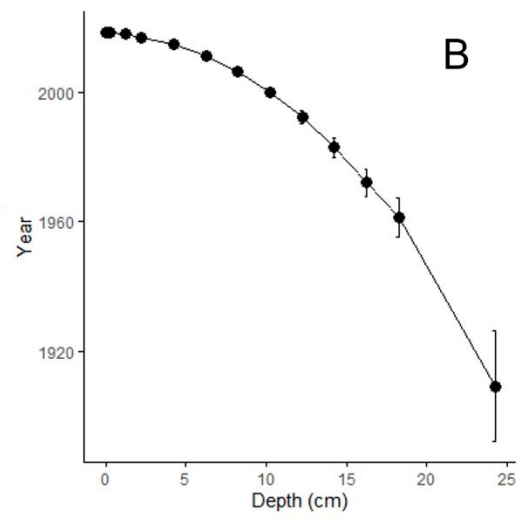
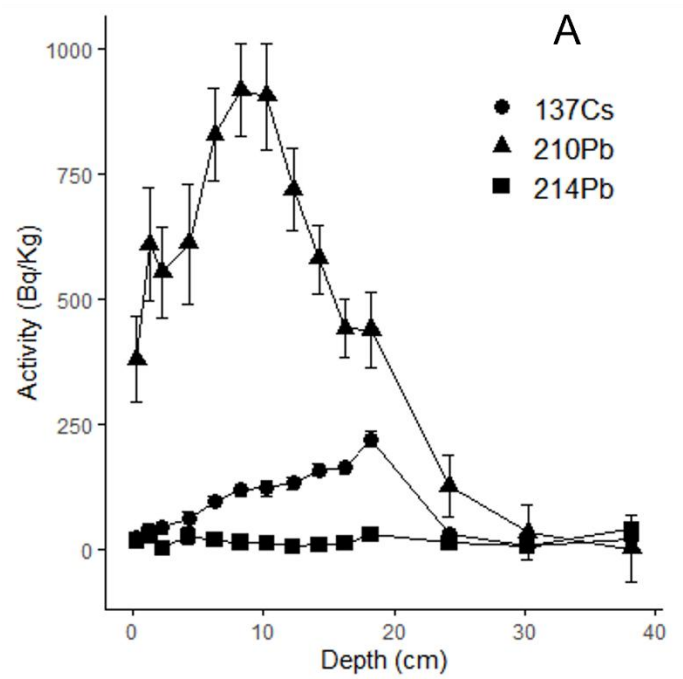
SC4



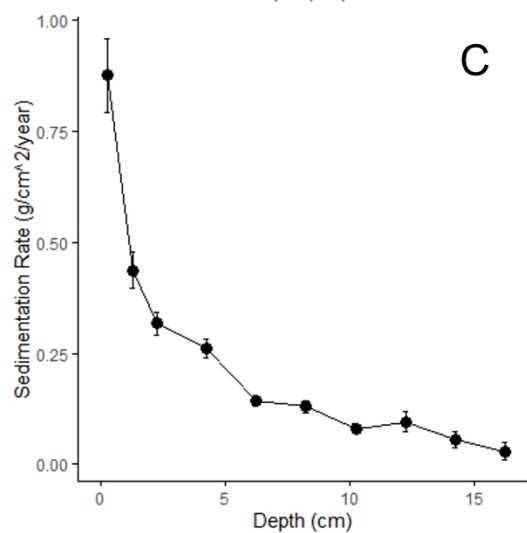
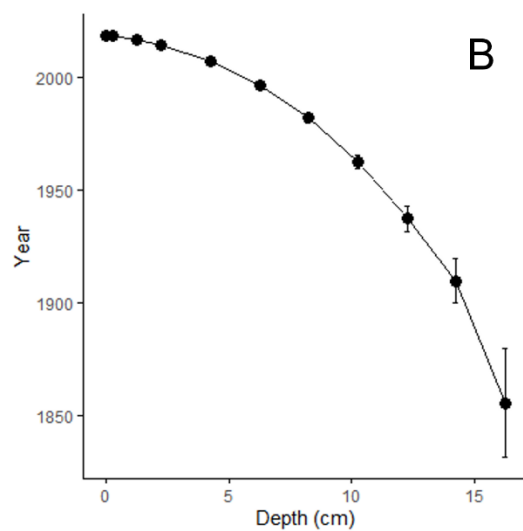
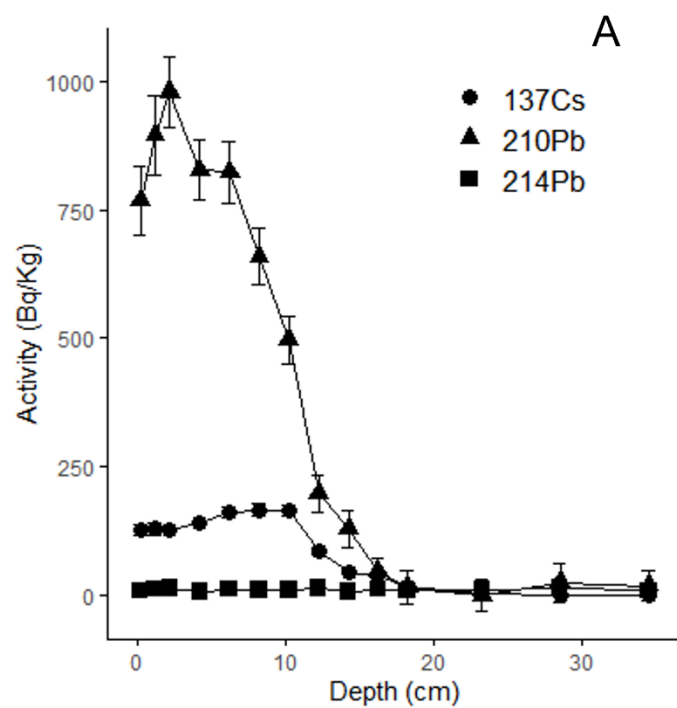
SC5



SC6

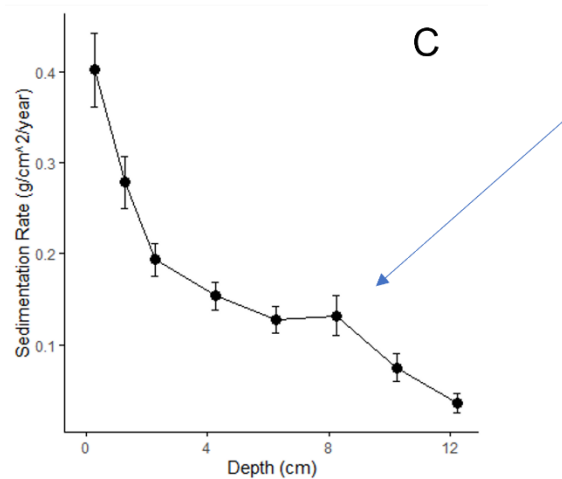
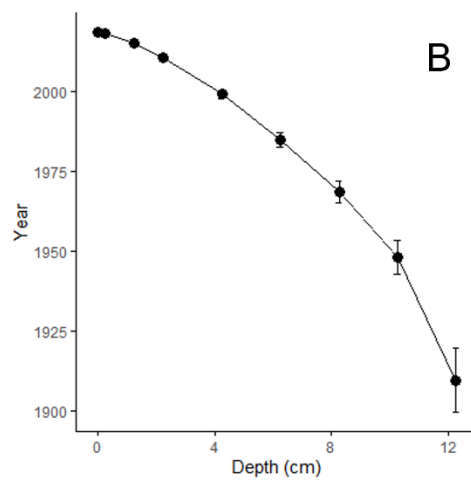
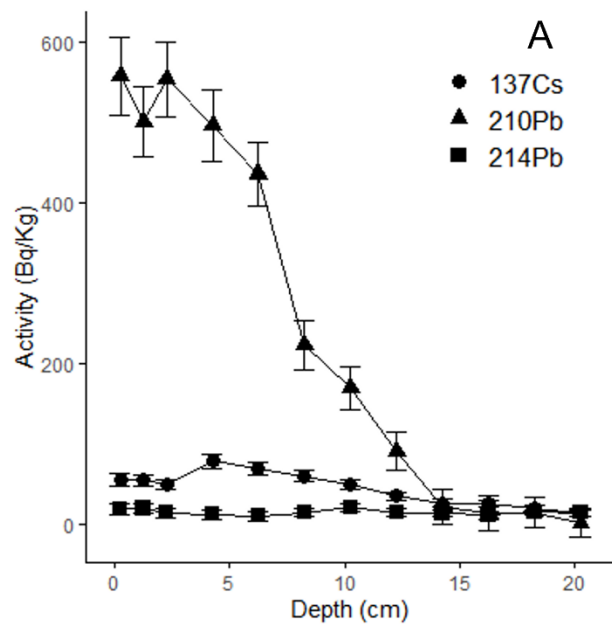


SC8

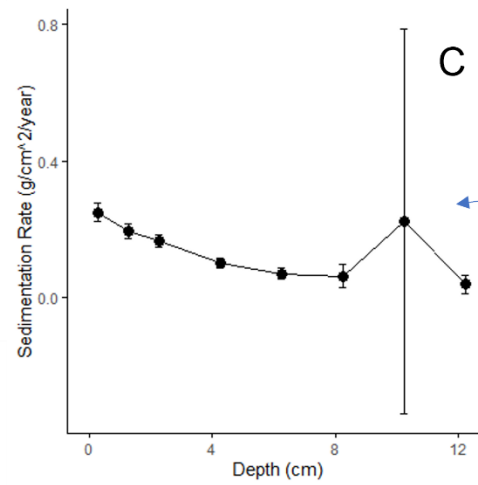
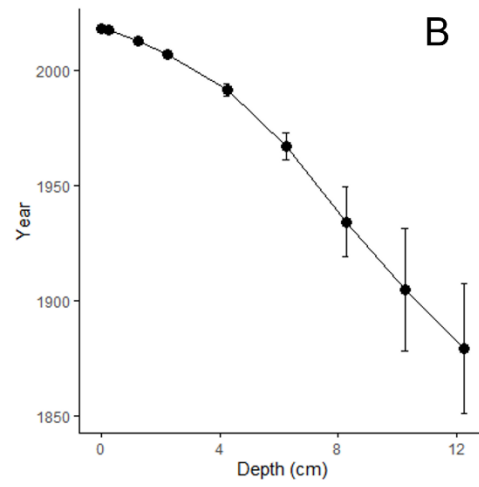
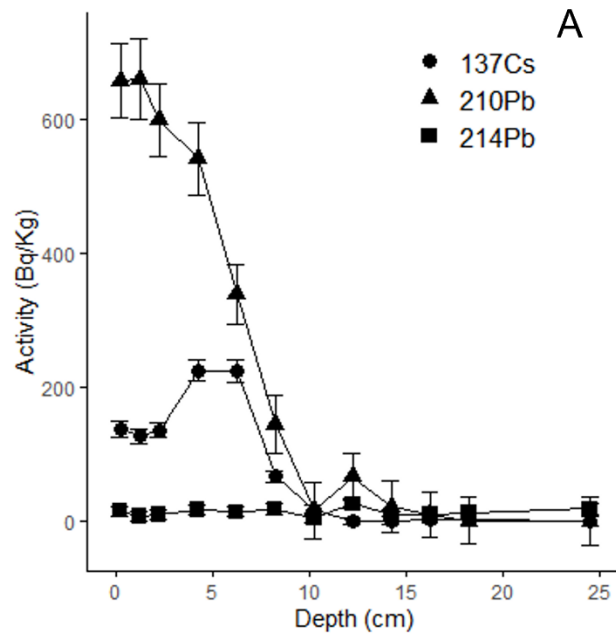


Appendix L

SC9

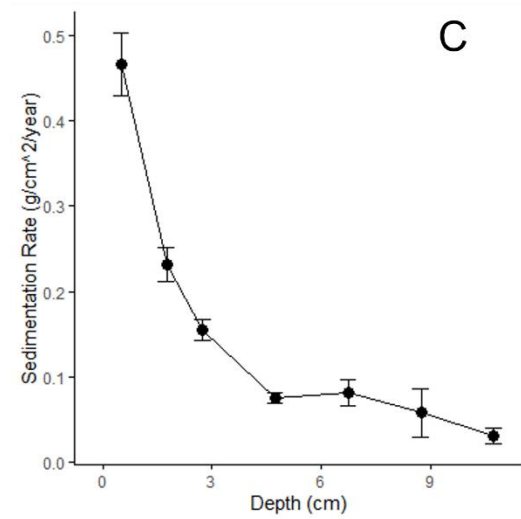
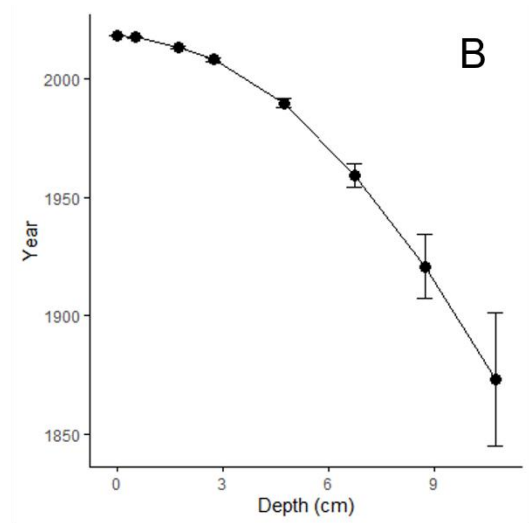
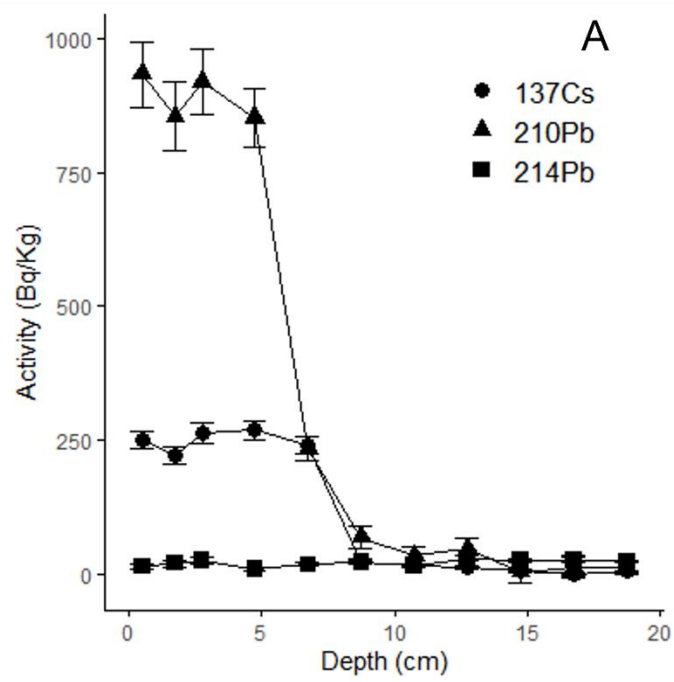


SC10



Appendix N

SC11



SC12

