

**Development and Application of Periphyton-Based Biomonitoring Methods to
Elucidate Aquatic Ecosystem Responses of Lakes in a Water-Rich Northern Landscape
(Old Crow Flats, Yukon, Canada) to Climate Change**

by

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Abstract

Shallow freshwater lakes are abundant in Arctic and subarctic regions, where they provide important wildlife habitat and sustain the cultural heritage and traditional land use of Indigenous communities. Concern over effects of climate change on shallow northern lakes, including warming and associated increase of evaporation and shifts in precipitation, however, elicits a need for agency-led, long-term, biomonitoring programs to implement protocols applicable across large, remote landscapes. My research focuses on lakes of the Old Crow Flats (OCF), a 5,600 km² lake-rich thermokarst landscape in northern Yukon recognized as a Ramsar Wetland of International Importance for ecosystem services provided to wildlife and the Vuntut Gwitchin First Nation (VGFN). There, climate warming has raised uncertainty about sustainability of traditional activities in the landscape and challenges natural resource stewardship. The research employs analysis of periphytic diatom community composition accrued on artificial-substrate samplers and water chemistry in lakes of the Old Crow Flats (Yukon Territory, Canada), where spatial and temporal variation in input water sources and water balance has been characterized using water isotope tracers, to explore the ability of diatoms to discern ecological responses to shifts in basin hydrology. The findings are reported in two data chapters. One chapter explores spatial variation across a set of lakes that span the hydrological gradients of OCF during ice-free seasons of 2008 and 2009. The other chapter assesses temporal variation at 14 lakes during a 12-year-long monitoring period (2008-2019) when water isotopes document increasing input of rainfall and possibly permafrost thaw on their water balance.

Results of multivariate analyses based on the spatial data set (33 and 48 lakes sampled in 2008 and 2009, respectively) demonstrate that water chemistry and diatom community composition differ among three isotope-defined hydrological lake categories based on differences in input water sources (snowmelt-dominated, rainfall-dominated, intermediate). Some snowmelt-dominated lakes support moderate percent abundances of *Rossithidium pusilla*, *Sellaphora laevissima*, *Tabellaria flocculosa* str. III and *T. fenestrata*, associated with relatively high concentrations of major nutrients and dissolved organic carbon (DOC). Rainfall-dominated lakes have higher pH and ion content, yet diatom composition overlapped extensively with intermediate and snowmelt-dominated lakes. Water chemistry and diatom community composition did not differ between study years, despite almost four-fold greater snowfall in 2009. Overall, the results reveal that periphytic diatom communities on artificial-substrate samplers capture ecological differences across hydro-limnological gradients of Old

Crow Flats, but longer time-series of data are required to assess their ability to track temporal responses to hydro-climatic variation.

The spatial dataset of OCF lakes sampled during 2008 and 2009 for analysis of periphytic diatom community composition and water chemistry was used to inform interpretations of temporal changes in diatom community composition that accrued on artificial substrate samplers deployed during thaw seasons of a 12-year period (2008-2019) at 14 long-term monitoring (LTM) lakes and infer shifts in water chemistry. Ordination by CCA reveals that periphytic diatom communities at 10 of the 14 LTM lakes (71.4%) converged towards composition typical of lakes with rainfall-dominated input waters by 2019 due to relatively high or rising percent abundance of the diatom taxa *Achnantheidium minutissimum*, *Gomphonema angustum*, *G. capitatum*, *Diatoma tenuis*, and/or *Eunotia obscurum*. These include 4 of the 5 lakes that were dominated by rainfall input water at the beginning of the monitoring period (OCF 29, 37, 38, 49), where diatom community composition remained relatively unchanged, as well as 5 of the 6 lakes that began in the intermediate category (OCF 19, 34, 35, 46, 48), and one of the 3 lakes that began in the snowmelt-dominated category (OCF 58). Four of the 14 LTM lakes reveal patterns of change that are not consistent with a shift towards diatom communities typical of rainfall-dominated lakes. These include two lakes (OCF 26, 55) where diatom community composition remained relatively constant during the entire monitoring period and indicative of conditions typical of lakes with snowmelt-dominated inflow. They also include a lake that recently drained (OCF 6) and a lake with a particularly large catchment area (OCF 11) where *Cocconies lineata* dominated diatom communities and where basin hydrology appears to be strongly influenced by both rainfall and snowmelt input. Overall, these findings suggest that composition of periphytic diatom communities on artificial-substrate samplers tracks aquatic ecosystem responses to temporal trends in climate-mediated hydrological change.

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Dedication

This thesis is dictated to my mother Fraiha K. Alwan, my daughters Tuqa, Zahraa, and Noora, and to my son Mohammed-Ali.

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Chapter 1

Introduction

The research presented in this PhD Thesis has been motivated by a need to advance methods capable of generating informative long-term monitoring records of changes in hydrological and ecological conditions of shallow lakes within remote northern landscapes where concern is growing over effects of climate warming (Rouse et al., 1997; Wolfe et al., 2011; Bouchard et al., 2013; Heino et al., 2020; Kahlert et al., 2020). I began my PhD program shortly after substantial multidisciplinary research had been completed at the Old Crow Flats in northern Yukon Territory, funded by the Government of Canada's International Polar Year (IPY) program and led by the Government of the Vuntut Gwitchin First Nation, in partnership with academic researchers and stakeholder agencies (Figure 2.1). The IPY project was entitled "Environmental change and traditional use of the Old Crow Flats in northern Canada (Yeendoo Nanh Nakhweenjit K'atr'ahanahyaa) and it focused on addressing the complex effects of climate change on aquatic and terrestrial ecosystems within the Old Crow Flats (OCF) and the nearby First Nation community of Old Crow (population ~300) (Wolfe et al., 2011). OCF is a Ramsar Wetland of International Importance that spans an area of 5,600 km² of flat terrain that supports over 2,700 shallow, mainly thermokarst, lakes. The landscape offers important habitat to an abundance of migrating and resident wildlife, and it supports the traditional lifestyle of the Vuntut Gwitchin First Nation VGFN (Yukon Ecoregions Working Group, 2004). OCF is protected within Vuntut National Park (VNP) and the OCF Special Management Area, which are cooperatively managed by the Vuntut Gwitchin Government (VGG), Parks Canada Agency (PCA), and North Yukon Renewable Resources Council (NYRRC). The landscape is situated within a region of continuous permafrost, where the estimated active layer depth is 18–56 cm (Ovenden and Brassard, 1989). The active layer is underlain mainly by relatively uniform glaciolacustrine sediments (clay, sand, silt) with patches of gravel and alluvial sediments covered by organic detritus and peat residues (Hughes, 1972; Ovenden, 1981). The continuous permafrost layer that underlies the low-relief terrain is thought to prevent sub-permafrost inflow and outflow from altering lake water balances (Zazula et al., 2004; Turner et al., 2014). However, runoff from small outcrops of carboniferous rocks in the north-central region, named Timber Hill (Morell and Dietrich, 1993), probably affects water chemistry variables of some nearby lakes (MacDonald et al. 2012b). OCF is surrounded by

the Old Crow, British, Barn, and Richardson mountains along the southwest, west, north, and east margins, respectively, which provide downslope runoff to the peripheral areas (Hughes, 1972).

The abundant lakes within OCF are typically shallow, flat-bottomed and thermokarst in origin (Allenby, 1989). They are perched above the streams and rivers, thus any outflow from the lakes is eventually exported via distributary channels toward the Porcupine River. A few oxbow lakes occur at locations adjacent to the rivers, and they are deeper than the thermokarst lakes (Balasubramaniam et al., 2017). Dendrochronological evidence reveals a marked warming in recent decades that exceeds any other interval during the previous 300 years (Porter et al., 2010). The warming is consistent with observations of residents who also have witnessed fluctuations in lake water levels, which range from marked declines to stable and increasing water levels across the landscape (Wolfe et al., 2011; Lantz and Turner, 2015). The ongoing hydrological variations, and their potential to alter terrestrial vegetation and access to wildlife, have raised concern about ability of Indigenous residents to maintain their traditional lifestyle (Wolfe et al., 2011).

Meteorological data have been recorded since 1951 at the Environment Canada meteorological station located at the Old Crow airport. The 1971-2000 climate normal indicates the region is characterized by a continental sub-Arctic regime, with long cold winters, short cool summers, and comparatively low precipitation (Environment and Climate Change Canada, 2019). Mean annual air temperature is $-9.0 \pm 6.1^{\circ}\text{C}$ and mean annual precipitation is 257 mm, with nearly 60% as rain (station ID 2100200, Environment Canada, 2007). Mean annual air temperatures were higher between 1977 and 2001 period than the preceding period (1951-1975). Breakup of lake ice occurs between late May and mid-June, while freeze-up happens between mid-September and late October. During the ice-free season, lakes are exposed to 24 h of sunlight (Yukon Ecoregion Working Group, 2004).

As detailed in chapters 2 and 3, the small volume and large surface area-to-volume ratio of the shallow lakes within OCF makes them particularly responsive to effects of climatic changes. This has generated concern that alteration of hydrological processes could trigger widespread decline of lake levels, with associated consequences for water quality and ecological conditions (Wolfe et al., 2011; MacDonald et al., 2021). Thus, a major goal of the IPY project was to leave a legacy for the local community through the establishment of a long-term monitoring program capable of tracking trends in,

and identifying drivers of, aquatic ecosystem change, with an intention to inform decisions and policies for adaptation (Wolfe et al. 2011a).

A foundational component of the IPY project was an intensive three-year (2007–2009) assessment of spatial variation in water balance, water quality and community composition of aquatic biota at the base of the food webs of 58 lakes in OCF (Turner et al., 2014; Balasubramaniam et al., 2015, 2017). Variation in water balance was assessed using isotope tracers ($\delta^{18}\text{O}$, $\delta^2\text{H}$; Turner et al. 2014), water quality was assessed using analysis of water chemistry variables (pH, alkalinity, concentrations of major nutrients, dissolved organic carbon, ions; Balasubramaniam et al., 2015, 2017), and community composition was assessed from analysis of remains of diatom algae and chironomids in surficial sediment samples (Balasubramaniam et al., 2017). As summarized in the Introduction sections of chapters 2 and 3, the results revealed complex interactions among hydrological processes, catchment characteristics and meteorological conditions, which enabled prediction of possible trajectories in hydrological conditions, water quality and biological communities in response to anticipated changes in climate. As demonstrated in chapters 2 and 3, research presented in this thesis builds on this foundation via development, evaluation and application of the use of diatom algae accrued on artificial-substrate samplers for systematic repeated long-term monitoring of lakes across OCF to provide information about changes in water chemistry and ecological conditions in response to shifts in hydrological processes. The artificial-substrate samplers were deployed into most of the 58 ‘spatial-survey’ lakes during open-water seasons of 2008 and 2009 to assess ability of diatoms to capture limnological differences across the range of basin hydrology of OCF, including marked differences in input water sources (rainfall, snowmelt; see Chapter 2), and into a subset of 14 long-term monitoring lakes since 2008 where temporal changes in water isotope composition have also been recorded (see chapter 3; MacDonald et al., 2021).

I focus on analysis of periphytic diatom communities because periphytic algae are abundant in shallow lakes and diatoms typically dominate the periphyton. Tracking changes in diatom community composition and their relations with hydrological processes and water chemistry variables can be complicated in periphytic habitats because the taxa often occupy different benthic substrates (e.g., mud, aquatic moss, macrophytes), including specificity for the species of macrophytes and aquatic mosses to which they adhere, and it is rare that a single substrate remains consistently present across lakes and over time (Cattaneo & Amireault, 1992; Wiklund et al., 2010). Differences among sampled substrates in

duration of time for accrual of diatom communities can also confound ability to track environmental change (e.g., Wiklund et al., 2010). Artificial-substrate samplers provide a consistent substrate for periphytic diatom accrual, and they can be deployed for a consistent length of time, which may minimize these complications (Lowe & Pan, 1996; Wiklund et al., 2010). Artificial-substrate samplers have not been widely used in remote, shallow thermokarst lakes to track aquatic ecosystem responses to shifts in climate and hydrological processes. A prior study conducted by MacDonald et al. (2012a) revealed that deploying artificial-substrate samplers at a single location in a lake is sufficient to get a representative sample. In Chapter 2, I evaluate the potential of artificial-substrate samplers and periphytic diatom community composition to track ecological responses to spatio-temporal variation in hydrological and limnological conditions of shallow thermokarst lakes in OCF during 2008 and 2009 when samplers were deployed across the 58-lake set and retrieved from 33 and 48 lakes, respectively. The objectives included: 1) to determine if composition of diatom communities accrued on the samplers differs among the three hydrological lake categories determined from analysis of metrics based on water isotope composition (snowmelt-dominated, rainfall-dominated, intermediate); 2) to identify the water chemistry variables most strongly associated with the differences in community composition among lakes; and, 3) to evaluate if community composition differs between the two years of study which differed in amount snowfall (Turner et al., 2014). The research presented in Chapter 2 has been published as: Mohammed, W.J, L.A. MacDonald, B.B. Wolfe, R.I. Hall. 2021. Use of artificial-substrate samplers to identify relations between periphytic diatom community composition and hydro-limnological conditions in shallow lakes of the Old Crow Flats, Yukon Territory (Canada). *Hydrobiologia* 848 (19): 4551-4567 (<https://doi.org/10.1007/s10750-021-04661-3>).

In collaboration among multiple stakeholders (VGG, NYRRC, PCA and university researchers), 14 of the 58 lakes sampled during 2007-2009 were identified as the sites for a long-term hydro-ecological monitoring program, because they captured the range of hydrological and ecological conditions and catchment characteristics of lakes in OCF (Tondu et al., 2013). These lakes have been sampled annually in June and August/September for water isotope composition (since 2007) and for the diatom communities accrued on artificial-substrate samplers between the two visits (since 2008; except in 2015 when logistical problems occurred). Metrics based on the water isotope data (i.e., isotope composition of input water (δ_i) and evaporation-to-inflow (E/I) ratios) have been used to evaluate trends in the importance of snowmelt, rainfall and evaporation to the lakes since 2007 (Tondu et al., 2013; MacDonald et al., 2021). The water

isotope monitoring records spanning from 2007 to 2019 were recently published for the 14 long-term monitoring (LTM) lakes, and they identify a trend towards more positive water balances as a consequence of increasing inputs from rainfall and possibly also permafrost thaw (MacDonald et al., 2021). Rise of lake levels threatens to increase the frequency of catastrophic drainage events, with negative consequences for aquatic habitat (Turner et al., 2014; MacDonald et al., 2021). Integration of long-term monitoring of periphytic diatom community composition and inferred lake water chemistry with the water isotope data has potential to provide valuable additional information on aquatic ecosystem responses to the hydrological changes. I evaluate this in Chapter 3, where I use knowledge of relations among differences in input water sources, water chemistry variables, and composition of periphytic diatom communities accrued on artificial-substrate samplers gained from the 57-lake spatial dataset (obtained during 2008-2009) to infer limnological responses from analysis of periphytic diatom communities in biofilms accrued on artificial-substrate samplers deployed in the 14 LTM lakes in OCF during thaw seasons of 12 years spanning the same 13-year period of water isotope monitoring (2008-2019; data in 2015 were not available). Following feedback from the Examination Committee, I intend to submit Chapter 3 for publication to a Special Collection of the journal *Science Progress* on ‘Progress in Assessing Vulnerability of Freshwater Ecosystems’ as: Mohammed, W.J, L.A. MacDonald, K. Thomas, I. McDonald, K. Turner, B.B. Wolfe, R.I. Hall. Ecosystem responses of shallow thermokarst lakes to climate-driven hydrological change: Insights from long-term monitoring of periphytic diatom community composition at Old Crow Flats (Yukon, Canada).

Overall, research presented in this PhD thesis is intended to improve knowledge of aquatic ecosystem responses of shallow thermokarst lakes in remote northern regions to climate-driven hydrological changes and advance methods for integrated long-term hydro-ecological monitoring.

Chapter 2

Use of artificial-substrate samplers to identify relations between periphytic diatom community composition and hydro-limnological conditions in shallow lakes of Old Crow Flats, Yukon Territory (Canada)

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2.1 Introduction

Shallow lakes are abundant features of Arctic and subarctic landscapes, but concerns continue to grow about their vulnerability to climate warming and associated consequences for Indigenous communities and wildlife (Rouse et al., 1997; Wolfe et al., 2011; Bouchard et al., 2013; Heino et al., 2020). Shallow lakes cover substantial areas of mainland northwestern Canada, Alaska and Siberia (15–50% among regions), where they are often formed and influenced by thermokarst processes (Burn & Hag Elnur, 2002; Grosse et al., 2011). Due to small water volumes relative to surface area, water balance of shallow lakes is particularly responsive to changes in the distribution of rainfall and snowmelt inputs and evaporative losses (Bouchard et al., 2013). Shifts in air temperature, evaporation, and amount of rain and snow can cause marked changes in water levels, lake surface area, and timing and duration of ice-cover, which influence biogeochemical cycling and habitat availability (Rühland & Smol, 2005; Prowse et al., 2006; White et al., 2007; Labrecque et al., 2009). The magnitude and direction of recent hydrological change varies between regions, and among lakes within regions, which affects ability to predict lake responses to ongoing and future climate warming (Kahlert et al., 2020). Documented changes range from reductions in size and abundance of lakes in some areas due to sudden drainage events and increased net evaporation (Labrecque et al., 2009; Carroll et al., 2011; Lantz & Turner, 2015), to expansion of lake surface area and rise of water levels in other areas of increased permafrost thaw, shoreline erosion and precipitation (Payette et al., 2004; Jorgenson & Shur, 2007; Korosi et al., 2017). But, insufficient long-term monitoring data continues to impede progress in understanding responses of lakes and ponds in many remote northern regions (Heino et al., 2020; Kahlert et al., 2020).

Old Crow Flats (OCF) is a large (5,600 km²), water-rich thermokarst landscape in northern Yukon Territory where long-term monitoring has been identified as a priority to track ongoing and future hydrological and ecological changes in the abundant (>2,700) shallow lakes and ponds that provide important natural resources for wildlife and the Vuntut Gwitchin First Nation (VGFN) (Wolfe et al., 2011). OCF is a Ramsar Wetland of International Importance and is protected within Vuntut National Park and the OCF Special Management Area. Traditional knowledge and scientific data indicate pronounced changes have occurred during recent decades in temperature, precipitation, vegetation cover, and lake and river water levels (Wolfe et al., 2011; Porter & Pisaric, 2011; Lantz &

Turner, 2015), which raise uncertainty about sustainability of traditional activities in the landscape and challenge natural resource stewardship. Among the many concerns is that climate warming and associated changes to terrestrial vegetation is altering hydrological processes, water quality and ecological communities of the abundant shallow lakes (Wolfe et al., 2011; Balasubramaniam, 2012; Tondu et al., 2013).

The above concerns triggered scientific studies which have improved understanding of hydrological processes that influence lake water balance and their relations with limnological conditions and biotic communities. Coupled hydrological and limnological studies at a set of 57 shallow lakes repeatedly sampled across OCF during 2007-2009 have demonstrated systematic relations among catchment land cover, lake water balance, water chemistry and composition of biotic assemblages in recently-deposited surficial sediments (Turner et al., 2010, 2014; Balasubramaniam et al., 2015, 2017). Analyses of water isotope composition demonstrated that water balance varies among the lakes due to differences in catchment land cover, which influence snowmelt and rainfall inputs and evaporative losses (Turner et al., 2010, 2014). Lakes with sparsely vegetated catchments possess water balances dominated by rainfall inputs and experience stronger influence of evaporation during summer than lakes in catchments with tall and denser vegetation that entrap snow and receive greater and more protracted inputs of snowmelt during the thaw season. Lakes dominated by rainfall inputs possess higher conductivity, pH, alkalinity, and concentrations of ions and dissolved inorganic carbon (DIC), whereas lakes with inputs dominated by snowmelt have higher concentrations of nutrients (nitrogen, phosphorus) and dissolved organic carbon (Balasubramaniam et al., 2015). Larger lake surface area, which increases evaporative water loss, and more rapid influx of eroded shoreline soils from sparsely vegetated catchments have been suggested as processes that generate higher ionic content, conductivity and pH in the rainfall-dominated lakes (Turner et al., 2014; Balasubramaniam et al., 2015). Interaction between snowmelt and organic-rich terrestrial vegetation and soil has been proposed as a mechanism for greater supply of DOC and other nutrients (TP, TDP) to snowmelt-dominated lakes (Balasubramaniam et al., 2015). Collectively, these studies provided a framework to differentiate lakes in OCF into three functional hydrological categories based on differences in relative importance of input waters: snowmelt-dominated, rainfall-dominated, and intermediate lakes (Balasubramaniam et al., 2015). Lakes in the intermediate category receive relatively equal proportions of snowmelt- and

rainfall- input waters during the ice-free season, or begin the open-water season with substantial snowmelt input and rapidly transition to strong influence of rainfall and evaporation by mid-summer.

Hydrological and water-chemistry differences between lakes in the rainfall- and snowmelt-dominated categories are associated with distinctive composition of diatom algae and chironomid assemblages in surficial sediments (Balasubramaniam et al., 2017). The assemblages included mainly taxa known to occupy periphytic (epiphytic and benthic) habitats, which are abundant in OCF's shallow lakes. Thus, the ability of water isotope tracers to determine differences in water input sources and evaporation, and of periphytic diatoms and chironomids to discern hydro-limnological differences among the lake categories, suggests sampling and analyses of these media can provide an effective approach for long-term monitoring of lakes in OCF to track hydro-ecological effects of ongoing and future climatic changes.

Since 2007, partnerships among Parks Canada, VGFN and university researchers have been advancing these methods for long-term hydro-ecological monitoring of lakes in OCF, as a legacy of the Government of Canada International Polar Year Program (Wolfe et al., 2011). Tondu et al. (2013) analyzed water isotope samples collected between 2007 and 2011 from a set of 14 lakes that span the hydrological and land cover gradients captured by the 57-lake set of the above scientific studies by Turner et al. (2010) and Balasubramaniam et al. (2015, 2017). Tondu et al. (2013) used the coupled-isotope tracer method of Yi et al. (2008) to compute the isotope composition of input waters (δ_i) and evaporation-to-inflow (E/I) ratios for each lake, and proposed use of Mann-Kendall trend tests as an effective method to detect if and when shifts in hydrological processes begin to alter lake water balances. Annual monitoring of these 14 lakes has been ongoing since 2007 and demonstrates a trend of increasingly positive lake water balances as a consequence of increasing rainfall and possibly permafrost thaw, which has offset evaporative water loss during the ice-free season (MacDonald et al., 2021). These trends have stimulated interest by natural resource stewardship agencies to couple hydrological monitoring with a long-term ecological monitoring program capable of assessing if and when hydrological changes elicit shifts in biological communities at the base of the aquatic food webs. To address these interests, our research group has developed protocols for a long-term ecological monitoring program suitable for shallow lakes in OCF using periphytic diatoms and artificial-substrate samplers (MacDonald et al., 2012a).

Diatom communities in shallow lakes of OCF are dominated by taxa that occupy mainly periphytic habitats (Balasubramaniam et al., 2017). Tracking changes in diatom community metrics and relating them to variation in hydrological processes and water chemistry is challenging in these habitats since periphytic taxa often exhibit specificity for type of benthic substrate (e.g., mud, aquatic moss, macrophytes) and host macrophyte species, and it is typically rare that a single substrate remains consistently present across lakes and over time (Cattaneo & Amireault, 1992; Wiklund et al., 2010). Signals of environmental change over space and time obtained from periodic sampling of periphytic diatoms on naturally occurring substrates also can be confounded by differences in duration of diatom community accrual (Wiklund et al., 2010). Artificial-substrate samplers can be used to overcome some of these limitations, as they present a consistent substrate for periphytic diatom accrual across lakes and can be deployed for a known, controlled period of time (Lowe and Pan, 1996; Wiklund et al., 2010). MacDonald et al. (2012a) determined that deployment of the samplers during the entire ice-free season was most appropriate at a shallow lake near OCF to ensure samples are representative of environmental conditions. However, to our knowledge, artificial-substrate samplers have not been widely used in remote, shallow thermokarst lakes to track ecological and limnological shifts associated with variation in climate and hydrological processes. Thus, there is a need to explore the potential of artificial-substrate samplers and periphytic diatom community composition to track ecological responses to differences in hydro-limnological conditions of shallow thermokarst lakes across the OCF landscape.

For this study, we deployed artificial-substrate samplers in lakes spanning the hydro-limnological gradients of OCF at the beginning of the ice-free seasons of 2008 and 2009 and retrieved them from 33 and 48 lakes, respectively, at the end of the season to determine: 1) if community composition of diatoms that accrue on the samplers differs among the three hydrological lake categories (snowmelt-dominated, rainfall-dominated, intermediate); 2) environmental variables that are most strongly associated with the floristic differences; and, 3) if community composition differs between the two years of study as a consequence of inter-annual differences in snowmelt runoff. For the third objective, seasonal air temperature variations were similar between the two study years, but winter precipitation differed substantially (Turner et al., 2014), which provided opportunity to assess if and how inter-annual differences in snowmelt runoff affect water chemistry and periphytic diatom community composition.

2.2 Methods:

2.2.1 Meteorological data

Ice breakup on lakes of OCF occurs during late May to mid-June, and freeze-up occurs mid- to late September. Lakes are exposed to 24 hr sunlight during most of the ice-free season. Mean annual air temperature is -9.0 ± 6.1 °C, and annual precipitation is 265.5 mm with 54.3% falling as rain (1971–2000 climate normal, station ID 2100800; Environment Canada, 2007). As reported by Turner et al. (2014), cumulative winter snowfall was well below average before the 2008 ice-free season (snow water equivalent = 35 mm; 1951–2009 mean = 100 mm) and above average before the 2009 ice-free season (153 mm). Cumulative rainfall was comparable during ice-free seasons of 2008 (169 mm) and 2009 (166 mm).

2.2.2 Water sample collection and laboratory analyses

During ice-free seasons of 2008 and 2009, a set of 57 lakes spanning the hydrological gradients of OCF were visited by helicopter (fitted with floats) three times per year (early June, late July, early September) to characterize hydrological and limnological conditions (Figure 2.1; Appendix A, B). On each lake visit, in situ measurements of pH and specific conductivity (SpCond) were obtained at 30-cm depth from a central location in each lake (or, at least 200-300 m from shore) using a YSI 600QS multimeter. Also, water samples were collected at ~15-cm depth for analysis of water isotope composition (in 30 ml HDPE bottle without air space) and water chemistry (4 L in plastic carboys). All samples for water chemistry analysis were kept cool (4 °C) and in the dark until processed at the field base in the town of Old Crow. A coarse Nitex mesh (200 µm) was used to eliminate large particles before assessing concentrations of total nitrogen (TN), ammonia (NH₃), total phosphorus (TP), silica (SiO₂) and major ions (Na⁺, Cl⁻, SO₄²⁻, Mg²⁺, Ca²⁺, K⁺) and alkalinity (Alk). Subsamples of water were filtered through cellulose acetate filters (0.45 µm) to determine concentrations of dissolved inorganic carbon (DIC), dissolved organic carbon (DOC), and total dissolved phosphorus (TDP). Samples for determination of TP and TDP concentration were preserved with 1 mL of 30% H₂SO₄. All water samples were kept cold and in the dark during transport to and storage at the Environment and Climate Change Canada's National Laboratory for Environmental Testing (NLET) in Burlington, Ontario, prior to analysis following standard protocols (Environment Canada, 1996). Chlorophyll *a* (Chl-*a*)

concentration was determined following methods in Balasubramaniam et al (2015). The water chemistry and Chl-a data are available in Appendices A and B.

We used water isotope data reported in Turner et al. (2010, 2014) for the mid-summer (July) sampling period and methods of Turner et al. (2014) to estimate the oxygen isotope composition of input waters ($\delta^{18}\text{O}_\text{I}$). Following methods of Balasubramaniam et al. (2015, 2017), the $\delta^{18}\text{O}_\text{I}$ values from July were used to place lakes into one of three input-water categories based on the full lake set in 2008 (snowmelt-dominated <-24.3 ‰, intermediate -24.3 to -22.6 ‰, rainfall-dominated >-22.6 ‰; $n = 54$ lakes) and 2009 (snowmelt-dominated <-24.3 ‰, intermediate -24.3 to -22.7 ‰, rainfall-dominated >-22.7 ‰; $n = 56$ lakes). These threshold values differ slightly from those reported in Balasubramaniam et al. (2015, 2017) because of differences in the sample years, site locations and sample sizes among the data sets. The $\delta^{18}\text{O}_\text{I}$ data are available in Appendix A.

2.2.3 Deployment and retrieval of artificial-substrate periphyton samplers

During 2008 and 2009, artificial-substrate samplers were deployed in June (shortly after ice-off) at a central location of each lake and retrieved in September (end of the growth season) to collect a biofilm of periphytic algae. The artificial-substrate samplers follow the design of Wiklund et al. (2010) and MacDonald et al. (2012a), which include a wood float (62 cm long x 6.3 cm wide x 1.6 cm thick) holding two sampling units, each composed of five rectangular sheets of polyethylene (each 4 x 14 cm) that serve as the artificial substratum. After deployment, the artificial substrates were suspended 25 cm below the water surface, and the sampler was anchored to the lake bottom with rocks. During September sampling, we were able to retrieve samplers from 33 lakes in 2008 and 48 lakes in 2009. Samplers were recovered from 29 of the same lakes in both years. The sheets in each unit were removed carefully from the retrieved samplers, placed individually into opaque plastic film canisters and preserved frozen until analysis.

2.2.4 Diatom analysis

Diatom analysis was conducted on samples of accrued periphyton biofilm prepared from the polyethylene sheets of the retrieved artificial-substrate samplers. To do this, one of the 10 sheets from each sampler was randomly chosen, placed in a beaker and submerged in 10% HCl (by volume) to dissolve carbonates. Then, samples were digested at 90 °C in 30% H_2O_2 to remove organic matter.

After that, diatoms in each sample were allowed to settle to the bottom of the beakers for 24 hr. The supernatant was gently drawn off and substituted with deionized water to remove acid residues from the slurry, and this process was repeated many times until the pH of the deionized water was reached. The resulting cleaned diatom slurries in water were then placed on circular coverslips and allowed to dry. Finally, these coverslips were mounted onto microscope slides using NaphraxTM. Using a Zeiss Axioskop II Plus compound light microscope and 1,000X magnification under oil immersion, at least 300 diatom valves were tallied and identified to the lowest achievable taxonomic level (typically species or lower) using the taxonomic references by Krammer & Lange-Bertalot (1986–1991) and Lavoie et al. (2008). The diatom data were expressed as relative (%) taxon abundances of the total diatom sum, as a metric of community composition. For each year, we removed rare diatom taxa from subsequent numerical analyses and included only those taxa that were present in at least three lakes and achieved maximum abundance $\geq 2\%$ in at least one lake. Appendix C presents the percent abundance data for the diatom taxa meeting this criterion, including their taxonomic authorities.

2.2.5 Numerical analyses

We employed multivariate data analyses to explore the distribution of water chemistry variables and composition of periphytic diatom communities among the study lakes, and statistical tests to determine if water chemistry and diatom community composition differ among the three hydrological categories (rainfall-dominated, snowmelt-dominated, intermediate) and between the two study years, as described below.

Principal components analysis (PCA) was used to explore patterns of variation in water chemistry variables among lakes during 2008 and 2009. The PCAs were performed using values from the July samples, which best reflect limnological conditions at the time of peak algal growth (Balasubramaniam et al., 2015). For the PCAs and all other subsequent analyses, we included only the lakes where artificial-substrate samplers were successfully retrieved and July water chemistry data were also available (33 lakes in 2008, 48 lakes in 2009). Water chemistry variables, except pH, were $\log(x+0.5)$ -transformed prior to numerical analyses. Lake surface area was added as a supplementary variable to explore relations between lake area and water chemistry. All variables were centered and standardized in the PCAs. In the resulting ordination plots, sample scores for lakes were coded according to their hydrological category. All ordinations, including those used for analyses of the

diatom data below, were performed using the software CANOCO version 5 (ter Braak & Šmilauer, 2002).

Ordinations were used to explore patterns of variation in periphytic diatom community composition among the three hydrological categories (using indirect gradient analysis) and relations with explanatory water chemistry variables (using direct gradient analysis). Unimodal-based ordination methods were used because a preliminary ordination by detrended correspondence analysis (DCA), with linear detrending, indicated the floristic gradient along the first axis was 2.7 SD units in 2008 and 2.8 SD units in 2009 (Lepš & Šmilauer, 2003). For all ordinations of the diatom data, taxon abundances were square-root-transformed and rare taxa were down-weighted.

To explore how periphytic diatom community composition differs among the hydrological categories, correspondence analysis (CA) was run separately for each study year (2008, 2009). In the resulting ordination plots, sample scores for lakes were coded according to their hydrological category.

One-way analysis of similarities (ANOSIM) tests were performed separately on the 2008 and 2009 water chemistry and diatom datasets to determine if water chemistry and periphytic diatom community composition, respectively, differ significantly among lakes of the three hydrological categories. For the ANOSIM tests on the water chemistry data, Euclidean distances were computed from $\log(x+0.5)$ transformed values (except pH, which was not transformed). For the ANOSIM tests on the diatom data, Bray-Curtis similarity coefficients were computed on square-root-transformed diatom percent abundances. The ANOSIM test statistic (global R) represents the differences of water chemistry variables or diatom community composition among the three input-water categories contrasted with the differences among replicates within each category, and the value ranges from 0 to 1. A value of 0 indicates that the similarity between and within hydrological categories is the same on average, while a value of 1 indicates that replicates within a category are more similar to each other than to all other replicates of the other categories. P-values were calculated for each test by comparing the distribution of within- and across-group rank Bray-Curtis similarities (based on 9,999 random computations) to the initial rank similarity, as reported by the global R value. Two-way nested ANOSIM tests were also conducted to determine if water chemistry and diatom community composition differ significantly between the two study years (2008, 2009). These tests were performed on the subset of 29 lakes from which periphyton samplers were obtained in both 2008 and 2009. Nesting

by lakes within years provided a paired-samples design to determine if water chemistry and diatom community composition differ between the two years of sampling. All ANOSIM tests were performed using PRIMER version 7 software (Clarke & Warwick, 2001; Clarke & Gorley, 2006). For all statistical tests, significance was assessed at $\alpha = 0.1$, consistent with assessment of benthic algal biomonitoring protocols for temperate lakes by Thomas et al. (2011) to reduce the risk of Type II error.

Relations between periphytic diatom community composition and water chemistry variables measured in July were explored using canonical correspondence analysis (CCA) for each of the study years (2008, 2009). Water chemistry variables that individually explained a significant amount of variation in diatom community composition among lakes (at $\alpha = 0.1$, based on 499 random Monte Carlo permutations) were included as active variables in the CCAs. The remaining variables were included as supplementary variables to identify their associations with the significant water chemistry variables and the lake hydrological categories, but without influencing the positions of taxon and sample scores.

2.3 Results

Use of PCA identified systematic differences in water chemistry among the lake hydrological categories for both years (Figure 2.2). In 2008, the first two PCA axes explain 65.7% of the variation in the data set (axis 1 = 40.2%; axis 2 = 25.5%). Lakes in the snowmelt-dominated category are generally located towards the right along axis 1, associated with relatively low concentrations of major ions, and low alkalinity, specific conductivity and pH, and moderate to high concentrations of DOC and other nutrients. In contrast, the rainfall-dominated lakes are positioned to the left along axis 1, associated with relatively high concentrations of major ions, and high pH, alkalinity and specific conductivity. Lake surface area is relatively large for the rainfall-dominated lakes, relatively small for the snowmelt-dominated lakes and positively correlated with concentrations of major ions, and high pH, alkalinity and specific conductivity. Lakes in the intermediate category are scattered among those of the other two hydrological categories, demonstrating high variability of the water chemistry values. In 2009, the first two PCA axes explain 62.2% of the variation in the dataset (axis 1 = 42.5%; axis 2 = 19.7%) and captured similar patterns of variation as in the PCA of the 2008 data (Figure 2.2).

One-way ANOSIM tests reveal that July water chemistry differs significantly among hydrological categories in both 2008 (global $R = 0.243$, $p = 0.002$) and 2009 (global $R = 0.170$, $p =$

0.002). Based on pairwise comparisons, water chemistry differs between snowmelt- and rainfall-dominated lakes in both years (2008: $R = 0.504$, $p = 0.0004$; 2009: $R = 0.283$, $p = 0.007$). Water chemistry differs significantly between rainfall-dominated and intermediate lakes in 2008 ($R = 0.212$, $p = 0.011$), but not in 2009 ($R = -0.020$, $p = 0.540$). Water chemistry of snowmelt-dominated and intermediate lakes does not differ significantly in 2008 ($R = 0.045$, $p = 0.166$), but differs significantly in 2009 ($R = 0.233$, $p = 0.001$). The two-way nested ANOSIM test identified that water chemistry does not differ significantly between 2008 and 2009 ($R = -0.025$, $p = 0.941$), despite almost four-fold greater cumulative snowfall in 2009.

A total of 47 diatom taxa were identified in samples analyzed from the periphyton samplers retrieved from the 33 lakes in 2008. In 2009, a total of 37 diatom taxa were identified from samplers retrieved from 48 lakes. In both years, 31 of these taxa occurred in at least three lakes and at $\geq 2\%$ relative abundance in at least 1 lake and were included in all subsequent analyses. *Achnanthydium minutissimum*, *Cocconeis lineata* and *Gomphonema angustum* are the most abundant and widespread taxa across the entire hydrological spectrum of OCF lakes in both years (Figure 2.3). These three taxa, as well as *Nitzschia palea* and *Fragilaria capucina*, occur in all three hydrological categories. Percent abundance of *A. minutissimum* is slightly higher in rainfall-dominated (average = 56.3%) than intermediate (39.8%) and snowmelt-dominated lakes (38.8%). On average, *G. angustum* is twice as abundant in rainfall-dominated (20.0%) and intermediate (17.3%) lakes than in snowmelt-dominated lakes (8.8%). Relative abundance of *C. lineata* is almost three-fold higher in intermediate lakes (average = 20.1%) than rainfall-dominated (7.6%) or snowmelt-dominated lakes (6.9%). A few other taxa are relatively abundant in several snowmelt-dominated lakes and present in a few intermediate lakes but absent from rainfall-dominated lakes, including *Rossithidium pusillum*, *Eunotia subarcutoides*, *Epithemia adnata*, *Sellaphora laevissima*, *Tabellaria flocculosa* str. III, and *T. fenestrata*. No taxa are exclusive to the rainfall-dominated lakes.

Analysis by indirect gradient ordination reveals that periphytic diatom community composition differs between snowmelt- and rainfall-dominated lakes, but their compositions overlap substantially with intermediate lakes (Figure 2.4). For the 2008 dataset, the first two CA axes explain 30.9% of the variation in community composition among lakes. Axis 1 explains 18.8% of the variation and separates communities of the rainfall-dominated lakes, mainly positioned in the lower left quadrant, from many

of the snowmelt-dominated and intermediate lakes which were mainly positioned in the other three quadrants. Scores for the diatom taxa with relatively high abundance in several snowmelt-dominated lakes and absence from rainfall-dominated lakes are positioned to the right along axis one (*T. flocculosa* str. III, *T. fenestrata*, *R. pusillum*, *S. laevissima* and *E. subarcutoides*). For the 2009 dataset, the first two CA axes explained 32.3% of the variation in diatom taxon relative abundances among lakes (axis 1 = 20.4%, axis 2 = 11.9%), and also separates communities of the rainfall-dominated lakes, positioned mainly in the lower left quadrant, from the snowmelt-dominated positioned almost exclusively in the other three quadrants. A notable exception is OCF 6, which is positioned at the top left due to unusually high percent abundance of *C. lineata* relative to other lakes in the rainfall-dominated category. Sample scores for the intermediate lakes are distributed more equally among all four quadrants in 2009. In general, taxon scores are positioned consistently in the plots for both the 2008 and 2009 datasets.

One-way ANOSIM tests identified that composition of periphytic diatom communities differs significantly among hydrological lake categories in 2008 (global $R = 0.059$, $p = 0.067$) and in 2009 (global $R = 0.112$, $p = 0.024$). However, the low values of the global R test statistic suggest that periphytic diatom community composition differs due to other factors beyond those associated with the three hydrological categories. Based on pairwise comparisons, community composition differs in 2008 between rainfall-dominated and intermediate lakes ($R = 0.094$, $p = 0.069$), but not between rainfall- and snowmelt-dominated lakes ($R = 0.046$, $p = 0.168$) or snowmelt-dominated and intermediate lakes ($R = 0.045$, $p = 0.184$). In 2009, community composition differs between snowmelt-dominated and intermediate lakes ($R = 0.193$, $p = 0.003$) and between snowmelt- and rainfall-dominated lakes ($R = 0.098$, $p = 0.092$), but not between rainfall-dominated and intermediate lakes ($R = -0.022$, $p = 0.543$).

The two-way nested ANOSIM test identified no significant differences in periphytic diatom community composition between 2008 and 2009 ($R = 0.013$, $p = 0.207$), consistent with the above finding of no significant difference in water chemistry between the two study years.

Ordination by CCA was used to explore relations between periphytic diatom community composition and water chemistry variables (Figure 2.5). For the 2008 dataset, the first two CCA axes explain 21.2% of the variation in community composition and the water chemistry variables among lakes. Axis 1 captures 13.5% of the variation and separates the rainfall-dominated lakes from most of the snowmelt-dominated lakes. All but one of the rainfall-dominated lakes are positioned to the left

along CCA axis 1, and most of the rainfall-dominated lakes are in the lower left quadrant, associated with relatively high pH, alkalinity and conductivity, high concentrations of ions (Mg^+ , Na^+ , Cl^- , Ca^- , and SO_4^{2+}) and low concentrations of DOC, TDP and SiO_2 . The snowmelt-dominated lakes are generally positioned across the right half of the plot, associated with lower concentrations of ions (Mg^+ , Na^+ , Cl^- , Ca^- , and SO_4^{2+}) and alkalinity and pH, and relatively high concentrations of DOC, SiO_2 and TDP. The intermediate lakes are well dispersed across the ordination space. For the 2009 dataset, the first two CCA axes explain 25.4% of the variation in community composition and environmental variables among lakes and capture patterns of variation similar to the CCA of the 2008 dataset. Axis 1 captures 17.7% of the variation. As in 2008, the rainfall-dominated lakes are positioned mainly in the lower left quadrant, associated with relatively high concentrations of ions (Mg^+ , Na^+ , Cl^- , Ca^- , SO_4^{++}) and DIC and relatively high pH, alkalinity and conductivity, and lower concentrations of DOC, TDP, TP and NH_3 . In 2009, most snowmelt-dominated lakes are positioned in the upper half of the plot, associated with relatively high concentrations of DOC, SiO_2 , TP, TDP and NH_3 , and relatively low concentrations of ions and DIC and low pH, alkalinity and conductivity. For both study years, positions of the sample scores and taxon scores are broadly consistent between plots based on CA (taxa only; Figure 2.4) and CCA (taxa and environmental variables; Figure 2.5), indicating that variation in community composition among study lakes is well captured by the supplied water chemistry variables.

2.4 Discussion

Concern about effects of climate warming on shallow northern lakes elicits interest to track changes in communities at the base of aquatic food webs, but methods to achieve this effectively across large, remote lake-rich landscapes remain underdeveloped (Vincent et al., 2011; Heino et al., 2020; Kahlert et al., 2020). Here, we explored the ability of periphytic diatom community composition accrued on artificial-substrate samplers in shallow thermokarst lakes of OCF to discern ecological responses to differences in hydrological conditions and water chemistry, as needed to inform on their potential use by agency-led long-term monitoring programs.

Lakes of OCF span a hydrological gradient of dominance by snowmelt to rainfall input, with corresponding differences in water chemistry and periphytic diatom community composition. In both study years, snowmelt-dominated lakes possess higher concentrations of nutrients and DOC and lower ionic content and pH, and corresponding higher relative abundance of several diatom taxa not

encountered in the rainfall-dominated lakes (*R. pusillum*, *E. subarcuoides*, *S. laevis*, *E. adnata*, *T. flocculosa* str. III, *T. fenestrata*) (Figure 2.2, 2.3). Collectively, these findings identify that relationships exist among variation of basin hydrology, water chemistry and composition of diatom communities that accrue on artificial-substrate samplers. However, a few taxa (notably, *A. minutissimum*, *C. lineata*, and *G. angustum*) were dominant and widespread across the entire hydrological spectrum of OCF lakes in both years, and several other taxa abundant in intermediate lakes were also common in either the rainfall- or snowmelt-dominated categories. Despite the widespread taxa, which result in overlap of sample scores in multivariate ordination plots among the hydrological categories (Figure 2.4, 2.5), ANOSIM tests detected significant difference in diatom community composition among the hydrological categories in both 2008 and 2009. Community composition differs significantly between rainfall-dominated and intermediate lakes in 2008. In 2009, the year of greater antecedent snowfall, diatom community composition of snowmelt-dominated differs from that of rainfall-dominated and intermediate lakes. Community composition does not differ between the other pairwise-comparisons among categories in either year, however, likely due to lack of unique taxa in the rainfall-dominated lakes (Figure 2.3). Thus, use of diatom analysis and artificial-substrate samplers appears to have moderate ability to track differences among lakes along the hydro-limnological gradients of lakes in OCF and inter-annual variability of snowfall. For example, reduction in snowmelt runoff may be expected to result in lower relative abundance of the above taxa indicative of the snowmelt-dominated lakes. However, ability of the periphytic diatoms to discriminate the three hydrological lake categories is less than that of the water chemistry measurements, which differed significantly between snowmelt- and rainfall-dominated categories in both study years. Given that diatoms accrue over the entire ice-free season, whereas July water chemistry samples reflect a shorter duration ‘snapshot’ of limnological conditions, seasonally shifting water balance and water chemistry of the intermediate lakes may account for the substantial overlap in community composition of intermediate lakes with lakes in the other two categories.

Variation of periphytic diatom community composition among lakes in OCF is most strongly associated with gradients of pH, alkalinity and conductivity, and concentrations of major ions and DOC, as identified from use of constrained ordination. Snowmelt-dominated lakes possess higher concentrations of DOC, lower concentrations of the major ions and DIC, and lower conductivity, pH and alkalinity than lakes dominated by rainfall input (Figure 2.2, 2.5). Such differences in water

chemistry between snowmelt- and rainfall-dominated lakes have been demonstrated by prior limnological studies of the OCF (Balasubramaniam et al. 2015, 2017), and were attributed to differences in catchment vegetation and shoreline processes (Turner et al., 2010, 2014; Balasubramaniam et al., 2015). The shorelines of snowmelt-dominated lakes typically support growth of trees and tall shrubs, which entrap wind-distributed snow and contribute substantial snowmelt during the spring and summer. In contrast, vegetation surrounding most rainfall-dominated lakes is dominated by dwarf shrub/herbaceous and sparse vegetation, which accumulate considerably smaller snowpack. Interaction between snowmelt and organic-rich terrestrial vegetation and soil likely provides substantial supply of nutrients and DOC to snowmelt-dominated lakes (Balasubramaniam et al., 2015). Dilute ionic content of snowmelt may account for the generally lower ionic content of snowmelt- versus rainfall-dominated lakes (Balasubramaniam et al., 2015). Greater evaporative water loss from larger lake surface area and influx of eroded shoreline soils from sparsely vegetated catchments have been suggested as processes that support higher ionic content, conductivity and pH in the rainfall- versus snowmelt-dominated lakes (Turner et al., 2014; Balasubramaniam et al., 2015). Diatom communities on the artificial-substrate samples reflect these differences in water chemistry among hydrological categories. For example, the taxa *R. pusillum*, *E. adnata*, *S. laevissima*, *S. pupula*, *T. flocculosa* str. III, *T. fenestrata*, *E. bilunaris* and *E. subarcutoides* occurred at moderate percent abundance in several snowmelt-dominated lakes but were absent from rainfall-dominated lakes and rare in most intermediate lakes. These taxa have been characterized as relatively abundant in lakes with moderate to high concentrations of DOC and major nutrients, and low ionic content (Round et al., 1990; Pienitz, 2001; Furey, 2010). No diatom taxa were unique to the rainfall-dominated lakes. Taxa abundant in the intermediate lakes are broadly distributed among lakes of the other categories, including *A. minutissimum*, *C. lineata* and *G. angustum* (Figure 2.3). Of these taxa, only *C. lineata* occurs at distinctively higher percent abundance in intermediate lakes than lakes in the other categories. *A. minutissimum* and *G. angustum* were also relatively abundant in surface sediments of OCF lakes (Balasubramaniam et al., 2017) and on artificial-substrate samplers deployed in several locations within nearby Mary Nitro Lake (MacDonald et al., 2012a), and our study suggests they have weak ability to track hydro-limnological variation among lakes. As suggested by Remmer et al. (2019), ecological phenomena such as dispersal ability, stabilizing niche differences and priority effects may account for

high abundance of these taxa on the artificial-substrate samplers, which weakens ability of periphytic diatom community composition to discriminate differences in basin hydrology and water chemistry.

Composition of diatom communities that accrued on the artificial-substrate samplers are broadly similar with diatom assemblages in surface sediments of OCF lakes collected in 2008 and reported in Balasubramaniam et al. (2017). Consistent with composition on the artificial-substrate samplers, *T. flocculosa* and several *Eunotia* species, including *E. bilunaris*, commonly occur at moderate to high percent abundance in surface sediments of snowmelt-dominated lakes but are rare to absent in the intermediate and rainfall-dominated lakes (Balasubramaniam et al., 2017). Also, *Gomphonella calcarea* achieved moderate to high percent abundance in surface sediments of many rainfall-dominated lakes but was rare to absent from the snowmelt-dominated lakes. Surficial sediments capture a longer and more variable time period of diatom accrual (among lakes) than the periphyton samplers, and they have potential to sample diatoms that grow in a broader range of habitats (e.g., planktonic and epipelagic zones). The correspondence of diatom community composition between these media suggests that artificial-substrate samplers accrue diatom communities that are reasonably reflective of the main habitats in the lakes. This is likely promoted by the shallow depth of lakes in OCF and cool summer temperatures and winds of the region, which prevent formation of abundant planktonic habitat (Turner et al., 2014; Balasubramaniam et al., 2015). Also, light penetration to the lake bottom supports macrophyte growth across substantial portions of lake bottoms (Balasubramaniam et al., 2015). These are factors that favor dominance of diatom communities by periphytic taxa in lakes of OCF, which are taxa well adapted to accrue on artificial-substrate samplers. Despite these many similarities, diatom assemblages in surficial sediments samples were better able to discriminate between rainfall- and snowmelt-dominated lake categories than diatoms accrued on artificial-substrate samplers in our study. Weaker ability of the artificial-substrate periphyton samplers to discriminate diatom community composition of snowmelt-dominated versus rainfall-dominated lakes is due, in part, to a paucity of taxa with consistent occurrence in lakes of only one hydrological category, and suggests that methods to detect hydro-limnological change should consider composition of entire communities (e.g., using ordination) and avoid reliance on a few indicator taxa. Weaker discrimination is also attributable to a few taxa that dominated communities on the artificial-substrate from most lakes across OCF (e.g., *A. minutissimum*, *C. lineata*, *G. angustum*). *A. minutissimum*, for example, is widely regarded as a ‘generalist’ taxon in temperate and northern lake and stream habitats, and has been identified as an

indicator of a broad class of shallow, circumneutral to alkaline, nutrient-rich lakes and ponds spanning the Arctic tundra to sub-Arctic and boreal forest zones of Canada (i.e., Biotype 6 of Kahlert et al., 2020). Thus, it is not surprising *A. minutissimum* is the most abundant taxon in periphyton biofilms in lakes of OCF. To counteract influence of abundant generalists, enumeration of more diatom valves per sample is recommended in future studies to quantify more reliably percent abundances of non-dominant taxa, which may convey additional hydro-limnological information.

To be useful for a long-term monitoring program, diatom community composition on artificial-substrate samplers must be responsive to temporal changes in hydro-limnological conditions caused by climatic variations and trends. The two-year duration of our study offered preliminary opportunity to assess if water chemistry and composition of the periphytic diatom communities of the lakes differed in response to inter-annual variation in snowmelt input. Air temperatures and rainfall during the ice-free seasons were similar between the study years and comparable to the climate normal, but cumulative winter snowfall before the 2008 ice-free season (35 mm) was 65% below the 1951–2000 mean (100 mm) and 53% above average before the 2009 ice-free season (153 mm). Despite the almost four-fold difference in snowfall, neither the water chemistry variables measured in July nor the composition of seasonally-accrued periphytic diatoms differed significantly between 2008 and 2009. This suggests that greater meteorological differences or longer duration of temporal trends are required to elicit a detectable change in mid-summer water chemistry and periphytic diatom community composition than occurred in the OCF lakes between 2008 and 2009. Or, it suggests that vegetation structure and other catchment features, which are less responsive to inter-annual climate variability, exert an over-riding influence on lake chemistry and periphytic diatom community composition. Longer time series of data spanning a broader range of climatic variation are needed to decipher these possibilities and further assess the utility of diatom analysis on artificial-substrate samplers as an informative approach for long-term monitoring of biological and environmental change. MacDonald et al. (2021) recently reported a trend of increasingly positive water balances during the past 13 years in a set of 14 lakes in OCF due to rise of rainfall and possibly permafrost thaw. All 14 lakes shifted into the rainfall-dominated category, despite placement in all three hydrological categories in 2008-2009. Analysis of shifts in periphytic diatom communities in these lakes during the past 13 years will provide opportunity to determine if community composition tracks the demonstrated changes in hydrology or remains unchanged due to over-riding influence of less temporally variable catchment features.

Given widespread concern about consequences of climate warming for shallow lakes, especially at high latitude areas of pronounced warming, analysis of diatom community composition on artificial-substrate periphyton samplers provides a promising, additional source of scientific data, when coupled with measurement of water isotope tracers, to track ecological shifts at the base of aquatic food-webs. Exploration of catchment characteristics, basin hydrology from measurement of water isotope tracers, water chemistry and periphytic diatom community composition across other lake-rich landscapes may demonstrate sufficiently strong relations to serve as a basis of long-term lake monitoring, and to guide interpretations of paleolimnological analysis of diatom assemblages in sediments cores where periphytic taxa dominate shallow lake communities (e.g., Wiklund et al., 2010). Due to dominance of periphytic diatom communities by a few taxa, enumerating more than 300 diatom valves per sample may improve estimation of percent abundances of the non-dominant taxa and provide stronger ability to discern limnological and ecological change in response to climatic and hydrological processes.

2.5 Conclusions

Multivariate analyses of periphytic diatom communities accrued on artificial-substrate samplers across broad hydro-limnological gradients of 33 (2008) and 48 (2009) lakes in OCF identified that snowmelt-dominated lakes, with abundant trees and shrubs within their catchments, possess higher concentrations of nutrient and DOC and lower ionic content and pH, and corresponding higher relative abundance of several diatom taxa not encountered in the rainfall-dominated lakes (e.g., *Rossithidium pusilla*, *Eunotia subarcutoides*, *Sellaphora laevissima*, *Tabellaria flocculosa* str. III, *T. fenestrata*). The findings identify relations exist among variation of catchment characteristics, basin hydrology, water chemistry and composition of diatom communities that accrue on artificial-substrate samplers, consistent with prior study of diatom assemblages in lake surficial sediment. However, dominance by a few taxa in lakes of all three hydrological categories (snowmelt-dominated, rainfall-dominated, intermediate) and a paucity of taxa with consistent, unique occurrence in rainfall-dominated and intermediate lakes weakened ability to discriminate periphytic diatom community composition of snowmelt-dominated versus rainfall-dominated lakes. Water chemistry and diatom community composition did not differ between the two study years, despite almost four-fold difference in winter snowfall. These results identify that composition of periphytic diatom communities on artificial-substrate samplers captures ecological differences across the gradients of hydro-limnological conditions, but we require longer time-series of data to determine

ability of this approach to track responses to temporal trends in climate-mediated hydro-limnological change. The approach used in this study is readily transferrable to other landscapes with abundant shallow lakes. We suggest enumeration of more diatom valves per sample could better capture signals of environmental change potentially conveyed by the non-dominant taxa.

2.6 Figures and Tables:

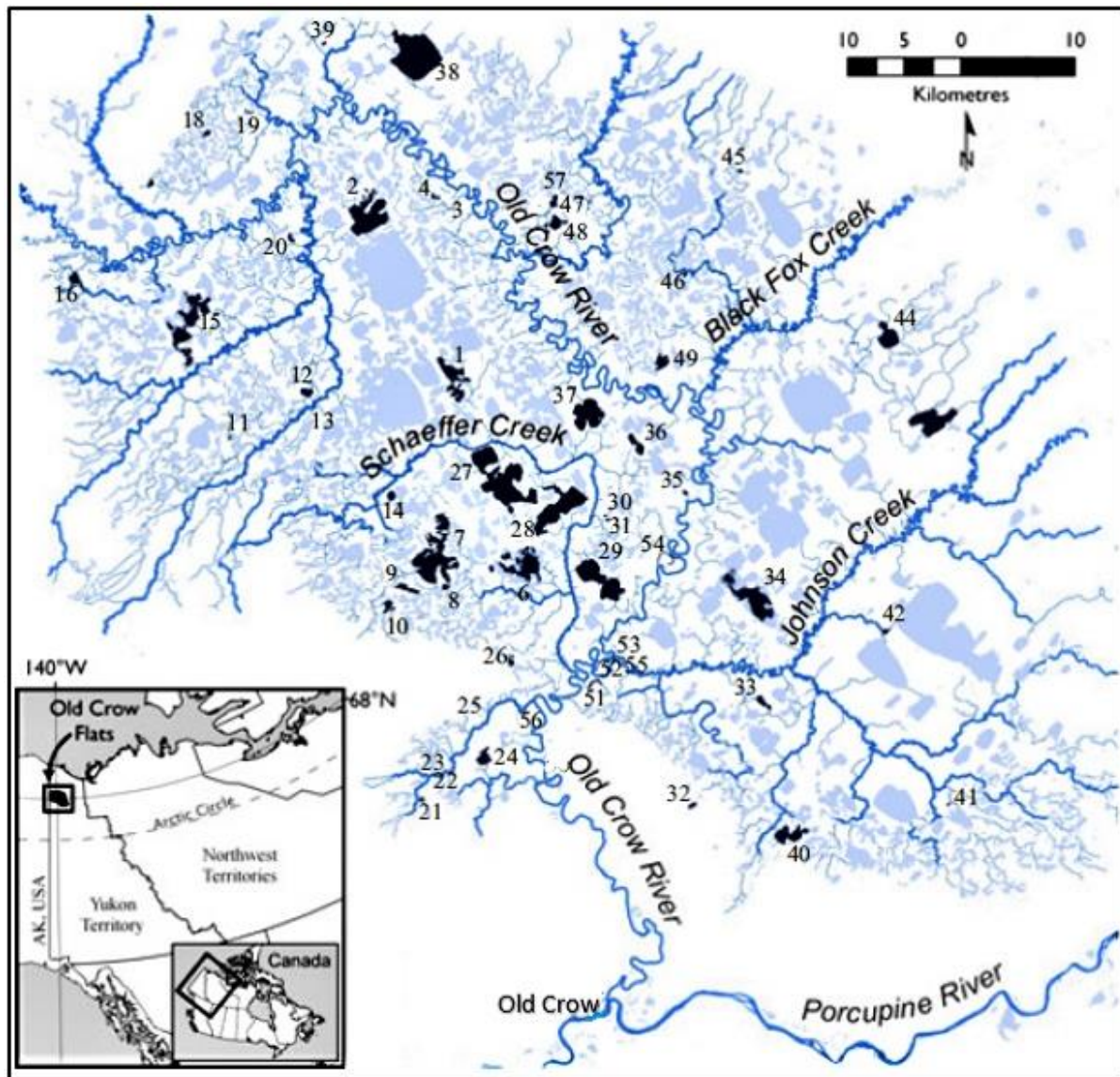


Figure 2.1: Map showing locations of Old Crow Flats (OCF), Yukon, and the study lakes sampled in 2008 and 2009.

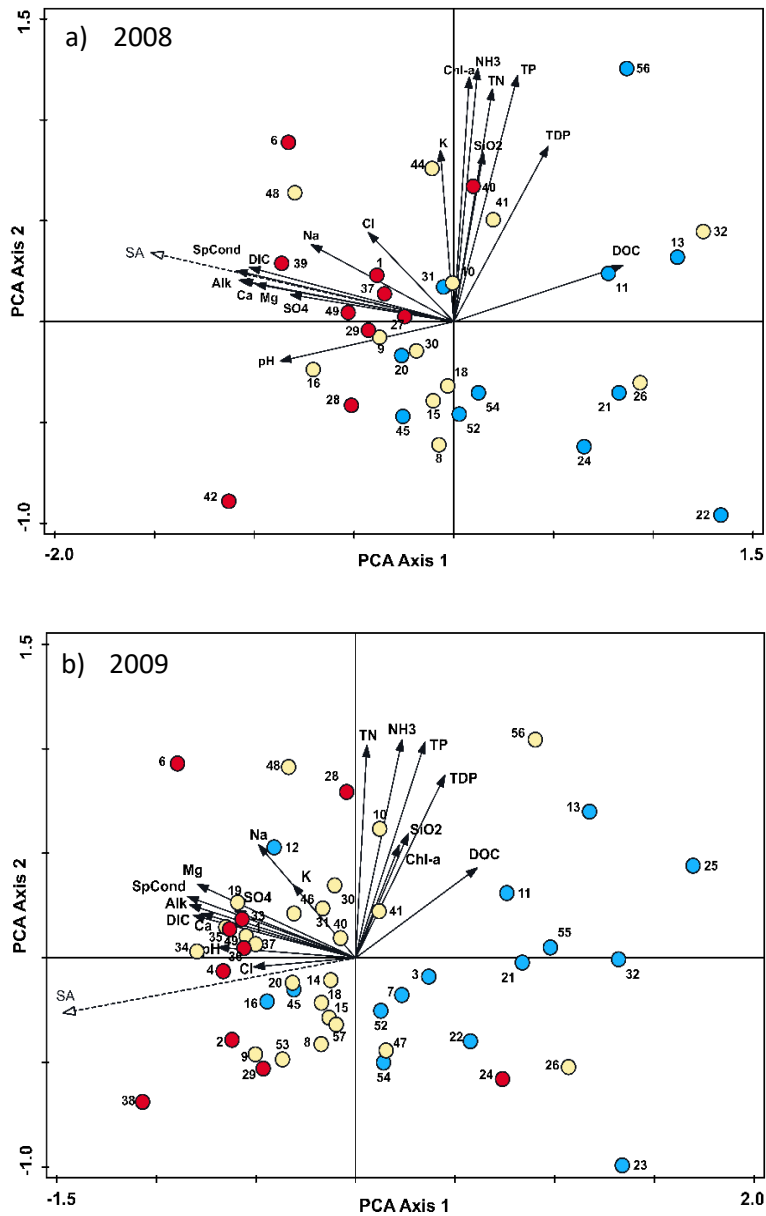
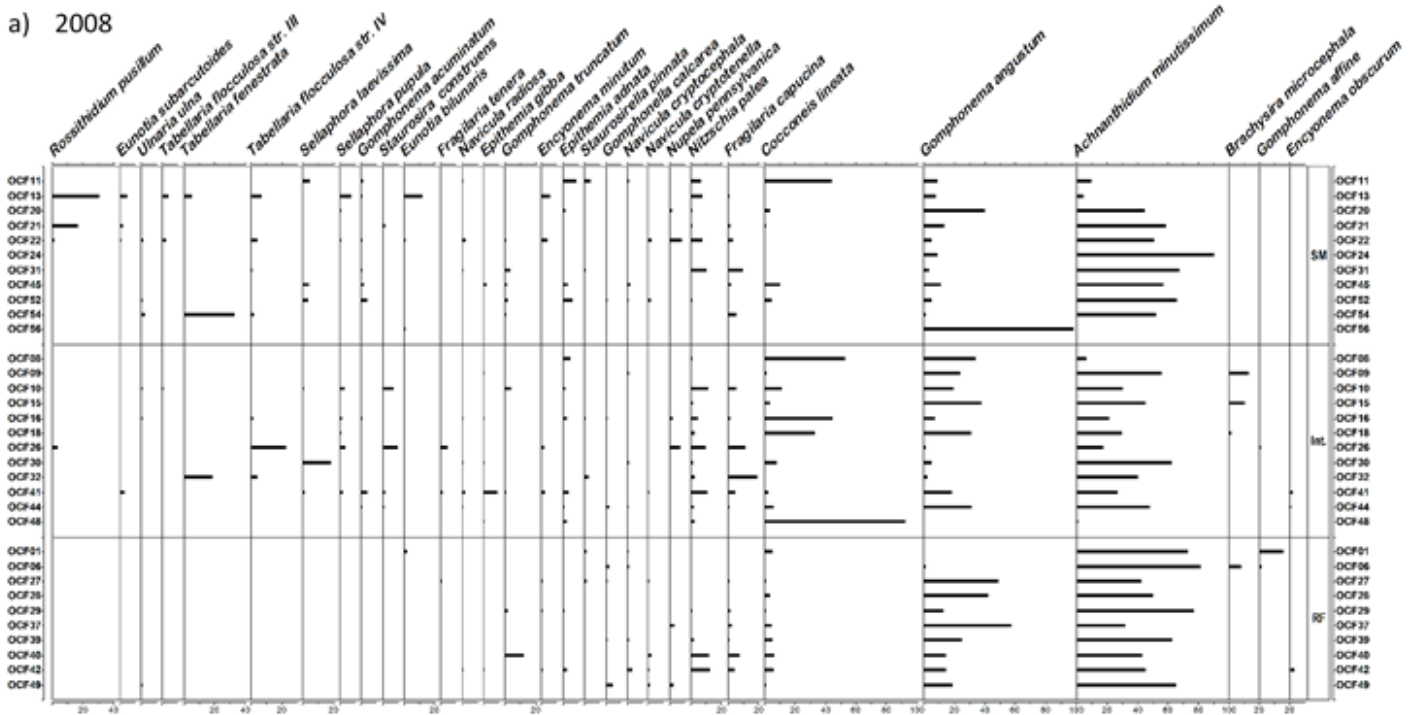


Figure 2.2: Scatterplots showing results of principal components analysis (PCA) of the water chemistry variables determined from samples obtained from the 33 and 48 lakes across Old Crow Flats in July 2008 (upper panel) and 2009 (lower panel), respectively. Water chemistry variables are shown as vectors and sample scores are presented as circles filled with blue for snowmelt-dominated lakes, red for rainfall-dominated lakes and yellow for lakes in the intermediate category. Numbers refer to the OCF lake designations shown in Figure 2.1.

a) 2008



b) 2009

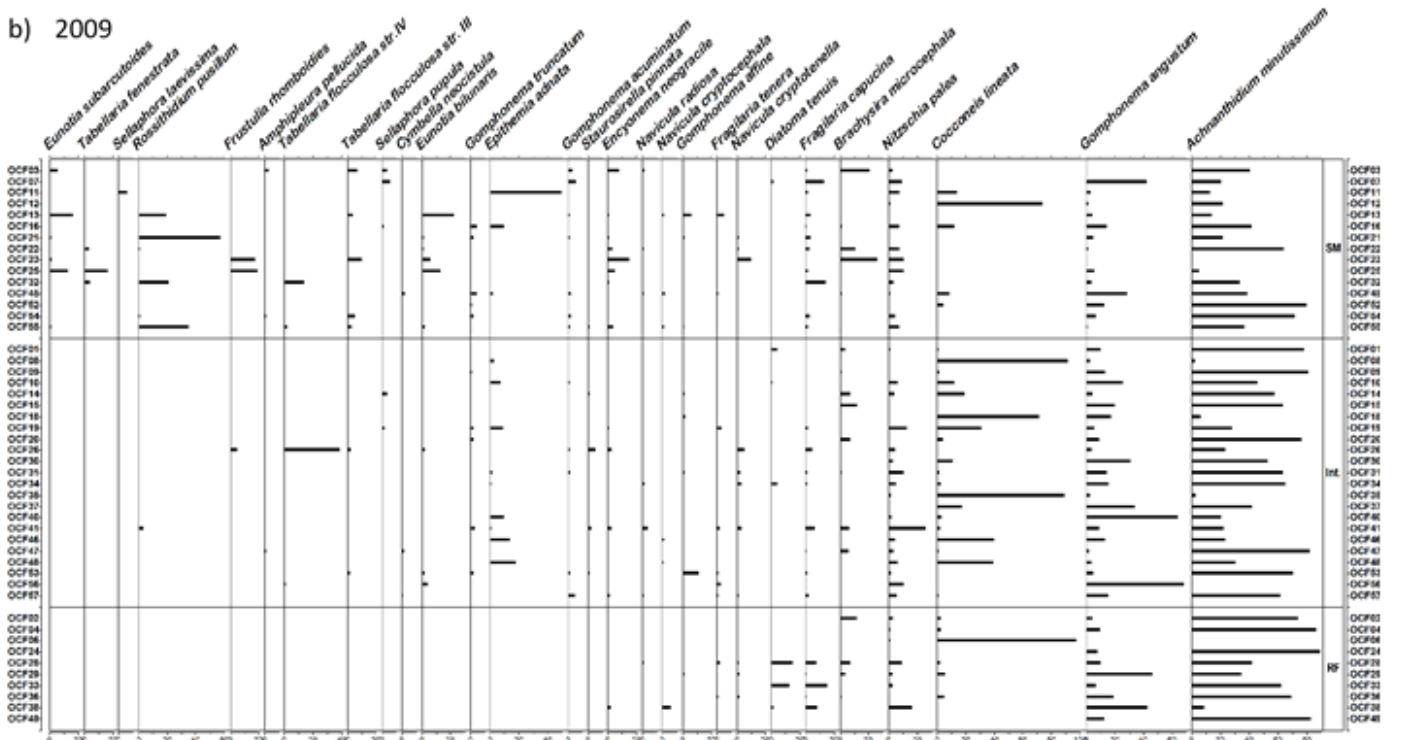
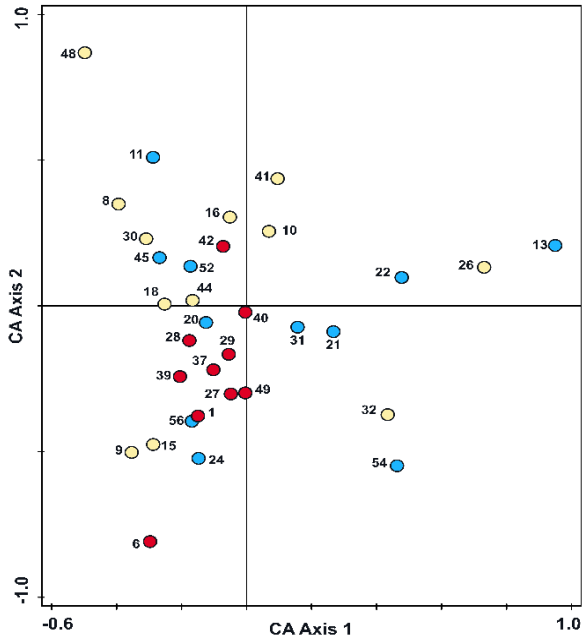
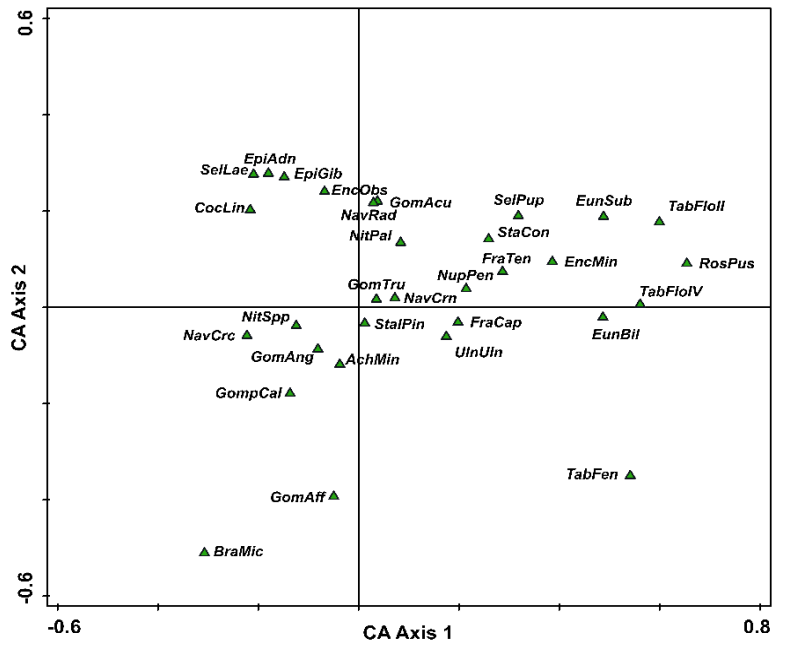


Figure 2.3: Horizontal bar graphs showing the percent abundances of the most common diatom taxa accrued on artificial substrate periphyton samplers retrieved from 33 lakes in 2008 (upper panel) and 48 lakes in 2009 (lower panel) across Old Crow Flats. Lakes are arranged along the vertical axis in both panels according to hydrological category, where SM = snowmelt-dominated lakes, Int.= intermediate lakes, and RF = rainfall-dominated lakes, and by their $\delta^{18}\text{O}_1$ values within each category.

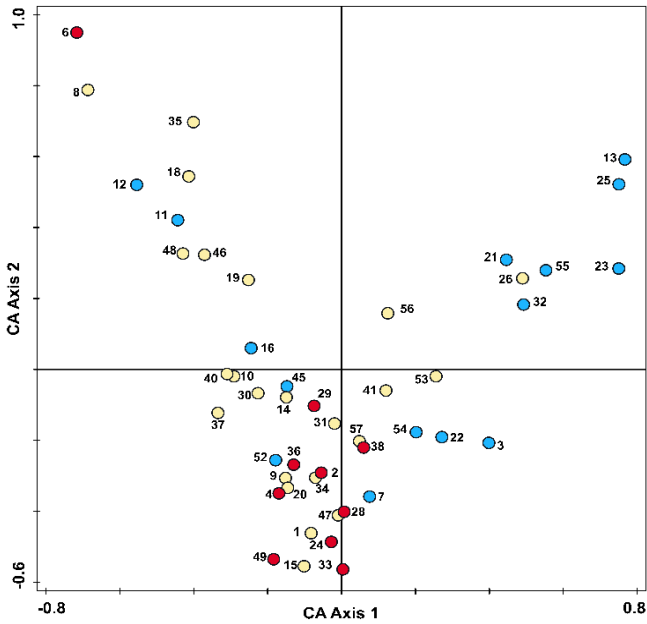
a) 2008 - sample scores



b) 2008 - taxon scores



c) 2009 - sample scores



d) 2009 - taxon scores

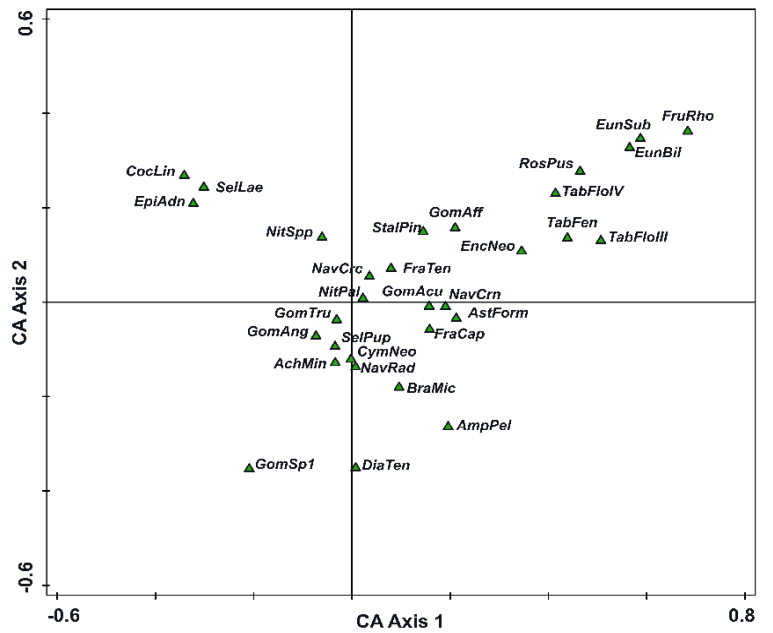


Figure 2.4: Scatterplots showing results of correspondence analysis (CA) on the relative abundances of diatom taxa accrued on artificial-substrate periphyton samplers retrieved from 33 lakes in 2008 (panels a and b) and 48 lakes in 2009 (panels c and d) across Old Crow Flats. Sample scores are presented in the left column (panels a and c) as circles filled with blue for snowmelt-dominated lakes, red for rainfall-dominated lakes and yellow for lakes in the intermediate category. Numbers refer to the OCF lake designations shown in Figure 2.1. Taxon scores are presented in the right column (panels b and d) and full names of the shortened diatom taxon codes are presented in Table 2.1.

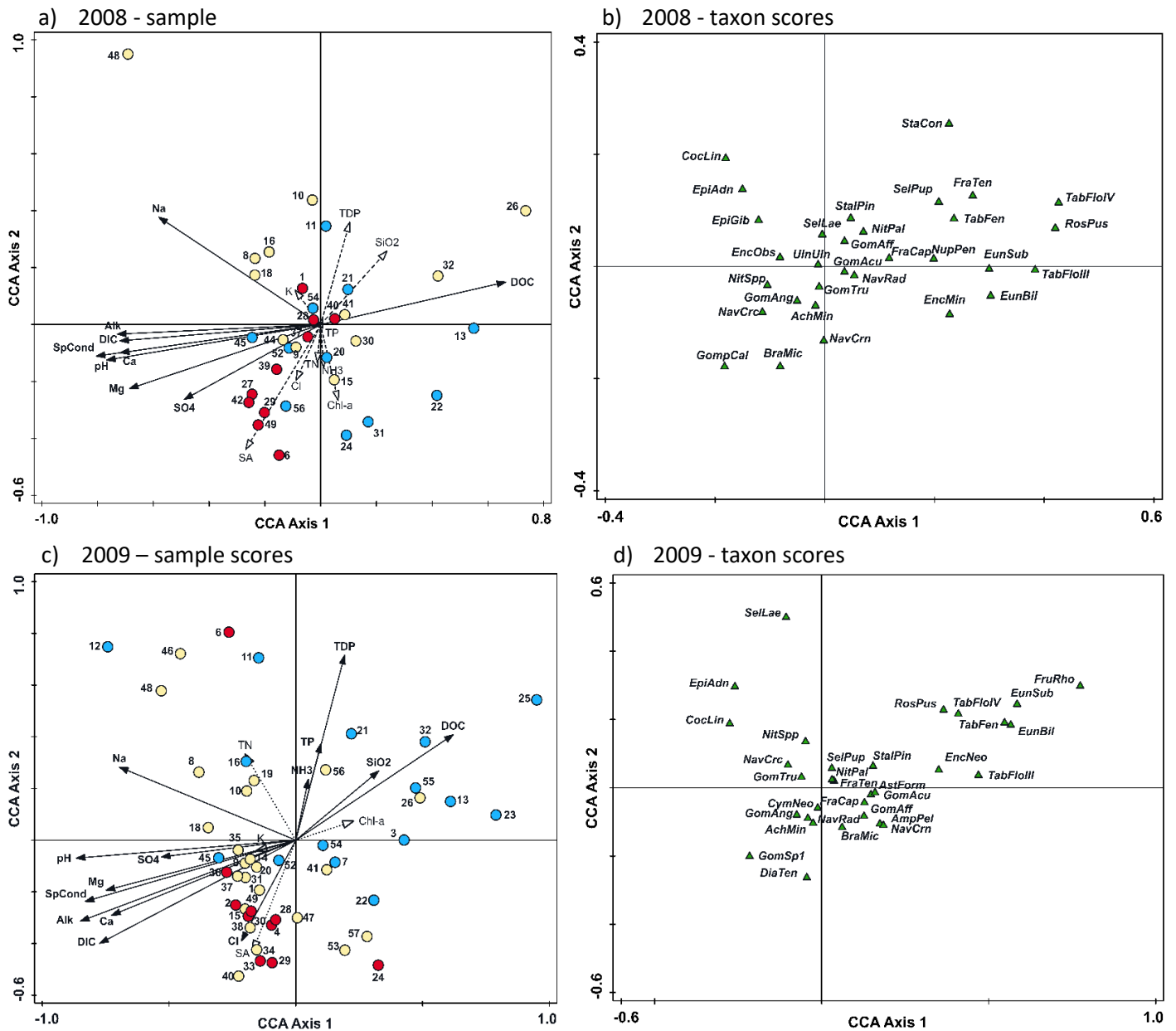


Figure 2.5: Scatterplots showing results of canonical correspondence analysis (CCA) of the water chemistry variables and diatom community composition accrued on artificial-substrate periphyton samplers retrieved from 33 lakes in 2008 (panels a and b) and 48 lakes in 2009 (panels c and d) across Old Crow Flats. Water chemistry variables are shown as vectors and sample scores are presented as circles in the left column (panels a and c). Circles filled with blue are snowmelt-dominated lakes, circles filled with red are rainfall-dominated lakes and circles filled with yellow are lakes in the intermediate category. Numbers refer to the OCF lake designations shown in Figure 2.1. Taxon scores are presented in the right column (panels b and d) and full names of the shortened diatom taxon codes are presented in Table 2.1

Table 2.1: List of diatom taxa found on artificial substrate sheets retrieved from OCF lakes sampled in 2008 and 2009, and the taxon codes used in ordination plots showing taxon scores. Note that taxon code *TabFloIII* appears as *TabFloII* in Figures 2.5 and 2.6 due to software restrictions.

Diatom taxon name	Authority	Taxon code
<i>Achnanthes imperfecta</i>	Schimanski	<i>AchImp</i>
<i>Achnantheidium minutissimum</i>	Kützing	<i>AchMin</i>
<i>Achnanthes pusilla</i>	(Grunow) De Toni	<i>AchPul</i>
<i>Amphipleura pellucida</i>	Kützing	<i>AmpPel</i>
<i>Asterionella formosa</i>	Hassall	<i>AstFor</i>
<i>Brachysira microcephala</i>	Grunow	<i>BraMic</i>
<i>Cocconies placentula</i> var. <i>lineata</i>	Ehrenberg	<i>CocPla</i>
<i>Cymbella cistula</i>	Ehrenberg	<i>CymCis</i>
<i>Cymbella gracilis</i>	Ehrenberg	<i>CymGra</i>
<i>Cymbella obscura</i>	Krasske	<i>CymbObs</i>
<i>Cymbella minuta</i>	Hilse and Rabenhorst	<i>CymMin</i>
<i>Diatoma tenuis</i>	Agardh	<i>DiaTen</i>
<i>Discostella stelligera</i>	(Cleve & Grunow)	<i>DisSte</i>
<i>Epithemia adnata</i>	Kützing	<i>EpiAdn</i>
<i>Eunotia bilunaris</i>	Ehrenberg	<i>EunBil</i>
<i>Eunotia subarcutoides</i>	Nörpel & Lange-Bertalot	<i>EunSub</i>
<i>Fragilaria capucina</i>	Desmazières	<i>FraCap</i>
<i>Fragilaria pinnata</i>	Ehrenberg	<i>FraPin</i>
<i>Fragilaria tenra</i>	Lange-Bertalot	<i>FraTen</i>
<i>Fragilaria ulna</i>	Lange-Bertalot	<i>FraUln</i>
<i>Frustulia rhomboides</i>	(Ehrenberg) De Toni	<i>FruRho</i>
<i>Gomphonema acuminatum</i>	Ehrenberg	<i>GomAcu</i>
<i>Gomphonema affine</i>	Kützing	<i>GomAff</i>
<i>Gomphonema angustum</i>	C.Agardh	<i>GomAng</i>
<i>Gomphonema olivaceum</i> var. <i>calcareum</i>	Van Heurck	<i>GompOli</i>
<i>Gomphonema species 1</i>		<i>GomSp1</i>
<i>Gomphonema truncatum</i>	Ehrenberg	<i>GomTru</i>
<i>Navicula cryptocephala</i>	Kützing	<i>NavCrc</i>
<i>Navicula cryptotenella</i>	Lange-Bertalot	<i>NavCrn</i>
<i>Navicula laevissima</i>	Kützing	<i>NavLav</i>
<i>Navicula pupula</i>	Kützing	<i>NavPup</i>
<i>Navicula radiosa</i>	Kützing	<i>NavRad</i>
<i>Nitzschia palea</i>	Kützing	<i>NitPal</i>
<i>Nitzschia species</i>		<i>NitSpp</i>
<i>Rhopalodia gibba</i>	O. Müller	<i>RhoGib</i>
<i>Stauroneis construens</i>	Ehrenberg	<i>StaCon</i>
<i>Tabellaria fenestrata</i>	Kützing	<i>TabFen</i>
<i>Tabellaria flocculosa</i> str. III	Kützing	<i>TabFloIII</i>
<i>Tabellaria flocculosa</i> str. IV	Kützing	<i>TabFloIV</i>

Chapter 3

Ecosystem responses of shallow thermokarst lakes to climate-driven hydrological change: Insights from long-term monitoring of periphytic diatom community composition at Old Crow Flats (Yukon, Canada)

Following feedback from the Examination Committee, I intend to submit Chapter 3 for publication to a Special Collection of the journal Science Progress on ‘Progress in Assessing Vulnerability of Freshwater Ecosystems’ as: Mohammed, W.J, L.A. MacDonald, K. Thomas, I. McDonald, K. Turner, B.B. Wolfe, R.I. Hall. Ecosystem responses of shallow thermokarst lakes to climate-driven hydrological change: Insights from long-term monitoring of periphytic diatom community composition at Old Crow Flats (Yukon, Canada).

3.1 Introduction

Arctic and subarctic permafrost landscapes support an abundance of shallow lakes and ponds which provide important wildlife habitat and sustain the cultural heritage and traditional land use of Indigenous communities (Wrona et al., 2006; White et al., 2007; Vincent et al., 2011; Heino et al., 2020). Due to their small water volume relative to surface area, hydrological and limnological conditions of northern shallow lakes and ponds respond rapidly to climate warming, including rising air temperature and longer thaw-season duration which increases evaporative water losses, shifts the amount and form of runoff from precipitation (snow, rain), and changes the amount of input from permafrost thaw (Schindler & Smol, 2006; Prowse et al., 2006; Rowland et al., 2010; Bouchard et al., 2013; IPCC, 2014; Woo & Young, 2014; Lantz & Turner, 2015; Roberts et al., 2017; Jones et al., 2020). Such hydrological changes can alter biogeochemical cycles, water chemistry, habitat availability, and the structure and function of biological communities of shallow northern lakes (Smol & Douglas, 2007; Medeiros & Quinlan, 2011; Turner et al., 2014; Rühland et al., 2015; Balasubramaniam et al., 2015, 2017; Lamhonwah et al., 2017; Mohammed et al., 2021).

Benthic algae play important roles in nutrient cycles, energy flow, and food web structure of shallow lakes, while their abundance and productivity are strongly influenced by habitat availability (Vadeboncoeur & Steinman, 2002). Diatoms (Class Bacillariophyceae), a group of eukaryotic algae that possess a siliceous cell wall or frustule, often dominate the phytoplankton of freshwater lakes and play key roles in the function of aquatic ecosystems (Smol, 2008). Diatom taxa have well defined ecological optima and rapid growth rates, and their communities typically have high taxonomic diversity which enables them to respond to a wide range of environmental changes including variations in water chemistry and habitat availability caused by alterations in basin hydrology and catchment-mediated processes (Julius & Theriot, 2010; Smol & Stoermer, 2010; Cantonati & Lowe, 2014; Evtimova & Donohue, 2016; Kahlert et al., 2020). These attributes have enabled broad use of diatoms in biomonitoring programs to track environmental changes in lakes in response to nutrient enrichment, acidification and climatic variations (Stevenson et al., 2010; Smol & Stoermer, 2010; Kelly et al., 2019; Kennedy & Buckley, 2021). Moreover, composition of diatom communities captures an integrated signal of environmental changes over time and space within a lake, which enables the ability to infer changes in water chemistry of shallow northern lakes in response to complex interactions among

hydrological processes, catchment features, and in-lake processes (Wiklund et al., 2010; Balasubramaniam et al., 2017; Mohammed et al., 2021).

Old Crow Flats (OCF) is a 5,600 km² thermokarst landscape in northern Yukon recognized as a Ramsar Wetland of International Importance for ecosystem services provided to wildlife and the Vuntut Gwitchin First Nation (VGFN) (Figure 3.1). Natural resources of OCF are protected within Vuntut National Park and the OCF Special Management Area and are cooperatively managed by the VGFN, Parks Canada Agency, and the North Yukon Renewable Resource Council. Concern has been expressed by the local community and natural resource stewardship agencies over climate-driven changes in the landscape, which range from lake expansion to lake drainage and desiccation, accelerated terrestriation of wetlands and proliferation of shrubs at desiccated aquatic basins, and changes in river water levels (ABEK Co-op, 2007; Turner et al., 2010; Lantz & Turner, 2015). To help address concerns regarding the effects of climate change on the landscape, a multidisciplinary International Polar Year (IPY) project was initiated in OCF during 2007 entitled ‘Yeendoo Nanh Nakhweenjit K’atr’ahanatyaa (Environmental change and traditional use of the Old Crow Flats in northern Canada)’ (Wolfe et al., 2011). One of the goals of this program was to develop and establish long-term monitoring programs for the community that would be able to track trends and identify drivers of environmental changes in the landscape.

Since 2007, partnerships among Parks Canada, VGFN, and university researchers have been advancing methods for long-term monitoring of the shallow, mainly thermokarst lakes in OCF to track hydrological and limnological changes (Turner et al., 2010, 2014; MacDonald et al., 2012a, 2017, 2021; Tondu et al., 2013; Balasubramaniam et al., 2015, 2017; Mohammed et al., 2021). Recently, increases in air temperature, thaw season duration and input of rainfall and, possibly, permafrost thaw to lakes have been identified based on water isotope monitoring of 14 lakes in OCF during 2007-2019, a legacy of the IPY program (MacDonald et al., 2021). Increasing rainfall and rising water levels threaten to increase the frequency of catastrophic lake drainage events via outlet erosion, with negative consequences for aquatic habitat (Turner et al., 2014; MacDonald et al., 2021).

One component of the IPY project included assessment of relations among input water sources, water chemistry and diatom community composition that accrue on artificial substrate samplers and in surficial sediments of lakes in OCF. This was based on systematic sampling of a set of 57 lakes during

2007-2009 that span the hydroecological gradients of OCF. Results demonstrated that lakes with water balance dominated by rainfall input possess higher lake-water pH, alkalinity, conductivity, and concentrations of major ions and dissolved inorganic carbon (DIC), and lower concentrations of major nutrients and dissolved organic carbon (DOC) compared to lakes dominated by snowmelt input (Balasubramaniam et al., 2015, 2017; Mohammed et al., 2021). The differences in water chemistry between rainfall- and snowmelt-dominated lakes were ascribed to differences in catchment vegetation and shoreline processes. Catchments of the rainfall-dominated lakes are dominated by dwarf shrubs and herbaceous or sparse vegetation (Turner et al., 2010, 2014; Balasubramaniam et al., 2015). Conversely, the shorelines of snowmelt-dominated lakes generally support growth of trees and tall shrubs, which entrap wind-distributed snow and provide considerable snowmelt runoff during the ice-free season. The organic-rich soil and greater biomass of vegetation in the catchment interact with snowmelt runoff, which elevates concentrations of nutrients and DOC in snowmelt-dominated lakes (Balasubramaniam et al., 2015). The lower ionic content of snowmelt- versus rainfall-dominated lakes may be attributed to the low ionic content of snowmelt (Balasubramaniam et al., 2015). In contrast, higher ionic content, conductivity, and pH in rainfall-dominated lakes may result from greater evaporative water loss from larger lake surface areas and release of ions via erosion of sparsely vegetated shoreline soils (Turner et al., 2014; Balasubramaniam et al., 2015). As consequences of the hydrological and limnological differences, periphytic diatom communities accrued on artificial-substrate samplers and sediments were found to have higher relative abundance of the diatom taxa *Achnantheidium minutissimum*, and *Gomphonema angustum* in lakes dominated by rainfall inputs, whereas lakes dominated by snowmelt input have higher relative abundance of *Rossithidium pusillum*, *Sellaphora pupula*, *Eunotia bilunaris*, and *Tabellaria flocculosa* (Balasubramaniam et al., 2017; Mohammed et al., 2021). The studies identified a third group of lakes with similar amounts of input from rainfall and snowmelt or that were snowmelt-dominated in spring and transitioned to rainfall-dominated during the thaw season (Balasubramaniam et al., 2015). These ‘intermediate’ lakes possess values of water chemistry variables, catchment features, and diatom community composition that overlap extensively with those of the rainfall- and snowmelt-dominated lakes (Balasubramaniam et al., 2015, 2017; Mohammed et al., 2021). Integration of available water isotope data with long-term monitoring of periphytic diatom community composition and inferred lake water chemistry may

provide valuable information on aquatic ecosystem responses to the recently shifting hydrological conditions reported by MacDonald et al. (2021) and their vulnerability to climate change.

Knowledge of relations among differences in input water sources, water chemistry variables, and composition of periphytic diatom communities accrued on artificial-substrate samplers gained from the 57-lake spatial dataset can be used as a ‘template’ to track physico-chemical and biological responses from analysis of periphytic diatom community composition at the 14 long-term monitoring (LTM) lakes in OCF (Tondu et al., 2013; MacDonald et al., 2021). Thus, this study aims to determine responses of diatom community composition in biofilms accrued on artificial substrate samplers deployed in the 14 LTM lakes in OCF during thaw seasons of 12 years spanning a 13-year period (2008-2019; data in 2015 were not available) associated with the documented rise in rainfall runoff and increasingly positive lake water balances (MacDonald et al., 2021). The findings are intended to improve knowledge of ecosystem responses of shallow thermokarst lakes to climate-driven hydrological changes.

3.2 Methods

3.2.1 Study area

Old Crow Flats, located ~55 km north of Old Crow village, is a dynamic wetland landscape that includes ~8700 shallow (typically 0.5–6 m deep) and mainly thermokarst lakes amongst an assortment of terrestrial and riparian ecosystems (Figure 3.1; Labrecque et al., 2009). The lakes are perched above the Old Crow River, thus, the landscape exports waters from precipitation, runoff, and lake drainage. Fine-grained glaciolacustrine sediments and ~60 meters of continuous permafrost underlie the low-relief landscape, which restricts influence of sub-permafrost inflow and outflow on lake water balances (Russell et al., 1978; Smith & Burgess, 2002; Zazula et al., 2004; Roy-Léveillé & Burn, 2010).

Climate at Old Crow is continental, with cold winters (mean January air temperature = -31 °C) and cool summers (mean July air temperature = 15 °C). Mean annual precipitation is 257 mm, and the majority (157 mm) falls as rain during the thaw season, as reported by Environment and Climate Change Canada’s meteorological station at Old Crow airport during 1981-2006. The 2007-2019 period of long-term lake monitoring was characterized by longer thaw-season duration than the 1981-2006 average (147 vs 141 days) and a rising trend in winter air temperature since 2013 (MacDonald et al., 2021). For years of available data, average total thaw season precipitation (rainfall) during 2007-2019

(187 mm) was greater than the 1981-2006 mean (146 mm) recorded at the Old Crow airport, and total thaw season precipitation recorded within OCF by VNP during 2007-2016 was one standard deviation above the 1981-2006 mean. Average winter snow water equivalent during 2007-2019 was close to the 1981-2006 mean (120.1 mm and 103.8 mm, respectively). The years 2009 and 2011 stand out as an anomaly when winter precipitation was well above average (153 mm and 360 mm, respectively).

For this study, the 14 LTM lakes were selected from a spatial set of 57 lakes across OCF that were sampled three times per thaw season (early June, late July, early September) for water isotope composition during 2007-2009 and for composition of periphytic diatoms accrued on artificial substrate samplers in 2008 and 2009 (Figure 3.1). As described in Tondu et al. (2013), the 14 LTM lakes are well distributed across OCF and, at the time of selection, captured a representative range of hydrological conditions and catchment characteristics based on observations and data obtained during 2007-2009. The LTM lakes are typically shallow (< 2.6 m), except for OCF 55 which exceeds 5 m, and they span a range of surface area (0.02 to 12.67 km²) and catchment area (0.28 to 395.19 km²; Table 3.1). The catchments of the LTM lakes regularly include small portions of barren ground consisting of exposed rock, sand, and fire scar, which range from 1-8% of the catchment area. An exception is OCF 6 (Zelma Lake) where barren areas cover almost half (43%) of the catchment area following a sudden catastrophic lake drainage event that occurred in June 2007 (Tondu et al., 2013). Based on paleolimnological evidence and aerial images, OCF 48 experienced a drainage event in ~1989 and has since refilled (MacDonald et al., 2012b; Bouchard et al., 2017). Additionally, paleolimnological evidence for OCF 46 suggests increased thermokarst activity began in the 1970s and was followed by a possible drainage event (Bouchard et al., 2017). OCF 11 also has notably unique catchment characteristics with dense willow shrub surrounding the lake that suggests previous higher water-levels, but remote sensing images suggest surface water levels have remained relatively stable since 1951 (Lantz & Turner, 2015).

3.2.2 Sample collection and laboratory analyses

During 2007-2009, the LTM lakes were visited 3 times per year (early June, late July, late August/early September) as part of the 57-lake spatial data set. Since 2010, they have been visited twice per year (early June, early September) within the long-term monitoring program. Here we use water isotope data from late July 2008 and 2009 to classify lakes into hydrological categories following

methods presented in Mohammed et al. (2021) and we utilize water isotope data from consistent sample collections in early June and late August/early September during 2007-2019 (MacDonald et al., 2021). Water chemistry data utilized in this study were collected during visits in late July of 2008 and 2009, as reported in Balasubramaniam et al., 2015, 2017; Mohammed et al., 2021). Water chemistry measurements have been discontinued since then.

Use of artificial substrate periphyton samplers began in 2008, and they were deployed in early June shortly after ice-off and retrieved in late August/early September shortly before ice-on. In 2015, inclement weather prevented retrieval of periphyton samplers; thus, diatom data are missing for that year. Occasionally, periphyton samplers were not retrieved from some lakes in some years (see Table 3.1). Each artificial substrate sampler consisted of two groups of five polyethylene sheets suspended 25 cm below a wooden float at the lake's surface and anchored to the lake bottom, as described in Wiklund et al. (2010) and MacDonald et al. (2012a). Upon retrieval from each lake, the individual polypropylene sheets were placed in individual sample containers and kept in the dark. The retrieved samples were preserved frozen until analysis, and one sheet was randomly chosen from each sampler and analyzed for diatom community composition (as taxon percent abundances) that accrued during the thaw season, following methods described in Mohammed et al. (2021). For each sample, the polyethylene sheet was placed in a beaker and submerged in 10% HCl to remove carbonate. Then, samples were reacted with 30% H₂O₂ to remove organic matter. Before changing fluids, samples were left for at least 24 h to allow diatoms to settle to the bottom. After that, the supernatant was carefully withdrawn, and the residual diatom slurry was rinsed repeatedly with deionized water to remove acid residues until the pH of the deionized water was reached. The resulting cleaned diatoms in water were then deposited on circular coverslips and allowed to dry slowly over a 24-hr period. Naphrax™ was used to mount the coverslips onto microscope slides. A Zeiss Axioskop II Plus compound light microscope and 1,000X magnification under oil immersion was used to enumerate at least 300 diatom valves per sample and classify them to the lowest attainable taxonomic level (typically species or lower) using the references by Krammer & Lange-Bertalot (1986–1991) and Lavoie et al. (2008).

3.2.3 Numerical analyses

Multivariate ordination of the spatial dataset of 57 OCF lakes sampled during 2008 and 2009 for analysis of periphytic diatom community composition was used to inform interpretations of temporal

changes in diatom community composition and infer shifts in water chemistry at the 14 LTM lakes. Samplers were retrieved from 33 and 48 of the lakes in 2008 and 2009, respectively. These data were analyzed and reported for each year individually by Mohamed et al. (2021) to explore inter-annual differences. Here, we combined all the data from 2008 and 2009 in a single ordination to inform the interpretations of limnological change associated with shifts in community composition at the 14 LTM lakes during 2008-2019. For this analysis, the 38 diatom taxa that were identified in samples from at least 2 lakes and attained $\geq 2\%$ relative abundance in at least 1 lake were included in the ordinations (Table 3.2). Constrained ordination of the spatial data set of water isotope composition, water chemistry variables and periphytic diatom community composition obtained in 2008 and 2009 served as a 'template' for inferring temporal shifts in water chemistry from observed changes in diatom community composition at the 14 LTM lakes. Canonical correspondence analysis (CCA) was used because the gradient length of the 2008-2009 spatial diatom dataset was 2.9 standard deviation units based on analysis by DCA, which suggested a unimodal-based ordination method was more suitable than a linear-based method (ter Braak & Šmilauer, 2002). The combined 2008-2009 spatial dataset of the sampled lakes was entered as active samples in the CCA, whereas diatom percent abundance data obtained from 14 LTM lakes during 2008-2019 were entered as passive samples (i.e., they did not influence the ordination axes or the sample and taxon scores of the spatial dataset). This allowed interpretation of change over time in diatom community composition at the LTM lakes and inferred water chemistry in the context of the spatial variation of hydrolimnological conditions that existed across lakes of OCF in 2008 and 2009. Water chemistry variables that individually explained a significant amount of variation in diatom community composition among lakes (at $\alpha = 0.05$, based on 499 random Monte Carlo permutations) were incorporated as explanatory variables in the CCA. The variables lake surface area, oxygen isotope composition of input water ($\delta^{18}\text{O}_\text{I}$) (Turner et al., 2014), isotope-inferred evaporation-to-inflow (E/I) ratio (Turner et al., 2014) and concentrations of TN, NH_3 , K, and Chl-*a* were included as supplementary variables to assess their relationships with the active water chemistry variables without influencing the position of taxon and sample scores. Ellipses were added to the CCA plots to identify portions of the ordination space occupied by sample scores of the rainfall-dominated, intermediate and snowmelt-dominated lake categories and to identify temporal patterns of variation in diatom community composition at each of the 14 LTM lakes over the period of record (2008-2019). All ordinations were performed using the software CANOCO version 5 and the

ellipses were generated using the 2D-Normal based ellipses option to span 66% of the distribution of samples within each category (ter Braak & Šmilauer, 2012).

3.3 Results

3.3.1 Spatial analysis of the combined 2008-2009 OCF lake data set: a template for assessing temporal changes in the long-term monitoring lakes

The first two CCA axes of the combined 2008-2009 spatial dataset explained 20.6% of the variation in periphytic diatom community composition and water chemistry variables (Axis 1 = 15.0%, Axis 2 = 5.6%; Figure 3.2). Sample scores of the snowmelt-dominated lakes are mostly situated to the right along CCA axis 1, whereas sample scores of the rainfall-dominated lakes are positioned to the left along axis 1 and mainly within the bottom left quadrant. These differences are illustrated by small overlap of the ellipses for sample scores from these lake categories. Sample scores of the intermediate lakes, however, overlap extensively with those of the snowmelt- and rainfall-dominated lakes and are well scattered throughout the ordination space. Based on the environmental vectors, sample scores for the snowmelt-dominated lakes are associated with relatively high concentrations of TP, TDP, DOC and SiO₂, whereas rainfall-dominated lakes are associated with relatively high pH, alkalinity and higher concentrations of major ions (Mg⁺, Na⁺, Cl⁻, Ca⁻) and DIC.

Composition of periphytic diatom communities varied systematically among the three hydrological categories in the 2008-2009 spatial dataset. Taxa including *R. pusillum*, *S. pupula*, *E. bilunaris*, and *T. flocculosa* are relatively more abundant in several snowmelt-dominated lakes, as indicated by the position of their sample scores to the right along CCA axis 1 (Figure 3.2), while they were mostly absent from the rainfall-dominated lakes (Appendix D Figure 1.a). Other species such as *A. minutissimum*, *G. angustum*, *G. capitatum*, *Diatoma tenuis*, and *Encyonema obscurum* have higher relative abundance in the rainfall-dominated lakes than in the snowmelt-dominated lakes. Composition of periphytic diatom communities in the intermediate lakes overlapped with that of the other two categories, however *Cocconeis lineata* was relatively more abundant in the intermediate category (Appendix D Figure 1.b). These findings are consistent with those reported in Mohammed et al. (2021) based on analysis of the data for 2008 and 2009 individually.

3.3.2 Temporal changes at the long-term monitoring lakes

The CCA ordination of the 2008-2009 spatial dataset was used to track temporal changes in periphytic diatom communities and infer shifts in water chemistry at the 14 LTM lakes from 2008 to 2019 (Figure 3.3). At the beginning of the long-term monitoring period, five of the LTM lakes were classified as rainfall-dominated (OCF 6, 29, 37, 38, 49), three as snowmelt-dominated (OCF 11, 55, 58), and six as intermediate lakes (OCF 19, 26, 34, 35, 46, 48), based on the estimated isotope composition of input waters (δ_I) obtained in July 2008 and 2009 (Turner et al. 2014) and following lake classification methods outlined in Mohammed et al. (2021). Thus, if shifts in composition of periphytic diatom communities track limnological changes caused by the increase in rainfall input to lake water balances documented by MacDonald et al. (2021), sample scores of lakes that were in the intermediate and snowmelt-dominated categories at the start of the monitoring period would be expected to shift leftward and downward towards the bottom left quadrant and within the ellipse for the rainfall-dominated lakes in the CCA plots shown in Figures 3.2 and 3.3, associated with decline in relative abundance of *R. pusillum*, *S. pupula*, *E. bilunaris* and *T. flocculosa* and rise in relative abundance of *A. minutissimum*, *G. angustum*, *D. tenuis*, and *E. obscurum*. Such shifts also infer a decline in concentrations of TP, TDP, DOC and SiO₂ and increase in pH, alkalinity and concentrations of DIC and major ions.

Sample scores for four of the five LTM lakes that were classified as rainfall-dominated in 2008-2009 (OCF 29, 37, 38, 49) spanned a narrow range located within or adjacent to the ellipse of the rainfall-dominated lakes in the CCA of the 2008-2009 spatial dataset, indicating that periphytic diatom community composition and inferred water chemistry remained relatively consistent over the course of the monitoring period (Figure 3.3a, b). *A. minutissimum* and *G. angustum* dominated the diatom communities in these four lakes for nearly the entire monitoring period, with their combined relative abundances occasionally exceeding 80% (Appendix D Figure 1.a). Diatom community composition in these lakes infer consistent and relatively high lake-water pH, alkalinity and concentrations of DIC and major ions (Figure 3.3a, b). For these four lakes, the sample from 2011 at OCF 29 is the only exception to this pattern when the sample score shifted abruptly to the upper left quadrant of the CCA plot caused by an increase in the relative abundance of *C. lineata* from <5% in all other years to ~95% in 2011. OCF 6, the fifth lake that began in the rainfall-dominated category, displayed a markedly different

trajectory of change in diatom community composition during the monitoring period than the other four rainfall-dominated lakes (Figure 3.3b). Its sample score in 2008 was positioned in the lower left quadrant of the 2008-2009 CCA plot close to the other lakes in the rainfall-dominated category and associated with high relative abundance of *A. minutissimum*. In 2009, however, assemblage composition became dominated by *C. lineata* which resulted in a marked shift in sample scores to the upper left quadrant. After 2009, relative abundance of *C. lineata* varied 20-91% among years as illustrated by shifts in sample scores along axis 2. Declining relative abundance of *C. lineata* and increase of *A. minutissimum* and *G. angustum* during the past few years resulted in a decline of sample scores along axis 2 to a location within overlapping ellipses of the snowmelt-dominated and intermediate lakes (Figure 3.3b, Appendix D Figure 1.a). The trajectory of sample scores for OCF 6 is largely orthogonal to the vectors for pH, alkalinity and concentrations of major ions, TP, DIC, DOC and SiO₂, which suggests diatom communities responded to variation in other factors. OCF 6 experienced rapid, partial drainage in June 2007 caused by outlet erosion after a winter of above-average snowfall and intense rainfall in spring (Wolfe and Turner, 2008; Tondu et al., 2017). More than 80% of the lake's volume was lost and surface area was reduced by nearly 43% (Wolfe & Turner, 2008; Turner et al., 2010, 2022). Ontogenetic changes in biogeochemical cycling and physical variables following the lake drainage may account for the unique changes in diatom community composition at OCF 6 relative to other the LTM lakes that were in the rainfall-dominated category in 2008.

Sample scores for three of the six lakes that began in 2008 or 2009 in the intermediate category (OCF 35, 46, 48) were positioned initially within the upper left quadrant and subsequently decreased along axis 2 to the lower left quadrant and fell within the ellipse for rainfall-dominated lakes by 2019 (Figure 3.3c, d). Diatom communities in these three lakes were dominated by *C. lineata* during the first two monitoring years (2008, 2009), along with substantial relative abundance of *A. minutissimum*, *G. angustum*, *N. palea*, *Epithema adnata*, and *F. mesolepta*. Relative abundance of *C. lineata* varied markedly between years during 2008-2017 but declined noticeably in 2018-2019 when relative abundance of *A. minutissimum* and/or *G. angustum* increased (Appendix D Figure 1.b). Sample scores for OCF 19 follow a similar temporal pattern as the above three lakes, but in 2019 they are positioned in the upper left quadrant of the CCA plots where ellipses of the intermediate and snowmelt-dominated lakes overlap due to increased relative abundance of *C. lineata* and *E. adnata*. Sample scores of all four of these lakes (OCF 19, 35, 46, 48) displayed substantial inter-annual variation and oscillated between

the ellipses of the intermediate and rainfall-dominated categories (Figure 3.3c-e). Overall, findings suggest diatom community composition at OCF 35, 46, and 48 converged towards that more typical of rainfall-dominated lakes by 2019, but the inferred change in water chemistry appears to have been more subtle based on movement of sample scores orthogonal to most of the vectors of the water chemistry variables. Diatom community composition at lakes OCF 26 and OCF 34 showed a different temporal pattern than the other lakes that began in the intermediate category in 2008-2009 (Figure 3.3c, e). At OCF 34, diatom community composition was dominated by *A. minutissimum* and *G. angustum* in 2009 and sample scores fell within the ellipse of the rainfall-dominated lakes and subsequently remained relatively unchanged through the monitoring period (Fig. 3.3c). In 2008 and 2009, OCF 26 was classified as an intermediate lake based on analysis of water isotope compositions, but the periphytic diatom communities were dominated by *T. flocculosa* and sample scores fell within the ellipse of the snowmelt-dominated lakes (Figure 3.3e). During the monitoring period, diatom community composition remained relatively unchanged and indicative of relatively dilute ionic content and higher nutrient concentration typical of snowmelt-dominated lakes. Overall, during 2008-2019, diatom community composition shifted towards that typical of lakes in the rainfall-dominated category at five of the six lakes that began in the intermediate category. OCF 26 was an exception because it possessed diatom community composition more reflective of snowmelt-dominated lakes in 2008 and remained relatively unchanged throughout the monitoring period.

Three of the LTM lakes began in the snowmelt-dominated category (OCF 11, 55, 58) and they showed individual patterns of change in diatom community composition during the monitoring period (Figure 3.3f). Sample scores for OCF 58 shifted rapidly (2010-2012) to within the ellipse of the rainfall-dominated lakes. The floristic changes infer increases in lake-water pH, alkalinity and concentrations of DIC and major ions, and decreases in concentrations of TP, TDP, DOC and SiO₂. At OCF 55, *R. pusillum* and *T. flocculosa* maintained consistent and moderate relative abundance, and the sample scores remained mainly within the ellipse of the snowmelt-dominated lakes during the monitoring period (Figure 3.3f, Appendix D Figure 1.c). One exception to this was in 2011, when abrupt increase in relative abundance of *A. minutissimum* shifted the sample score to within the ellipse of rainfall-dominated lakes. Sample scores for OCF 11 were consistently positioned within the upper left quadrant of the 2008-2009 'template' CCA plot, associated with high relative abundance of *C. lineata* and *E. adnata*. During the monitoring period, sample scores for OCF 11 varied in a direction orthogonal to

vectors for most water chemistry variables and displayed marked interannual variation and absence of gradual directional change towards the ellipse of rainfall-dominated lakes.

3.4: Discussion

Water isotope monitoring during 2007-2019 identified a trend to increasingly positive water balances at the 14 LTM lakes in OCF caused by rise of rainfall and possibly also input from permafrost thaw (MacDonald et al., 2021). This provides opportunity to assess the aquatic ecological responses of shallow northern lakes to climate-mediated hydrological changes. Biomonitoring can be particularly useful for tracking ecosystem changes as aquatic biota are integrative of the complex interactions and multiple trajectories of change (Scott et al., 2019), and time series allow ecosystem changes to be identified quickly (Heino et al., 2020). However, long-term biomonitoring records are rarely available from northern locations due to logistical challenges (Mallory et al., 2019; Heino et al., 2020; Kahlert et al., 2020; Goedkoop et al., 2021). To date, most biomonitoring programs in the North have been of short duration and have focused on rivers or on surveys of fish or abiotic variables in lakes rather than on long-term trends in composition of algal communities in lakes (e.g., Lento et al., 2019). Long-term records of lake algal assemblages, and specifically diatoms, can provide important information and they have been shown to respond sensitively to climate-induced shifts in nutrients and hydrological connectivity (Lento et al., 2020). Studies have provided broad spatial analysis of diatom assemblage composition in northern lakes via collection of surficial sediment samples, and some studies have assessed composition of periphytic communities on naturally occurring substrates (e.g., Michelutti et al., 2003; Smol et al., 2005; Ruhland et al., 2014; Lento et al., 2019; Kahlert et al., 2020). These have largely involved single episode sampling to assess for spatial variation in community composition and associations with environmental gradients, and generally have not included systematic, repeated monitoring at regular time intervals. Indeed, few studies have focused on repeated biomonitoring of lakes in the North. For example, Scott et al. (2019) sampled benthic invertebrates from lakes in the Mackenzie Delta, NWT for five consecutive years to assess relationships with hydrological connectivity, and Smol and Douglas (2007) monitored a suite of limnological and biological variables, including composition of diatom communities in periphytic and planktonic habitats, at 45 lakes and ponds on Ellesmere Island every ~3 years since 1983. To our knowledge, our study is among these few long-term lake biomonitoring records in the Canadian North that exceed 10 years in duration.

Our analysis of periphytic diatoms accrued on artificial substrate samplers reveals that community composition at 10 of the 14 LTM lakes (71.4%) converged towards composition typical of lakes with rainfall-dominated input waters by 2019. This is based on samples scores for the LTM lakes in a CCA ordination which fell within or closely adjacent to the ellipse of the rainfall-dominated lakes in a spatial data set from OCF lakes obtained in 2008-2009. These include 4 of the 5 LTM lakes that were dominated by rainfall input water at the beginning of the monitoring period (OCF 29, 37, 38, 49), where diatom community composition remained relatively unchanged during the monitoring period. It also includes 5 of the 6 lakes that began in the intermediate category (OCF 19, 34, 35, 46, 48), and one of the 3 lakes that began in the snowmelt-dominated category (OCF 58; Figure 3.3). Sample scores of these 10 lakes varied little along CCA axis 1 and mainly fell within the range of axis 1 values of rainfall-dominated lakes in the 2008-2009 spatial dataset (Figure 3.4a). Greater variation of sample scores for these 10 LTM lakes occurred along CCA axis 2, and they converged between 2014 and 2019 to values that fall within the ellipse for the rainfall-dominated lakes in the 2008-2009 spatial lake-set (Figure 3.4b). Four of these 10 lakes (OCF 19, 34, 46, 48) had the highest axis 2 scores during 2008 to 2013 and declined markedly thereafter along axis 2, due mainly to relatively high or rising percent abundance of the diatom taxa *A. minutissimum*, *G. angustum*, *G. capitatum*, *D. tenuis*, and/or *E. obscurum*. The patterns of change in diatom community composition captured along CCA axis 2 are consistent with rising $\delta^{18}\text{O}_\text{I}$ values determined from measurements of water isotope composition, which demonstrate increasing input of rainfall and possibly permafrost thaw after 2013 (Figure 3.4e, f; MacDonald et al., 2021). The shifts in diatom community composition infer rising lake-water pH and alkalinity and rising concentrations of major ions (Mg^+ , Na^+ , Cl^- , Ca^+) and DIC. Thus, the climate-driven increase in rainfall and associated runoff elicited ecological and water quality responses in a majority of the LTM lakes.

Four of the 14 LTM lakes (OCF 6, 11, 26, 55) reveal patterns of changes that are not consistent with a shift towards diatom communities typical of rainfall-dominated lakes (Figure 3.4c, d). OCF 6 was identified as a rainfall-dominated lake in 2008, based on water isotope composition, and the diatom community fell within the ellipse for rainfall-dominated lakes in the spatial lake-set with high relative abundance of *A. minutissimum*. Soon thereafter, the diatom community became dominated by *C. lineata* (except in 2016), which is unique compared to composition of diatom communities in the 2008-2009 spatial dataset. Wolfe and Turner (2008) reported that OCF 6 drained suddenly and catastrophically in 2007, one year before diatom monitoring began, which resulted in loss of over 80% of the lake volume

and 40% of the surface area. Exposure of former lake bottom promoted rapid encroachment of terrestrial vegetation (Tondu et al., 2017). These post-drainage physical and ontogenetic changes at OCF 6 appear to have altered diatom community composition and inferred water chemistry in unique directions compared to other lakes that had not drained shortly before onset of the monitoring program. Based on use of the 2008-2009 spatial dataset, diatoms infer that TN and ammonia concentrations increased markedly during early years of the monitoring program and remained elevated above values observed in 2008. This is consistent with sporadic mid-summer measurements of TN concentration reported for this lake by Turner et al. (2022) and may have been caused by higher rates of organic matter decomposition under conditions of shallower lake depth and aerial exposure of former lake bottom sediment after drainage (Watanabe et al., 2011; Vonk et al., 2015; Natali et al., 2019). Alternately, the shifts in diatom community composition may reflect both increase of rainfall runoff caused by climatic variation and increase of snowmelt runoff that resulted from greater winter snowpack captured by extensive shrub proliferation within the lake's immediate catchment; a situation which may not have been well captured within the 2008-2009 spatial dataset. Water isotope records provide some support for this, based on $\delta^{18}\text{O}_\text{I}$ values in spring which are comparable to snowmelt runoff and values of $\delta^{18}\text{O}_\text{I}$ in fall that are comparable to rainfall (MacDonald et al., 2021).

OCF 11 was identified as snowmelt-dominated in 2008 based on water isotope composition, but it displayed a similar trajectory of change in diatom community composition during the monitoring period as that observed at OCF 6, characterized by sample scores that were positioned within the upper left quadrant of the CCA and that shifted mainly along axis 2 due to relatively high and varying abundance of *C. lineata* and *E. adnata* (Figure 3.3f). Shifts in diatom community composition at OCF 11 infer that concentrations of TN and ammonia increased during the monitoring period. OCF 11 has a particularly large catchment area (395.2 km²) compared to the other lakes (Figure 3.1, Table 3.1). These conditions may have resulted in shifts in diatom community composition that reflect both an increase of rainfall runoff caused by a climatic trend (MacDonald et al., 2021) and increase of snowmelt runoff from the dense shrubs in the catchment area. Interestingly, at OCF 46 and OCF 48, diatom communities were also dominated by *C. lineata* and *E. adnata* at the beginning of the monitoring period, similar to communities at OCF 6 and OCF 11. Paleolimnological records at OCF 46 and OCF 48 suggest active thermokarst activity and possible occurrence of a drainage event in the recent past at OCF 48 (MacDonald et al., 2012b; Bouchard et al., 2017), which may have led to the inferred rise of TN and

ammonia concentrations from higher organic matter decomposition which altered diatom community composition. Shifts in catchment vegetation (i.e., shrubification following lake drainage) also may have maintained substantial snowmelt runoff to OCF 46 and OCF 48 during early to middle years of the monitoring record. However, rise in percent abundance of *G. angustum* at OCF 46 and *A. minutissimum* at OCF 48 infers that hydro-limnological conditions shifted to those typical of rainfall-dominated lakes by the end of the monitoring period. MacDonald et al. (2021) predicts that with continued climate change and water balances increasingly dominated by rainfall in the OCF there could be an increase in thermokarst activity and drainage events in this region.

Lakes OCF 26 and OCF 55 are two other lakes that did not converge towards diatom community composition typical of rainfall-dominated lakes during the monitoring period. Based on water isotope composition in 2008 and 2009, OCF 26 was classified in the intermediate category and OCF 55 was in the snowmelt-dominated category. However, both lakes had diatom community compositions that consistently fell within the ellipse for snowmelt-dominated lakes during the monitoring period and infer relatively higher concentrations of nutrients and DOC. The relative stability of diatom community composition and inferred water chemistry may be attributed to the small surface area of both lakes which normally reduces the influence of heating and evaporation by sunlight (Frost et al., 2018). Also, the catchment vegetation is dominated by tall shrubs at both lakes, which typically accumulates thick winter snowpack and reduces inter-annual variability (Turner et al. 2010, 2014; Tondu et al. 2013). The greater depth of OCF 55, which exceeds 5 m, also may dampen influence of hydrological processes on water chemistry and diatom community composition.

Overall, this study shows that 71.4% of the LTM lakes have displayed patterns of change in diatom community composition during the monitoring period (2008-2019) consistent with a shift to increased influence of rainfall as demonstrated from systematic measurement of lake water isotope composition (MacDonald et al., 2021). The biotic shifts infer that increased rainfall runoff and interactions with catchment substrates led to increase of pH, alkalinity and ionic content of the lake water and reduction in concentrations of nutrients and DOC. Coincidental and corresponding shifts in diatom community composition and isotope composition of input waters demonstrate that shallow thermokarst lake ecosystems are responsive and vulnerable to climate-driven increase in rainfall. Exceptions include two lakes (OCF 26, 55) where diatom community composition remained relatively

constant during the entire monitoring period and indicative of conditions typical of lakes with snowmelt-dominated inflow, a lake that has recently drained (OCF 6) and a lake with a particularly large catchment area (OCF 11) both of which are uniquely dominated by *C. lineata* and where basin hydrology appears to be strongly influenced by both rainfall and snowmelt input waters. These findings detect that composition of periphytic diatom communities on artificial-substrate samplers tracks aquatic ecosystem responses to temporal trends in climate-mediated hydrological change.

3.5 Figures and Tables:

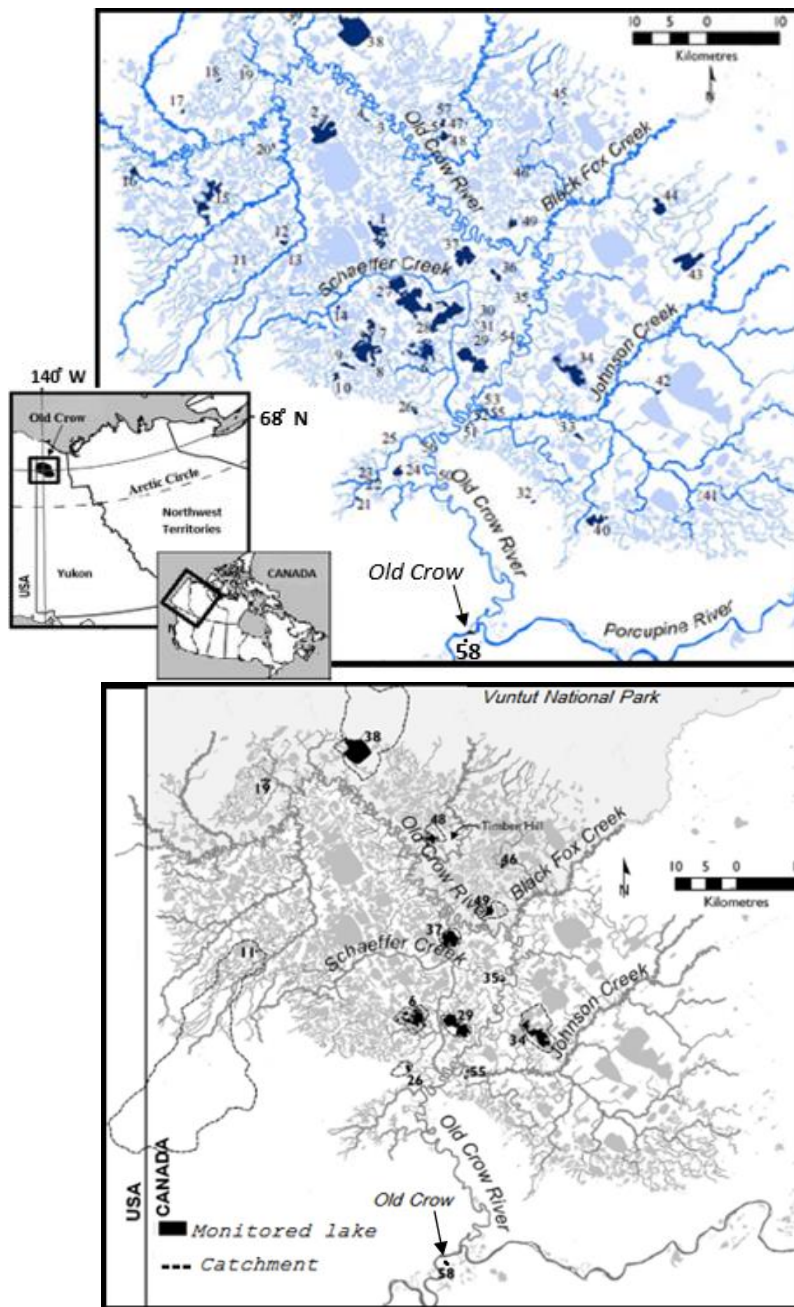


Figure 3.1: Maps for the study area, the upper panel showing locations of Old Crow Flats (OCF), Yukon, and the study lakes sampled in 2008 and 2009, and the lower panel showing locations of the 14 lakes that form the long-term monitoring study.

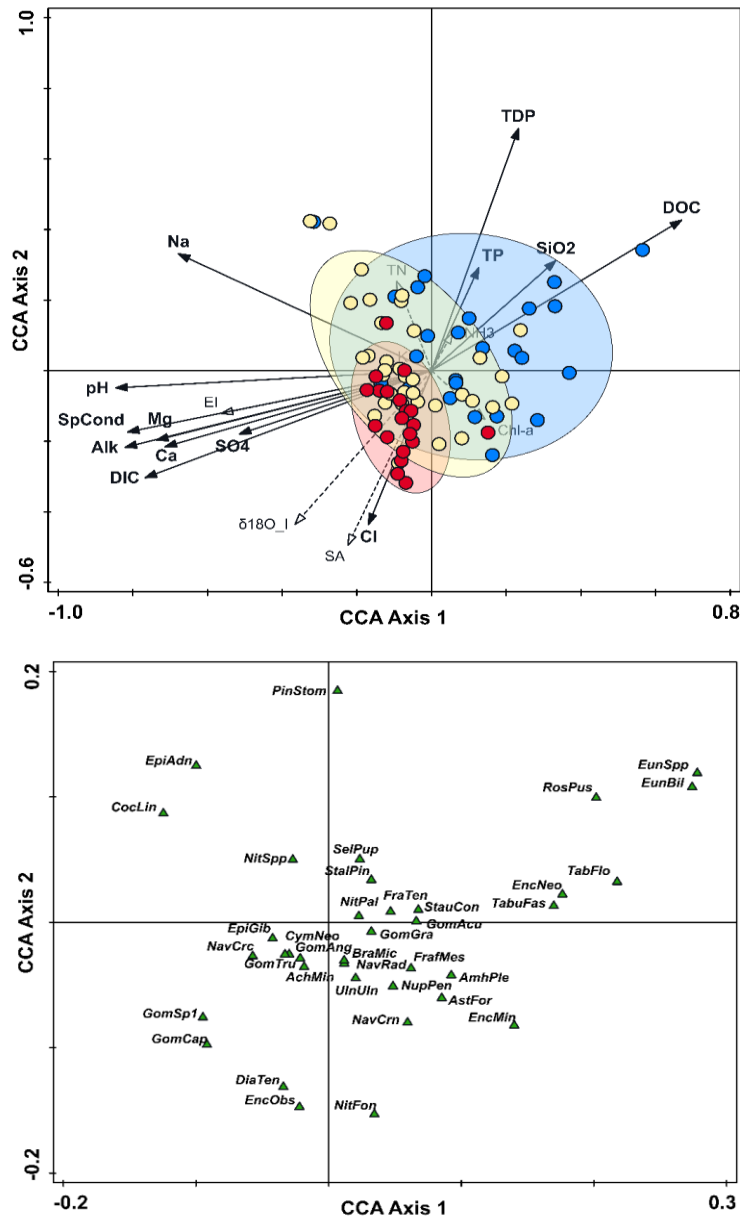


Figure 3.2: Graphs showing results of canonical correspondence analysis (CCA) of the water chemistry variables and diatom community composition (as taxon percent abundances) accrued on artificial-substrate periphyton samplers retrieved from 33 lakes in 2008 and 48 lakes in 2009 across Old Crow Flats. Water chemistry variables are shown as vectors and sample scores are presented as dots in the upper panel. Also shown in the upper panel are 2D-Normal based 66% ellipses for the snowmelt-dominated lakes (blue), rainfall-dominated lakes (red) and intermediate lakes (yellow). Species scores are presented in the lower panel and full names of the abbreviated diatom taxon codes are reported in Table 3.2.

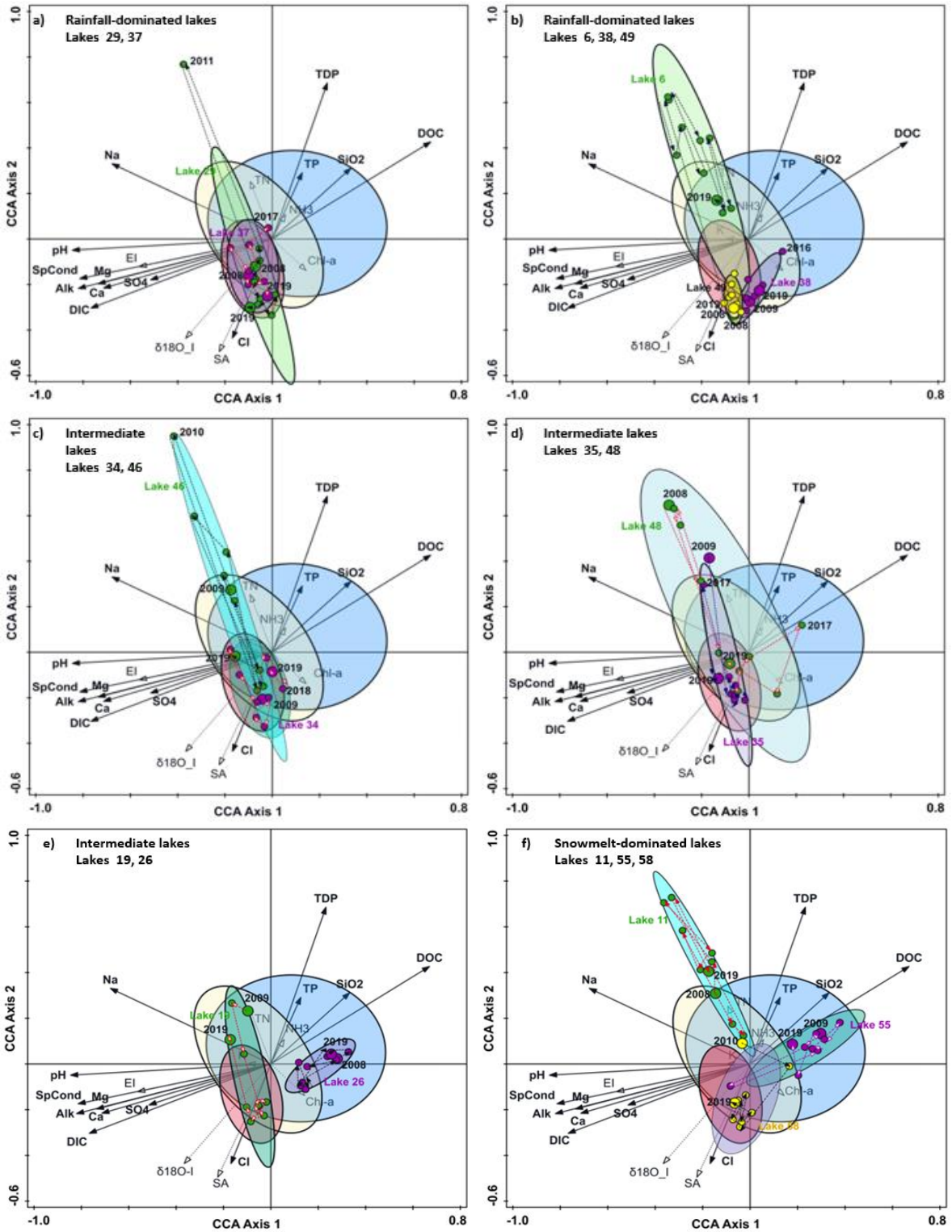


Figure 3.3: Graphs showing results of canonical correspondence analysis (CCA) based on the 2008-2009 spatial data set of epiphytic diatom percent abundances and water chemistry variables across lakes of the Old Crow Flats, and with the diatom percentage data from the 14 long-term monitoring lakes included passively. Red, yellow and blue ellipses are the same as presented in Figure 2 (2D-Normal based 66% ellipses) and identify a representative range of samples scores from the rainfall-, intermediate, and snowmelt-dominated lakes in the spatial data set from 2008 and 2009, respectively. Also provided are the 66% ellipses about sample scores of each of the 14 long-term monitoring lakes to assess temporal patterns of change in sample scores (circles) and inferred water chemistry during the monitoring period (2008-2019). Panels a & b present the lakes that began the monitoring periods in the rainfall-dominated category; panels c, d, & e present the lakes that began the monitoring periods in the intermediate category; and panel f presents the lakes that began the monitoring periods in the snowfall-dominated category.

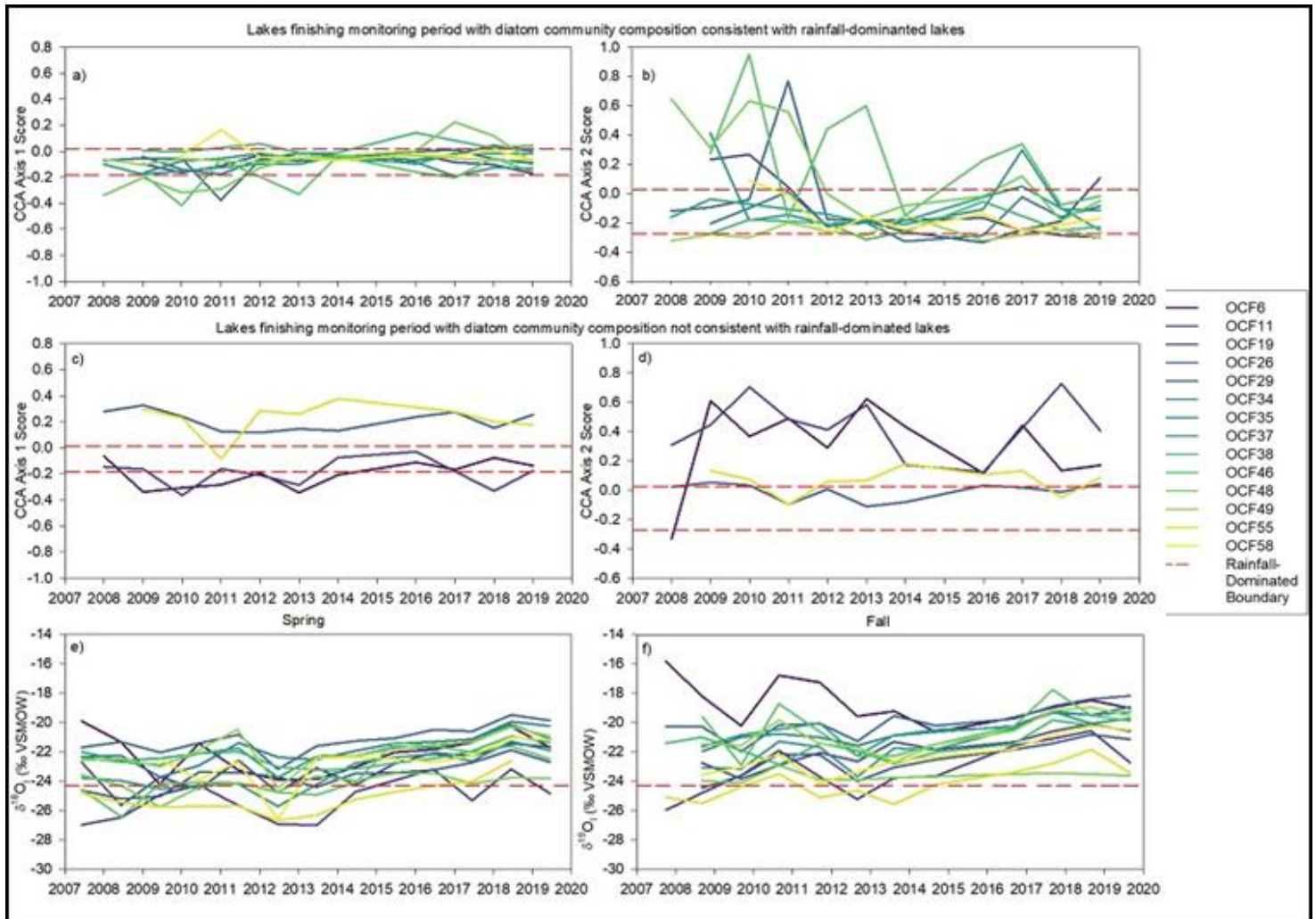


Figure 3.4: Graphs showing temporal patterns of variation in periphytic diatom community composition based on sample scores along axes 1 and 2 of the CCAs presented in Figure 3 and oxygen isotope composition of input waters ($\delta^{18}O_i$) at the 14 long-term monitoring lakes in OCF during 2008-2019. Panels (a) and (b) show temporal patterns of variation in sample scores along CCA axis 1 and 2, respectively, for the monitoring lakes that possessed diatom community composition consistent with rainfall-dominated lakes in 2019. Panels (c) and (d) show temporal patterns of variation in sample scores along CCA axis 1 and 2, respectively, for the monitoring lakes that possessed diatom community composition not consistent with rainfall-dominated lakes in 2019. Panels (e & f) represent spring and fall water isotope composition ($\delta^{18}O_i$) of lakes during monitoring period, and red dashed lines represent the threshold value for rainfall-dominated lakes as reported by MacDonald et al. (2021).

Table 3.1. Selected characteristics of the 14 OCF long-term monitoring lakes (LTM) based on Tondu et al. (2013) and list the years in which the deployed artificial samplers were successfully retrieved from each monitored lake during the long-term monitoring period (2008-2019).

Lake	Local Name	Original Category	Catchment Area (km ²)	Lake Surface Area (km ²)	Depth (m)	Periphyton Sample Retrieved											
						2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019
OCF 11		Snow	395.19	0.07	0.8	Y	Y	Y	Y	Y	Y	Y	N	Y	N	Y	Y
OCF 55		Snow	0.59	0.02	>5.0	N	Y	Y	Y	Y	Y	Y	N	Y	Y	Y	Y
OCF 58	Mary Nitro	Snow	-	-	2.6	N	N	Y	Y	Y	Y	Y	N	Y	Y	Y	Y
OCF 19		Inter.	0.58	0.11	0.9	N	Y	Y	Y	Y	Y	Y	N	Y	Y	Y	Y
OCF 26		Inter.	5.21	0.42	1.7	Y	Y	Y	Y	Y	Y	Y	N	Y	Y	Y	Y
OCF 34	Netro	Inter.	29.16	6.11	1.5	N	Y	Y	Y	Y	Y	Y	N	Y	Y	Y	Y
OCF 35		Inter.	0.80	0.14	1.1	N	Y	Y	Y	Y	Y	Y	N	Y	Y	Y	Y
OCF 46		Inter.	0.28	0.12	0.5	N	Y	Y	Y	Y	Y	Y	N	Y	Y	Y	Y
OCF 48	Hotspring	Inter.	7.41	1.31	0.7	Y	Y	Y	Y	Y	Y	Y	N	Y	Y	Y	Y
OCF 06	Zelma	Rain	15.99	5.01	0.3	Y	Y	Y	Y	Y	Y	Y	N	Y	Y	Y	Y
OCF 29	John Charlie	Rain	11.71	6.86	1.2	Y	Y	Y	Y	Y	Y	Y	N	Y	Y	Y	Y
OCF 37	Ts'iivii zhit	Rain	8.84	5.14	1.2	Y	Y	N	N	Y	Y	Y	N	Y	Y	N	Y
OCF 38	Husky	Rain	137.9	12.67	1.1	N	Y	Y	N	Y	Y	Y	N	Y	N	Y	Y
OCF 49	Marten	Rain	10.75	1.15	1.2	Y	Y	Y	Y	Y	Y	Y	N	Y	N	Y	Y

Table 3.2: Diatom taxon names, authority names, and codes presented in the CCA ordination for the combined 2008-2009 data.

Taxon Name	Authority	Code
<i>Achnantheidium minutissimum</i>	(Kützing) Czarnecki	<i>AchMin</i>
<i>Amphipleura pellucida</i>	(Kützing) Kützing	<i>AmhPle</i>
<i>Asterionella formosa</i>	Hassall	<i>AstFor</i>
<i>Brachysira microcephala</i>	(Grunow) Compère	<i>BraMic</i>
<i>Cocconeis lineata</i>	Ehrenberg	<i>CocLin</i>
<i>Cymbella neocistula</i>	(Krammer)	<i>CymNeo</i>
<i>Diatoma tenuis</i>	Agardh	<i>DiaTen</i>
<i>Encyonema minutum</i>	(Hilse) D. G. Mann	<i>EncMin</i>
<i>Encyonema neogracile</i>	(Krammer)	<i>EncNeo</i>
<i>Encyonema obscurum</i>	(Krasske)	<i>EncObs</i>
<i>Epithemia adnata</i>	Kützing	<i>EpiAdn</i>
<i>Epithemia gibba</i>	(Ehrenberg) Kützing	<i>EpiGib</i>
<i>Eunotia bilunaris</i>	Ehrenberg	<i>EunBil</i>
<i>Eunotia species</i>		<i>EunSpp</i>
<i>Fragilaria tenera</i>	(W. Smith) Lange-Bertalot	<i>FraTen</i>
<i>Fragilariforma mesolepta</i>	(Hustedt) Kharitonov	<i>FrafMes</i>
<i>Frustulia amphipleuroides</i>	(Grunow) A. Cleve	<i>FruAmpl</i>
<i>Gomphonema acuminatum</i>	Ehrenberg	<i>GomAcu</i>
<i>Gomphonema angustum</i>	Kützing	<i>GomAng</i>
<i>Gomphonema capitatum</i>	Ehrenberg	<i>GomCap</i>
<i>Gomphonema gracile</i>	Ehrenberg	<i>GomGra</i>
<i>Gomphonema species 1</i>		<i>GomSp1</i>
<i>Gomphonema truncatum</i>	Ehrenberg	<i>GomTru</i>
<i>Navicula cryptocephala</i>	Kützing	<i>NavCrc</i>
<i>Navicula cryptotenella</i>	Lange-Bertalot	<i>NavCrn</i>
<i>Navicula radiosa</i>	Kützing	<i>NavRad</i>
<i>Nitzschia fonticola</i>	(Grunow) Grunow	<i>NitFon</i>
<i>Nitzschia palea</i>	(Kützing) W. Smith	<i>NitPal</i>
<i>Nitzschia species</i>		<i>NitSpp</i>
<i>Nupela pennsylvanica</i>	(R. M. Patrick) Potapova	<i>NupPen</i>
<i>Pinnularia stomatophora</i>	(Grunow) Cleve	<i>PinStom</i>
<i>Rosithidium pusillum</i>	(Grunow) De Toni	<i>RosPus</i>
<i>Sellaphora pupula</i>	(Kützing) Mereschkovsky	<i>SelPup</i>
<i>Stausosirella pinnata</i>	(Ehrenberg) D. M. Williams & Round	<i>StalPin</i>
<i>Stausosira construens</i>	Ehrenberg	<i>StauCon</i>
<i>Tabellaria flocculosa</i>	(Roth) Kützing	<i>TabFlo</i>
<i>Tabularia fasciculata</i>	(C. Agardh) D. M. Williams & Round	<i>TabuFas</i>
<i>Ulnaria ulna</i>	(Nitzsch) Compère	<i>UlnUln</i>

Chapter 4

Synthesis, Implications and Recommendations

In my thesis research, I evaluated the ability of periphytic diatom communities that grew on artificial-substrate samplers during the open-water season to track changes in hydrological and limnological conditions of shallow northern lakes in Old Crow Flats (OCF) across space and time. The use of artificial substrate samplers reduces confounding influence of differences in accrual time and substrate inherent in sampling natural substrates and surficial sediments in lakes, and, fortunately, the taxa abundant on the artificial-substrate samplers deployed between early June and early September are also the ones abundant in surficial sediments that integrate across multiple lake habitats (based on comparison of data generated in my thesis research and by Balasubramaniam et al., 2017). Results from two years of spatial surveys (2008, 2009) that spanned the broad hydro-limnological gradients of lakes in this vast thermokarst landscape reveal distinctive differences in water chemistry and diatom community composition across three isotope-inferred hydrological lake categories that differ in the source of input waters (snowmelt-dominated, rainfall-dominated, intermediate). This supports that analysis of diatom community composition on the artificial-substrate samplers has potential for application in a long-term lake monitoring program to track limnological changes over time in response to shifts in hydrological conditions. However, undetectable differences in water chemistry and diatom community composition between the two years of the spatial lake surveys, despite about four-fold higher snowfall in the second year (Turner et al., 2014), suggest that longer time-series of data are required to assess their ability to track temporal responses to hydro-climatic variations because water chemistry and diatom communities may respond to climate-mediated changes in catchment processes and land cover that operate at longer timescales. To address this, I integrated information gleaned from the spatial lakes surveys of 2008-2009 with long-term monitoring data sets obtained during 12 years spanning a 13-year period (2008-2019; data in 2015 were unavailable) from 14 representative lakes to explore temporal patterns of variation in diatom community composition and infer changes in lake water chemistry during a documented hydrological trend towards increasingly positive lake water balances, as demonstrated by MacDonald et al. (2021). The results reveal that 71.4% (10/14 lakes) of the long-term monitoring lakes display patterns of change in diatom community composition between 2008 and 2019 consistent with the documented shift to increased influence of rainfall on lake water

balance. Temporal changes in diatom community composition in these lakes infer that increased rainfall runoff, likely via interactions with catchment substrates, fostered increases in lake-water pH, alkalinity and ionic content of the lake water and reduction in concentrations of nutrients and DOC. Coincidental and corresponding shifts in diatom community composition and isotope composition of input waters demonstrate ecological responses of shallow thermokarst lakes in OCF and, by inference, shifts in water chemistry to climate-driven increase in rainfall. Exceptions include two lakes with snowmelt-dominated input waters in 2008 (OCF 26, OCF 55) where diatom community composition remained relatively constant during the entire monitoring period. At two other lakes (OCF 6, OCF11), diatom community composition did not converge towards that typical of rainfall-dominated lakes in OCF. OCF 6 was classified as rainfall-dominated in 2008 based on water isotope composition, following recent catastrophic drainage, but substantial changes in catchment vegetation cover ensued as shrubs proliferated across the former lakebed (Turner et al., 2022). OCF 11 was classified as snowmelt-dominated in 2008, likely as a result of its particularly large catchment area that includes hillslopes that deliver snowmelt to the lake through protracted periods of the open-water season. In the latter two lakes, diatom communities are uniquely dominated by the species *Cocconeis lineata*, where water isotope compositions indicated their strong influence by both rainfall and snowmelt input waters. Despite these few exceptions, the results reported in my thesis support that composition of periphytic diatom communities on artificial-substrate samplers tracks aquatic ecosystem responses to climate-mediated hydrological changes with sufficient ability to be useful in long-term monitoring programs of shallow northern lakes of OCF, and likely elsewhere.

Water balance and ecological conditions of shallow northern lakes are influenced by interactions among several factors, including air temperature, precipitation, catchment vegetation and permafrost dynamics (Myers-Smith et al., 2011; Derksen and Brown, 2012; Lantz et al., 2013; Lantz and Turner., 2015; Arndt et al., 2019). Consequently, complex and multiple hydroecological trajectories are possible under scenarios of future climate change (Vincent et al., 2011; Tondu et al., 2013; Turner et al., 2014; MacDonald et al., 2017). Tondu et al. (2012) and Turner et al. (2014) postulated multiple trajectories for lakes in OCF in response to climate warming, but analysis of 13-year-long hydrological monitoring records by MacDonald et al. (2021) has revealed a trend of increasingly positive lake water balance because of rising rainfall and potentially permafrost thaw which have outpaced inputs from snowmelt runoff and losses by evaporation. Based on these findings, MacDonald et al. (2021) predicted

that increasingly positive water balances will lead to lake expansion and greater hydrological connectivity, which will increase incidence of lateral lake drainage. Information provided from analysis of periphytic diatom community composition at the long-term monitoring lakes provides additional insight into trajectories of change in chemical and physical conditions and biological responses (Figure 4.1). The rapid convergence of diatom community composition in 10 of the 14 lakes between 2010 and 2013 to that typical of lakes with rainfall-dominated input waters, characterized by a shift to higher relative abundance of *Achnanthydium minutissimum*, *Gomphonema angustum*, *Diatoma tenuis* and *Encyonema obscurum*, infers a rise in pH, alkalinity, conductivity and concentrations of major ions and DIC over a relatively short time period, likely in response to erosion of shoreline substrates during lake expansion and increased hydrological connectivity. Sudden lateral drainage also elicits a rapid response as substantial lake volume is lost and shrubs proliferated across the exposed lake bottom, but results in marked rise in concentration of total nitrogen and ammonia (Tondu et al., 2017) with associated increase in relative abundance of *Epithemia adnata* and *Cocconeis lineata*. These ‘fast responses’ likely occur at lakes located more centrally within OCF, where flat terrain, larger lake surface area and sparse terrestrial vegetation provide less resistance to lake expansion and shoreline erosion. For some of the lakes at peripheral locations and immediately downslope of the surrounding mountains, where catchment characteristics foster dominance of snowmelt input on their water balance, chemical and physical conditions likely respond at a slower pace to rise in rainfall runoff. Here, dense, tall vegetation and thicker, organic-rich soils have developed over many years to decades, and long-lasting seasonal input of snowmelt runoff from the hillslopes permits input waters to accumulate substantial amounts of major nutrients and DOC on their route to the lakes. Greater topographic relief and denser shrub growth along the shorelines also reduce rates of erosion as water balance rises. These counterbalancing forces may overwhelm or, at least, slow the pace of influence from rising rainfall input.

The research in this thesis contributes in important directions to a long-term lake monitoring program at OCF that in its 15th year, sustained by active partnerships among Vuntut National Park, Vuntut Gwitchin First Nation, North Yukon Renewable Resource Council and university-based researchers. Given that concern about the effects of climate change on shallow lakes in OCF is likely to grow, I recommend that the long-term monitoring program that has been ongoing since 2008, and which integrates information provided by analyses of water isotope composition and periphytic diatom community composition, be continued for many years and decades to track hydrological and ecological

changes and infer shifts in water chemistry. As climatic conditions change over time, effectiveness of the framework developed in my thesis can likely be improved by periodic ‘re-calibration’ of relations among water isotope inferred hydrological metrics, water chemistry and diatom community composition. Thus, I recommend spatial surveys be conducted across the OCF landscape at approximately 10-year intervals, consistent with the methods presented in Chapter 2. I advocate to collect water samples for analysis of isotope composition and water chemistry three times during the open-water season of those ‘re-calibration’ years in spring, mid-summer and fall. Addition of surface sample collection to the periodic spatial surveys and analysis of diatom community composition in those samples may reveal changes to diatom community composition in several other lake habitats beyond the periphytic taxa captured on the artificial-substrate samplers (e.g., planktonic and benthic habitats). Because composition of diatom communities accrued on the artificial-substrate samplers is often dominated by a small number of taxa with wide distribution across the lakes in OCF, additional information about shifting hydro-ecological conditions may be provided by increasing the number of diatom valves enumerated per sample. In this thesis, at least 300 diatom valves were identified and enumerated from each sample. Increasing the count size to 500 valves per sample may increase the information content of the data by estimating taxon percent abundances of the less-abundant taxa with greater precision, which would allow a larger number of the less-abundant taxa to be included in the numerical analyses.

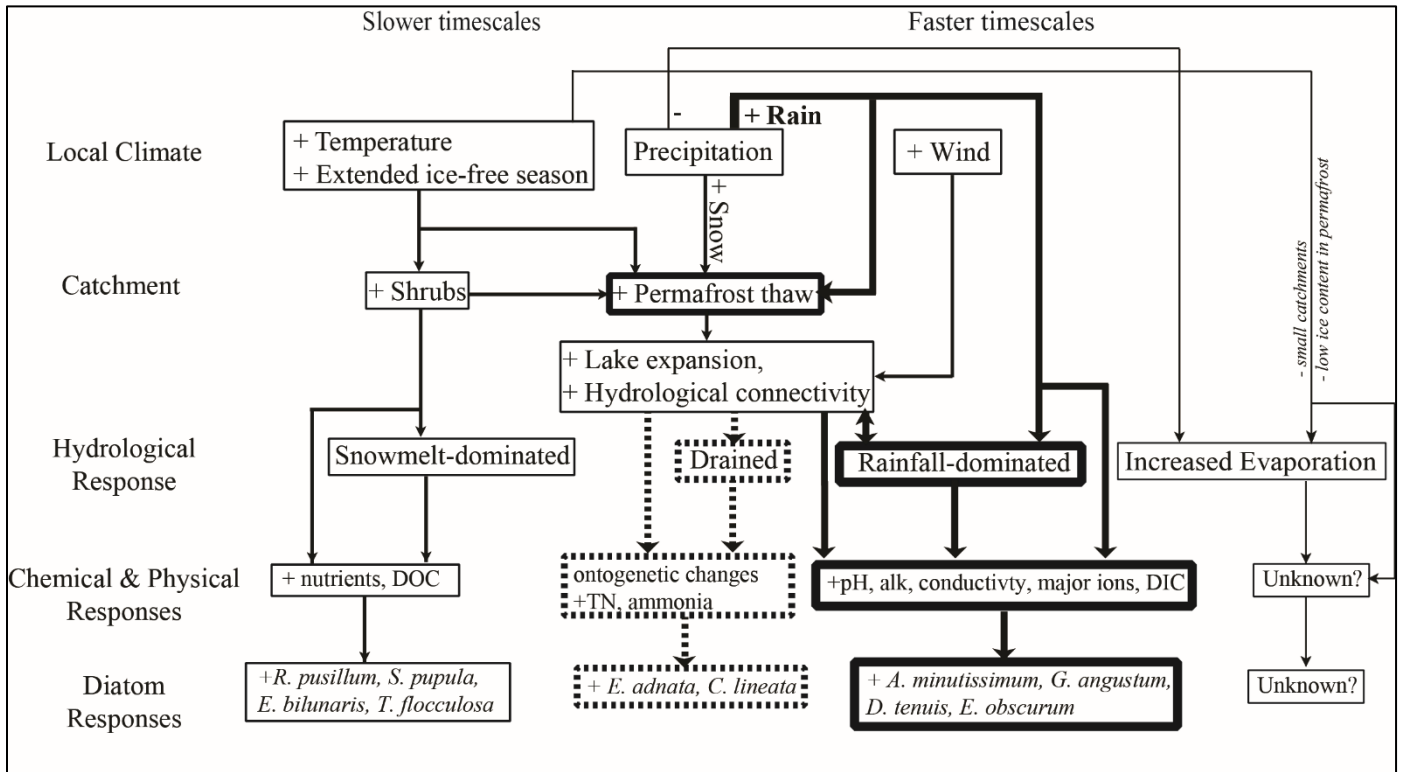


Figure 4.1: Schematic diagram, modified from MacDonald et al. (2021), representing the possible hydrological and limnological trajectories for lakes in OCF in response to climatic changes. Bold lines represent the pathways that have become dominant in OCF during the past 13 years and the dashed box around 'Drained' represents a potential trajectory that may become more common. Limnological changes are separated into chemical and physical responses and responses of periphytic diatom community composition.

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Appendices :
Appendix A
Lake locations and calculated oxygen isotope composition of input waters ($\delta^{18}\text{O}_I$) for lakes sampled in July 2008 and July 2009 and the associated input-water hydrological category for each year (2008 snowmelt-dominated <-24.264 ‰, intermediate = -24.264 to -22.553 ‰, and rainfall-dominated >-22.553 ‰; 2009 snowmelt-dominated <-24.313 ‰, intermediate = -24.313 to -22.728 ‰, and rainfall-dominated >-22.728 ‰).

Lake	Latitude (°N)	Longitude (°W)	July 2008 $\delta^{18}\text{O}_I$ Values (‰)	2008 Classification	July 2009 $\delta^{18}\text{O}_I$ Values (‰)	2009 Classification
OCF1	68.077	-140.11	-22.0	Rainfall	-23.0	Intermediate
OCF2	68.202	-140.296			-21.2	Rainfall
OCF3	68.214	-140.097			-25.4	Snowfall
OCF4	68.215	-140.134			-22.2	Rainfall
OCF6	67.919	-139.991	-19.2	Rainfall	-19.7	Rainfall
OCF7	67.921	-140.15			-24.6	Snowfall
OCF8	67.907	-140.124	-23.4	Intermediate	-24.2	Intermediate
OCF9	67.906	-140.205	-23.2	Intermediate	-23.9	Intermediate
OCF10	67.891	-140.235	-24.0	Intermediate	-23.9	Intermediate
OCF11	68.028	-140.57	-25.4	Snowfall	-25.8	Snowfall
OCF12	68.061	-140.411			-25.5	Snowfall
OCF13	68.059	-140.364	-25.3	Snowfall	-24.8	Snowfall
OCF14	67.977	-140.234			-24.0	Intermediate
OCF15	68.107	-140.674	-23.2	Intermediate	-24.1	Intermediate
OCF16	68.152	-140.893	-23.7	Intermediate	-25.1	Snowfall
OCF18	68.267	-140.619	-23.0	Intermediate	-23.9	Intermediate
OCF19	68.283	-140.522			-23.1	Intermediate
OCF20	68.185	-140.444	-24.6	Snowfall	-24.2	Intermediate
OCF21	67.739	-140.18	-25.0	Snowfall	-24.5	Snowfall
OCF22	67.764	-140.152	-26.8	Snowfall	-25.8	Snowfall
OCF23	67.765	-140.154			-25.8	Snowfall
OCF24	67.771	-140.049	-24.8	Snowfall	-21.7	Rainfall
OCF25	67.806	-140.055			-24.3	Snowfall
OCF26	67.848	-139.992	-24.0	Intermediate	-23.5	Intermediate

OCF27	68.004	-140.052	-22.4	Rainfall		
OCF28	67.962	-139.898	-21.6	Rainfall	-21.2	Rainfall
OCF29	67.911	-139.794	-21.1	Rainfall	-20.5	Rainfall
OCF30	67.958	-139.781	-24.1	Intermediate	-23.1	Intermediate
OCF31	67.961	-139.787	-24.3	Snowfall	-23.5	Intermediate
OCF32	67.731	-139.615	-24.1	Intermediate	-24.4	Snowfall
OCF33	67.81	-139.461			-22.7	Rainfall
OCF34	67.884	-139.472			-23.1	Intermediate
OCF35	67.979	-139.62			-23.0	Intermediate
OCF36	68.015	-139.712			-21.4	Rainfall
OCF37	68.044	-139.806	-21.6	Rainfall	-22.9	Intermediate
OCF38	68.322	-140.129			-22.4	Rainfall
OCF39	68.337	-140.367	-19.8	Rainfall		
OCF40	67.71	-139.432	-21.9	Rainfall	-23.3	Intermediate
OCF41	67.726	-139.083	-23.8	Intermediate	-24.1	Intermediate
OCF42	67.865	-139.206	-20.1	Rainfall		
OCF44	68.103	-139.185	-22.6	Intermediate		
OCF45	68.231	-139.483	-24.9	Snowfall	-26.1	Snowfall
OCF46	68.15	-139.606			-23.3	Intermediate
OCF47	68.205	-139.808			-24.0	Intermediate
OCF48	68.192	-139.879	-23.7	Intermediate	-24.1	Intermediate
OCF49	68.082	-139.662	-22.3	Rainfall	-21.0	Rainfall
OCF51	67.829	-139.823			-24.4	Snowfall
OCF52	67.843	-139.808	-26.4	Snowfall	-24.4	Snowfall
OCF53	67.848	-139.777			-23.0	Intermediate
OCF54	67.931	-139.671	-24.9	Snowfall	-24.4	Snowfall
OCF55	67.843	-139.758			-25.2	Snowfall
OCF56	67.812	-139.937	-25.1	Snowfall	-24.0	Intermediate
OCF57	68.208	-139.807			-22.9	Intermediate

Appendix B Water chemistry data from July 2008 from the monitored lakes in Old Crow Flats.																		
OCF Lake	NH3	pH	SPCOND	Alk	Cl	SO4	DOC	DIC	Ca	Mg	K	Na	SiO2	TN	TDP	TP	Chl-a	Surface Area
	µg/L		µS/cm	mequiv./L	mg/L	mg/L	mg/L	mg/L	mg/L	mg/L	mg/L	mg/L	mg/L	µg/L	µg/L	µg/L	µg/L	km ²
1	102	9.36	131	56.3	0.27	8.56	13.8	10.1	15.6	5.6	1.65	1.49	1.28	1180	10.3	20.3	4.60	3.901
6	178	8.47	212	56.6	1.22	45.6	11.8	12.2	21.5	9.93	2.41	3.02	0.48	1170	15.8	57.8	17.37	5.005
8	52	9.82	102	41.5	0.09	0.94	13.4	6.6	10.1	3.91	0.35	1.9	0.25	691	12.8	19.9	0.70	0.283
9	94	8.23	127	67.2	0.2	1.21	12.1	14.6	17.3	5.94	0.79	1.61	0.42	692	10.4	22.9	6.09	0.847
10	81	7.8	100	47.4	0.29	1.69	16.6	10.5	13.2	3.97	1.2	2.41	0.92	874	28	49.7	2.27	0.710
11	91	7.55	50	18.3	0.28	0.73	22.1	4.6	6.05	1.99	1.58	1.63	0.41	956	50.5	66.6	3.74	0.071
13	164	6.96	43	17.8	0.1	0.04	30.8	3.9	6.47	1.95	0.52	0.5	3.17	1140	31	41.7	4.34	0.023
15	68	8.49	94	46.8	0.15	2.7	11.6	9.3	12.3	4.3	0.93	0.75	0.13	709	13.5	21.9	1.55	6.909
16	54	8.41	193	90.2	0.15	12.4	15.2	19	27.6	6.7	0.37	1.97	1.3	623	11.4	20.3	1.97	0.978
18	75	9.4	96	45.4	0.14	0.47	12.1	8.3	13.3	3.2	0.48	0.94	0.24	837	12.6	22.9	2.84	0.271
20	75	8.39	133	71.3	0.14	0.16	17.2	14.2	19.9	6.04	0.48	1.24	0.52	852	8.3	20.3	3.94	0.277
21	61	7.4	42	16.4	0.22	0.019	20.1	4.4	5.9	1.82	0.49	1.02	0.44	841	17.6	27.2	1.77	0.159
22	41	6.65	21	7.33	0.15	0.06	21.4	2.1	2.61	1.1	0.58	0.38	0.34	555	4.5	12	1.79	0.016
24	58	7.22	44	20.2	0.22	0.06	12.5	5.2	6.16	1.91	0.36	0.36	0.28	772	7.7	18	1.76	1.220
26	66	7.03	33	21.4	0.25	0.13	18.3	3.9	4.77	1.53	0.61	0.45	0.51	688	15.9	31.7	4.72	0.423
27	112	10.2	131	48.3	0.18	3.04	12.7	7.5	12.4	5.54	0.09	1.27	0.86	962	9.5	36.6	8.65	13.209
28	62	9.32	126	65.2	0.24	2.86	13	12.7	15.3	7.35	0.17	1.79	0.32	805	6.7	14.3	2.51	7.999
29	110	9.83	117	55.8	0.33	3.34	9.2	10.2	11.6	6.69	0.08	1.34	1.09	806	6.5	36	7.12	6.858
30	91	8.18	118	55.1	0.19	4.72	19.6	11.6	16.8	5.3	0.65	0.96	0.31	849	9.7	23.5	2.48	0.085
31	120	7.68	111	48.3	0.31	5.63	21.1	10.7	14.7	5.19	1.57	0.74	0.33	972	16.4	24.7	4.11	0.062
32	223	6.75	31	12.6	0.14	0.25	21.5	3.3	4.74	1.33	0.47	0.62	1.54	1110	30.7	55.8	18.82	0.282
37	127	9.64	125	55.3	0.12	7.68	14.1	10.1	13.5	6.79	0.54	1.51	0.37	1080	8.9	34	8.97	5.143
39	107	9.32	175	86.6	0.56	8.31	13	17.8	16.8	12.1	1.88	3.08	0.41	853	11	25.7	6.46	12.670
40	171	7.63	90	46.5	0.23	1.06	11.8	10.2	13	3.7	0.67	1.18	0.8	1460	7.6	139	25.22	2.750
41	118	7.49	85	40.8	0.5	1.06	21.3	9.3	11.1	3.68	2.68	1.18	3.14	966	14.6	35.5	5.63	0.056

42	28	8.76	181	99	0.41	5.11	6.4	21.9	25	9.05	1.07	1.83	0.48	337	3.6	10.5	0.43	0.280
44	232	8.44	117	64	0.24	0.5	13.3	13.4	18.8	4.26	1.32	0.78	2.81	1240	8.1	64.8	21.69	2.839
45	65	9.6	132	42.6	0.12	22.5	11.9	7.8	22.4	2.93	0.12	0.23	1.26	733	11.2	19.4	1.05	0.127
48	116	9.36	186	100	0.28	0.86	9.2	20	16.5	7.88	2.05	13.1	2.87	909	30.5	38.2	6.43	1.305
49	98	9.81	137	59.2	0.19	9.64	12.3	12	12.7	8.92	0.45	1.73	0.81	985	8.2	27.2	6.10	1.148
52	48	9.02	101	51.2	0.12	0.24	19.4	10.3	16.4	3.64	0.57	0.41	0.46	766	11.1	19.3	1.50	0.032
54	28	7.73	90	45.3	0.42	0.52	20.7	10.1	15.6	2.65	1.23	0.44	1.84	625	10.3	18.2	2.05	0.355
56	198	6.93	73	33.4	0.13	0.25	25.9	8.9	10.7	2.23	2.93	0.33	2.98	1140	249	327	15.78	0.002

Water chemistry data from July 2009 from the monitored lakes in Old Crow Flats																		
OCF Lake	NH3	pH	SPCOND	Alk	Cl	SO4	DOC	DIC	Ca	Mg	K	Na	SiO2	TN	TDP	TP	Chl-a	Surface Area
	µg/L		µS/cm	mequiv./L	mg/L	mg/L	mg/L	mg/L	mg/L	mg/L	mg/L	mg/L	mg/L	µg/L	µg/L	µg/L	µg/L	km ²
1	93	8.56	148	61.3	0.25	11.6	11.9	13.1	19	5.75	1.85	1.3	0.72	896	8.4	17.3	1.62	3.901
2	42	9.84	124	56.5	0.24	6.88	9.1	9	10.8	7.91	1.11	1.79	0.37	685	7.9	12.9	1.07	7.785
3	45	7.34	74.3	26.6	0.28	2.08	31	5.8	11.3	2.66	1.25	0.51	2	1070	9.5	14.5	1.50	0.009
4	64	8.33	165	79.2	0.3	4.66	13.3	17.6	19.5	8.31	1.03	1.43	0.42	776	8.9	17.9	1.25	0.226
6	121	9.03	252	75.7	0.42	51.4	16.3	15.2	27.7	13.3	2.52	2.75	0.79	1280	21.1	53.3	2.43	5.005
7	46	7.64	71.4	31	0.21	1.84	13.1	7.1	8.69	2.98	1.48	1.13	1.13	563	18.1	40.7	2.04	10.116
8	41	9.56	92.2	44.5	0.15	1.33	13.8	7.1	10.4	4.1	0.73	2.07	0.29	690	12	14.4	0.70	0.283
9	41	8.76	131	66.8	0.18	1.17	11.6	14	16.5	5.98	0.8	1.62	0.19	605	8.9	14.3	0.86	0.847
10	158	8.38	94.7	45.5	0.21	1.34	18.2	8.7	11.7	3.79	0.94	2.21	1.35	1220	24.9	49.9	0.67	0.710
11	101	7.48	54.3	21.2	0.1	0.75	20.2	4.5	6.35	2.12	1.32	1.39	0.35	866	41.8	67.2	2.41	0.071
12	74	10	140	71.3	0.2	0.5	18	9.9	12.7	7.33	1.61	6.19	0.32	1200	16.7	27.3	5.46	0.650
13	141	6.84	50.2	22.6	0.07	0.09	37	4.6	7.82	2.53	0.39	0.52	2.93	973	49.5	67.6	9.03	0.023
14	70	9.13	102	52.1	0.19	0.25	14.4	9.7	12.5	5.05	0.26	1.62	0.27	843	9.1	21.2	3.36	0.481
15	61	9.63	91	42.8	0.12	1.88	11	6.6	10.1	4.33	1.38	0.86	0.35	770	8.4	16.2	2.08	6.909
16	52	8.8	145	64.7	0.21	8.68	15	13.3	21.6	5.03	0.24	1.54	0.98	647	19.8	12	0.44	0.978
18	72	9.09	104	52.8	0.18	0.43	12.4	10.1	14.8	3.63	0.51	1.17	0.16	846	12	24	0.39	0.271
19	54	9.78	166	59.6	0.12	20.9	14.7	9.6	15.9	9.27	3.47	1.88	1.4	872	12.4	20.7	2.40	0.106
20	64	8.9	135	69.2	0.15	0.25	17.5	14.3	18.9	5.83	0.68	1.19	0.33	797	9	19.4	1.40	0.277
21	86	7.35	46.9	17.8	0.17	0.04	21.6	4.1	6.1	1.96	0.56	0.92	0.5	857	21	34.6	2.59	0.159
22	51	7.48	54.9	23.4	0.14	0.1	16.8	5.4	6.1	2.71	1.06	0.52	0.55	594	13	21.3	4.08	0.016
23	39	6.4	23.5	6.61	0.1	0.1	23.6	1.6	2.5	1.12	0.51	0.33	0.52	557	7.8	12.9	0.77	0.005
24	70	7.38	42	18.9	0.12	0.05	13.6	4.4	5.68	1.7	0.21	0.28	0.22	821	8.4	17.9	1.22	1.220
25	117	6.03	30.4	9.11	0.05	0.31	43.1	1.4	4.14	1.73	0.6	0.33	3.18	970	33.1	74.7	5.11	0.011
26	62	7.1	32.3	11.1	0.12	0.19	17.5	2.9	4.25	1.42	0.43	0.37	0.28	620	16.9	29	1.83	0.423
28	169	8.03	120	58.7	0.33	2.4	17.6	12.6	14.9	5.68	0.69	1.51	1.04	1030	17.5	119	5.69	7.999

29	50	9.54	117	57.5	0.17	3.57	8.1	10.2	12	7.17	0.04	1.33	0.36	594	7.34	17.8	0.71	6.858
30	103	7.86	131	59.1	0.1	5.9	19.4	13.2	19.2	5.11	0.76	0.89	0.33	879	8.5	73.5	4.89	0.085
31	101	8	135	59.8	0.12	5.89	18.9	12.9	19.5	5.07	0.79	0.93	0.31	844	9.2	24.5	12.40	0.062
32	120	6.86	29	10.2	0.19	0.4	19.1	2.1	4.04	1.18	0.32	0.6	0.9	626	29.9	50.6	8.03	0.282
33	92	8.49	160	77.3	0.33	4.6	16.9	16.7	21	7.6	1.8	0.92	0.29	845	8.1	28.9	3.03	0.679
34	70	9.12	158	75.7	0.48	6.79	11	16.1	19.5	7.37	2.89	1.11	0.45	759	9.9	19.4	2.39	6.108
35	66	8.17	181	80.2	0.32	9.36	20.6	18.4	24.2	7.76	2.28	0.98	0.23	906	13.5	20.2	1.09	0.135
36	68	9.41	147	69.9	0.19	5.62	15.9	12.9	16.3	8.78	0.81	1.78	0.22	903	9.5	21.5	1.40	1.124
37	87	8.94	139	61.5	0.22	9.18	12.8	12.2	15.8	7.3	0.91	1.51	0.28	850	10.6	24.8	1.24	5.143
38	39	8.17	189	80.1	0.64	15.1	6.7	18.7	28.9	5.33	1.96	0.95	0.37	361	6.1	15.2	0.96	12.670
40	80	9.36	94.3	50.8	0.24	0.93	12.3	8.6	13	3.68	0.6	1.07	0.53	881	6.9	48.6	7.26	2.750
41	111	7.55	85.1	35.1	0.4	1.29	21.1	8.2	10.2	3.57	2.55	1.13	1.14	879	13.5	29.7	1.33	0.056
45	49	8.83	162	60.1	0.13	20.6	12.3	12.3	27.8	3.02	0.23	0.39	1.24	658	9.2	21	7.09	0.127
46	44	10.1	149	56.1	0.14	13.1	19.8	7.9	19.4	6.6	0.1	1.52	0.39	1050	17.3	33.3	4.45	0.122
47	72	7.85	76.8	35.5	0.18	0.27	14.5	7.9	11	2.61	0.82	0.58	0.21	785	6.5	12.5	1.61	0.044
48	124	9.65	151	78.2	0.16	0.28	8.9	14	10.6	6.45	1.33	12.2	5.42	826	45	67.5	1.91	1.305
49	75	9.36	156	65	0.28	14.5	12.4	11.8	15	9.64	0.87	1.84	0.56	822	7.4	24.4	4.73	1.148
52	43	9.63	103	52.1	0.04	0.52	20.7	7.4	18	3.63	0.08	0.28	0.85	798	12.3	23.7	1.56	0.032
53	40	8.04	122	60.6	0.34	0.04	14.6	13.4	15.7	5.55	1.51	0.94	0.76	582	6	12	1.50	0.044
54	24	7.75	86.8	38.9	0.27	0.41	21.4	8.4	14.4	2.58	1.11	0.4	0.68	629	11.1	17.5	2.91	0.355
55	101	7.07	44	14.8	0.12	0.45	24.9	3.4	5.75	2.11	0.96	0.37	0.66	922	18	36.5	3.04	0.020
56	174	6.91	70.7	32	0.13	0.17	25.6	7.5	10.2	2.44	1.39	0.38	1.68	1140	107	291	1.82	0.002
57	37	7.87	104	49.1	0.38	0.04	15.7	11	15.3	3.05	1.23	0.92	2.89	693	7.3	13.3	1.82	0.050

Appendix C

Percent abundances of the diatom taxa on artificial-substrate samplers deployed in and retrieved in 2008 from lakes of the Old Crow Flats and sufficiently abundant to meet the criterion for inclusion in numerical analyses.

OCF Lake	AchMin	BraMic	CocLin	EreMin	EreObs	EpiAdn	EpiGib	EunBil	EunSub	FraCop	FraTen	GomAcu	GomAjf	GomAng	GomThu	GompCal	NavCrc	NavCrm	NavRad	NitPol	NitSpp	NupPen	RosPlus
1	73.0	0.0	5.5	0.0	0.0	0.0	0.0	2.3	0.0	0.0	0.0	0.0	16.6	0.0	0.0	0.0	1.2	0.0	0.0	0.0	0.0	0.0	0.0
6	81.6	8.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.8	1.5	0.0	2.1	1.5	0.0	0.0	0.0	0.0	0.0	0.0
8	6.7	0.0	53.1	0.0	0.0	4.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	34.4	0.0	0.0	0.0	0.0	0.0	1.2	0.0	0.0	0.0
9	56.0	13.5	1.8	0.0	0.0	0.0	1.2	0.0	0.0	0.0	0.0	0.0	0.0	24.6	0.0	0.0	1.8	0.0	0.0	0.0	1.2	0.0	0.0
10	30.6	0.0	11.7	0.0	0.6	1.8	0.0	0.0	0.0	6.0	0.0	0.0	0.0	19.5	4.2	0.0	0.0	0.0	0.6	11.7	0.0	0.0	0.0
11	10.2	0.0	44.6	0.0	0.6	9.0	0.0	0.0	0.0	0.0	0.0	1.7	0.0	9.6	0.0	0.0	1.4	0.0	0.8	7.1	0.0	0.6	0.0
13	4.7	0.0	0.0	5.6	0.0	0.0	0.0	11.9	5.0	1.3	0.0	0.9	0.0	7.8	0.0	0.0	0.0	0.0	0.0	7.8	0.0	0.0	31.0
15	45.7	10.9	3.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	38.1	0.0	0.0	0.0	0.0	0.0	1.5	0.0	0.0	0.0
16	21.9	0.0	45.2	0.0	0.0	2.8	1.1	0.0	0.0	1.7	0.0	1.1	0.0	7.3	0.3	1.1	0.0	0.0	1.1	4.5	4.5	2.0	0.0
18	30.0	1.9	33.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	31.0	0.0	0.0	0.0	0.0	0.0	2.5	0.0	0.0	0.0
20	44.9	0.0	3.9	0.0	0.0	1.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	40.4	0.0	0.0	0.0	0.0	0.0	1.2	5.1	1.8	0.0
21	58.8	0.0	1.0	0.0	0.0	0.0	0.0	0.0	2.1	1.6	0.0	0.0	0.0	13.7	0.0	0.0	0.0	0.8	0.0	1.3	0.0	0.0	16.6
22	51.3	0.0	0.0	4.1	0.0	0.0	0.0	0.9	0.9	3.1	0.0	1.3	0.0	5.3	0.9	0.0	0.0	2.5	2.5	7.9	0.0	7.9	1.6
24	90.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	9.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
26	17.8	0.0	0.0	2.4	0.0	0.0	0.0	0.0	0.0	11.5	5.3	0.0	0.9	1.5	0.0	0.0	0.0	0.0	0.0	10.1	0.0	7.1	3.6
27	42.9	0.0	0.9	0.9	0.0	0.0	0.0	0.0	0.0	1.1	1.3	0.0	0.0	49.4	0.0	1.1	0.0	0.9	0.0	0.0	0.0	0.0	0.0
28	50.3	0.0	3.5	0.0	0.3	0.8	0.0	0.0	0.0	0.0	0.8	0.0	0.0	42.4	0.5	0.0	0.5	0.0	0.0	0.3	0.0	0.0	0.0
29	77.2	0.0	0.9	0.9	0.0	0.9	0.0	0.0	0.0	1.6	0.0	0.0	0.0	13.4	1.9	0.0	0.0	0.0	0.0	1.3	1.9	0.0	0.0
30	62.3	0.0	8.7	0.0	0.0	0.0	1.2	0.0	0.0	0.0	0.0	0.0	0.0	5.1	0.0	0.0	1.5	0.0	0.9	1.8	0.0	0.0	0.0
31	67.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	10.0	0.0	0.9	0.0	3.6	3.6	0.0	0.0	0.0	1.2	10.6	0.0	0.0	0.0
32	40.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	19.4	0.0	0.0	0.0	2.5	0.0	0.0	0.0	0.0	0.0	2.8	0.0	0.0	0.0
37	32.1	0.0	4.8	0.0	0.0	0.0	0.0	0.0	0.0	2.4	0.0	0.0	0.0	57.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.0	0.0
39	63.2	0.0	5.2	0.0	0.0	0.0	0.0	0.0	0.0	0.8	0.0	0.0	0.0	25.3	0.0	1.1	1.6	0.0	0.0	1.9	0.0	0.0	0.0
40	43.3	0.0	6.9	0.0	0.0	0.0	0.0	0.0	0.0	8.1	0.0	0.0	0.0	14.6	12.5	0.0	0.0	2.5	0.0	12.1	0.0	0.0	0.0
41	27.0	0.0	2.4	2.4	1.9	3.5	9.5	0.0	3.2	4.9	1.6	4.1	0.0	18.4	0.8	0.0	0.0	0.8	1.9	11.1	0.0	0.0	0.0
42	45.5	0.0	6.6	0.9	3.3	2.7	0.9	0.0	0.0	4.2	0.0	0.0	0.0	15.0	0.0	0.0	3.6	0.9	0.9	12.6	0.0	0.0	0.0
44	47.9	0.0	6.5	0.0	1.1	1.1	0.0	0.0	0.0	1.1	0.0	1.1	0.0	31.5	0.0	2.3	0.8	0.0	0.8	2.0	0.0	0.0	0.0
45	57.3	0.0	10.6	0.0	0.0	3.1	2.5	0.0	0.0	1.9	0.0	2.2	0.0	11.8	1.6	0.6	2.5	0.0	0.0	0.0	0.0	0.0	0.0
48	1.2	0.0	92.6	0.0	0.0	2.8	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.5	0.0	0.0	0.0
49	65.5	0.0	1.3	0.8	0.0	0.0	0.0	0.0	0.0	0.8	0.0	0.0	0.0	19.2	0.8	5.1	0.0	1.5	0.0	0.0	0.0	2.8	0.0
52	66.0	0.0	5.0	0.0	0.0	6.2	0.0	0.0	0.0	0.3	0.0	4.1	0.0	5.3	2.3	0.9	0.9	2.3	0.0	1.2	0.0	0.0	0.0
54	52.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.9	0.0	0.0	0.0	1.5	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
56	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.9	0.0	0.0	0.0	0.0	0.0	98.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

OCT Lakes	SeiLae	SeiPup	StoCon	StoPin	TobFen	TobFloBil	TobFloN	UlnUln
1	0.0	0.0	0.0	1.5	0.0	0.0	0.0	0.0
6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
10	0.9	3.0	7.2	0.0	0.0	0.9	0.0	1.2
11	4.8	0.0	0.0	4.0	0.0	0.0	0.0	0.0
13	0.0	7.2	0.0	0.0	5.0	4.1	6.6	0.0
15	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
16	0.0	1.7	0.0	1.1	0.0	0.0	1.7	0.8
18	0.0	1.2	0.0	0.0	0.0	0.0	0.0	0.0
20	0.0	1.2	0.0	0.0	0.0	0.0	0.0	0.0
21	0.0	0.0	1.8	0.0	0.0	0.0	0.0	0.0
22	0.0	0.9	0.0	0.0	0.0	2.8	4.4	1.6
24	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
26	0.0	3.8	9.8	0.0	0.0	0.0	23.1	0.0
27	0.0	0.0	0.0	1.7	0.0	0.0	0.0	0.0
28	0.0	0.0	0.8	0.0	0.0	0.0	0.0	0.0
29	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
30	18.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0
31	0.0	0.0	0.0	1.2	0.0	0.0	1.2	0.0
32	0.0	0.0	0.0	3.4	19.1	0.0	4.0	0.0
37	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
39	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
40	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
41	1.6	2.2	1.6	0.0	0.0	0.0	0.0	0.0
42	0.0	0.6	0.0	0.0	0.0	0.0	0.0	0.0
44	0.0	0.0	0.8	0.0	0.0	0.0	0.0	0.0
45	4.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0
48	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
49	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.3
52	3.5	0.0	0.0	0.0	0.0	0.0	0.0	0.9
54	0.0	0.0	0.0	0.0	33.0	0.0	2.4	2.7
56	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

OCT Lake	SelLoc	SelPup	StatPin	TabPen	TabRoll	TabRollV
1	0.3	0.3	0.0	0.0	0.0	0.0
2	0.0	0.0	0.0	0.0	0.0	0.0
3	0.0	3.7	0.0	0.0	7.1	0.0
4	0.0	0.0	0.0	0.0	0.0	0.0
6	0.0	0.0	0.4	0.0	0.0	0.0
7	0.0	5.7	0.0	0.0	0.0	0.0
8	0.0	0.0	0.0	0.0	0.0	0.0
9	0.0	0.0	0.0	0.0	0.0	0.0
10	0.0	0.0	0.0	0.0	0.0	0.0
11	6.2	0.7	0.0	0.0	0.0	0.0
12	0.0	0.0	0.0	0.0	0.0	0.0
13	0.0	0.0	0.0	0.0	3.9	0.0
14	0.0	3.7	0.9	0.0	0.0	0.0
15	0.0	0.0	0.0	0.0	0.0	0.0
16	0.0	1.6	0.3	0.0	0.0	0.0
18	0.0	0.0	0.0	0.0	0.0	0.0
19	0.0	1.9	0.0	0.0	0.0	0.0
20	0.0	0.0	0.0	0.0	0.0	0.0
21	0.0	0.0	0.0	0.0	0.0	0.0
22	0.0	0.0	0.0	3.5	0.0	0.0
23	0.0	0.0	0.0	0.0	10.5	0.0
24	0.0	0.0	0.0	0.3	0.0	0.0
25	0.0	0.0	0.0	16.1	0.0	0.0
26	0.0	0.0	5.1	0.0	1.9	38.7
28	0.0	0.0	0.0	0.0	0.0	0.0
29	0.0	0.0	0.0	0.0	0.0	0.0
30	0.0	0.0	0.0	0.0	0.0	0.0
31	0.0	0.0	0.0	0.0	0.0	0.3
32	0.0	0.0	0.0	4.3	0.0	14.0
33	0.0	0.0	0.0	0.0	0.0	0.0
34	0.0	0.0	0.0	0.0	0.0	0.0
35	0.0	0.0	0.0	0.0	0.0	0.2
36	0.0	0.0	0.0	0.0	0.0	0.0
37	0.0	0.0	0.0	0.0	0.0	0.0
38	0.0	0.0	0.0	0.0	0.0	0.0
40	0.0	0.0	0.0	0.0	0.0	0.0
41	0.0	0.0	2.7	0.0	0.0	0.0
45	0.0	0.0	0.3	0.0	0.0	0.0
46	0.0	0.0	0.0	0.0	0.0	0.0
47	0.0	0.0	0.0	0.3	0.0	0.0
48	0.0	0.0	0.0	0.0	0.0	0.0
49	0.0	0.0	0.0	0.0	0.0	0.0
52	0.0	0.0	0.0	0.3	0.0	0.0
53	0.0	0.0	0.9	0.0	1.9	0.0
54	0.0	0.0	0.0	0.0	5.6	0.0
55	0.0	0.0	0.9	0.0	2.6	2.0
56	0.3	0.0	0.0	0.0	0.0	1.2
57	0.0	0.3	0.0	0.3	0.0	0.0

OCF49-08	65.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.3	1.0	0.0	0.0	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.8	0.0	0.0	0.0	0.0	19.2
OCF49-09	83.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	12.8	
OCF49-10	40.8	0.0	0.0	0.0	0.0	3.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.9	0.0	2.0	0.0	49.0	
OCF49-11	79.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.8	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.1	0.0	0.0	0.0	13.7	
OCF49-12	79.9	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.9	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	15.0		
OCF49-13	80.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.0	0.9	0.0	16.2		
OCF49-14	73.2	0.0	0.0	0.0	0.0	0.6	0.0	0.0	1.1	0.8	0.0	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	19.5		
OCF49-16	80.8	0.0	0.0	0.0	0.0	1.7	0.0	0.0	0.0	0.0	0.3	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	13.8		
OCF49-18	76.1	0.0	0.0	0.6	0.0	0.3	0.0	0.3	0.9	0.3	0.0	8.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	9.6		
OCF49-19	82.7	0.0	0.0	0.3	0.0	5.3	0.0	0.6	0.3	0.6	0.0	0.9	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.4		
OCF55-09	37.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.3	0.0	0.0	0.0	4.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.3	0.9	0.0	0.0	2.3	0.0	0.0	1.4	0.9		
OCF55-10	31.3	0.5	0.0	0.0	0.0	2.8	0.0	0.0	0.0	0.0	0.0	0.0	3.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.1	11.9	0.0	0.0	0.0	0.0	2.3	0.0	4.4	4.7		
OCF55-11	86.3	0.0	0.0	0.0	0.0	2.7	0.0	0.0	2.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.2	0.0	3.0			
OCF55-12	59.6	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	1.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.1	0.9	0.0	0.0	0.6	0.0	2.3	0.0	2.6			
OCF55-13	61.9	0.0	0.3	0.0	0.0	4.6	0.0	0.0	0.0	0.0	0.0	0.0	1.5	0.0	0.0	0.6	0.0	0.0	0.0	0.0	0.6	3.1	0.0	0.0	0.0	0.0	0.6	0.0	0.9			
OCF55-14	44.4	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	1.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.6	6.9	0.0	0.0	6.3	0.0	2.6	0.0	0.0			
OCF55-16	28.5	0.0	0.0	0.0	0.0	0.6	0.0	0.0	0.0	0.0	1.2	0.0	0.0	5.1	0.0	0.0	0.6	0.0	0.0	0.0	1.8	2.7	0.0	0.0	2.4	0.0	0.3	0.0	1.8			
OCF55-17	34.2	0.0	0.0	0.0	0.0	2.2	0.0	0.0	0.8	0.3	0.0	0.0	0.0	1.4	0.0	0.0	0.0	0.8	0.0	0.0	0.5	1.6	0.0	1.1	3.6	0.0	0.5	0.0	3.3			
OCF55-18	52.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.2	0.0	0.0	0.0	0.0	1.2	0.3	0.0	3.8	10.3	0.0	1.2	0.0	6.9			
OCF55-19	52.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.5	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.6	2.5	0.0	0.0	4.1	0.3	4.1	0.0	5.3			
OCF58-10	43.7	0.9	0.0	0.0	0.0	0.0	0.0	0.0	5.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	6.4	1.5	0.0	0.0	0.0	1.7	0.0	0.9	0.0	6.1			
OCF58-11	42.7	0.0	0.0	0.0	0.0	3.9	0.0	0.0	0.0	0.0	0.0	0.0	3.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.6	0.0	1.8	0.0	0.0	1.5	0.0	3.9			
OCF58-12	82.5	0.0	0.0	0.0	0.0	2.4	0.0	0.0	0.0	0.0	0.0	1.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.1	0.0	11.7			
OCF58-13	71.9	0.0	0.0	0.0	0.0	8.5	0.0	0.0	3.8	1.2	0.0	1.8	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.5	0.0	6.4			
OCF58-14	67.7	0.0	0.0	0.0	0.0	0.3	0.0	0.0	2.3	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.6	0.0	0.0	0.0	21.0			
OCF58-16	42.7	0.0	0.0	0.6	0.0	0.3	0.0	0.0	3.9	0.0	1.2	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.9	0.6	0.0	0.6	0.0	0.0	3.0	0.0	0.6	0.0	30.6			
OCF58-17	82.9	0.0	0.0	1.2	0.0	6.1	0.0	0.0	1.2	0.6	0.0	0.9	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	1.8	0.0	0.3	0.0	1.2				
OCF58-18	60.7	0.0	0.0	0.6	0.0	0.3	0.0	1.6	1.0	0.0	0.0	1.6	0.3	0.3	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.6	1.0	0.0	1.6	0.0	19.8		
OCF58-19	56.2	0.0	0.0	0.6	0.0	0.0	0.0	0.0	3.9	0.0	0.0	1.3	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.6	0.0	0.0	0.0	3.6	0.0	0.3	0.0	0.0	21.8			

Appendix E. Table.2 hydrological data of LTM OCF lakes during Spring and Fall seasons of 2008-2018

Site	Spring data		Fall data	
	$\delta^{18}\text{O}_l$	EI	$\delta^{18}\text{O}_l$	EI
OCF06-08	-21.34559	0.49	-18.198	1.057
OCF06-09	-24.22149	0.35	-20.229	0.492
OCF06-10	-21.43167	0.78	-16.786	0.728
OCF06-11	-23.2634	0.52	-17.266	0.746
OCF06-12	-23.91531	0.39	-19.576	0.881
OCF06-13	-23.8739	0.36	-19.234	0.589
OCF06-14	-23.04325	0.42	-20.642	0.887
OCF06-16	-21.84974	0.33	-19.669	0.501
OCF06-17	-21.35796	0.41	-18.977	0.650
OCF06-18	-20.28354	0.4	-18.484	0.475
OCF06-19	-21.70848	0.31	-19.025	0.565
OCF11-08	-26.48231	0.09	-24.806	0.501
OCF11-09	-24.93783	0.06	-23.609	0.276
OCF11-10	-24.27133	0.21	-21.922	0.266
OCF11-11	-25.67908	0.1	-23.721	0.479
OCF11-12	-26.93532	0.1	-25.236	0.553
OCF11-13	-27.02517	0.14	-23.792	0.477
OCF11-14	-24.7389	0.23	-23.656	0.678
OCF11-16	-23.19384	0.08	-21.586	0.273
OCF11-17	-25.33293	0.18	-21.109	0.105
OCF11-18	-23.19113	0.16	-20.580	0.294
OCF11-19	-24.84696	0.1	-22.741	0.519
OCF19-08	-25.65833	0.78	-22.760	1.089
OCF19-09	-23.73644	0.48	-23.853	0.738
OCF19-10	-24.54249	0.72	-22.918	0.850
OCF19-11	-22.59381	0.47	-22.061	0.787
OCF19-12	-24.78263	0.52	-22.659	0.675
OCF19-13	-23.09696	0.37	-21.323	0.557
OCF19-14	-24.25887	0.58	-21.852	0.584
OCF19-16	-22.07985	0.42	-21.333	0.493
OCF19-17	-22.30247	0.43	-20.609	0.572
OCF19-18	-21.43905	0.45	-20.102	0.478
OCF19-19	-21.66369	0.37	-20.597	0.520
OCF26-08	-25.20795	0.23	-24.469	0.368
OCF26-09	-25.04148	0.21	-23.647	0.228

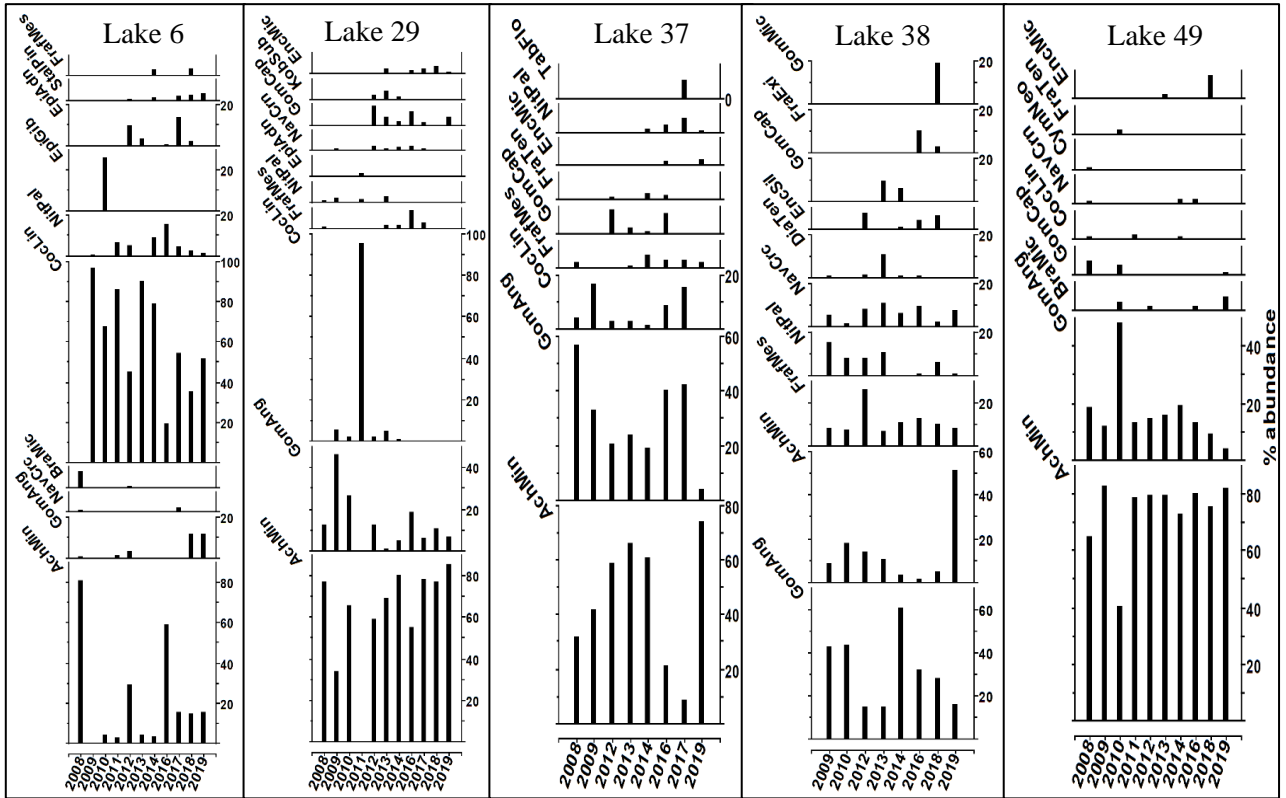
OCF26-10	-23.39672	0.21	-22.151	0.288
OCF26-11	-23.41853	0.19	-22.213	0.255
OCF26-12	-23.72264	0.17	-23.998	0.372
OCF26-13	-24.40545	0.2	-23.074	0.336
OCF26-14	-23.48103	0.21	-22.526	0.356
OCF26-16	-23.24585	0.16	-21.851	0.261
OCF26-17	-22.74227	0.15	-21.438	0.271
OCF26-18	-21.88312	0.17	-20.821	0.229
OCF26-19	-22.70499	0.15	-21.152	0.328
OCF29-08	-21.32858	0.41	-20.279	0.595
OCF29-09	-22.04167	0.37	-21.987	0.536
OCF29-10	-21.41074	0.41	-20.170	0.650
OCF29-11	-20.82654	0.38	-20.070	0.581
OCF29-12	-23.19937	0.5	-21.276	0.654
OCF29-13	-21.6104	0.39	-19.545	0.480
OCF29-14	-21.26632	0.37	-20.217	0.490
OCF29-16	-20.49886	0.31	-19.746	0.430
OCF29-17	-20.6084	0.36	-18.894	0.485
OCF29-18	-19.48621	0.36	-18.403	0.415
OCF29-19	-19.86326	0.31	-18.175	0.451
OCF34-08	-22.27489	0.32	-21.967	0.552
OCF34-09	-23.7296	0.41	-20.999	0.341
OCF34-10	-22.93463	0.43	-20.779	0.532
OCF34-11	-21.39545	0.3	-21.023	0.527
OCF34-12	-22.37418	0.32	-21.580	0.501
OCF34-13	-22.53259	0.32	-20.902	0.422
OCF34-14	-21.92679	0.33	-20.636	0.422
OCF34-16	-21.31224	0.26	-20.251	0.362
OCF34-17	-21.13478	0.29	-19.236	0.371
OCF34-18	-19.94511	0.28	-19.496	0.418
OCF34-19	-20.23917	0.25	-18.934	0.368
OCF35-08	-23.97618	0.32	-23.069	0.658
OCF35-09	-24.5306	0.29	-23.176	0.406
OCF35-10	-24.32449	0.49	-21.293	0.567
OCF35-11	-24.1564	0.32	-21.685	0.532
OCF35-12	-25.73184	0.38	-23.700	0.676
OCF35-13	-24.23671	0.32	-21.765	0.411
OCF35-14	-22.7688	0.29	-21.843	0.534
OCF35-16	-22.15659	0.28	-20.433	0.412
OCF35-17	-22.64089	0.35	-19.261	0.437

OCF35-18	-21.29346	0.29	-20.066	0.388
OCF35-19	-21.91118	0.27	-19.735	0.487
OCF37-08	-22.58578	0.51	-21.660	0.782
OCF37-09	-22.45236	0.43	-20.857	0.451
OCF37-11	-21.75474	0.44	-20.039	0.643
OCF37-12	-23.76818	0.48	-22.237	0.670
OCF37-13	-22.31058	0.38	-20.879	0.533
OCF37-14	-22.28497	0.39	-20.501	0.443
OCF37-16	-21.71326	0.34	-20.346	0.409
OCF37-17	-21.23657	0.36	-19.338	0.518
OCF37-18	-20.1285	0.34	-19.496	0.502
OCF37-19	-21.11505	0.3	-19.289	0.442
OCF38-08	-22.69804	0.4	-21.016	0.511
OCF38-09	-22.89272	0.3	-21.903	0.349
OCF38-10	-22.09492	0.25	-22.871	0.258
OCF38-11	-22.00194	0.2	-21.430	0.404
OCF38-12	-23.03427	0.25	-21.919	0.209
OCF38-13	-23.25953	0.18	-22.815	0.380
OCF38-14	-23.17387	0.19	-22.031	0.295
OCF38-16	-22.47407	0.1	-21.454	0.131
OCF38-17	-21.94049	0.15	-19.840	0.340
OCF38-18	-20.94721	0.23	-20.194	0.297
OCF38-19	-21.36319	0.19	-20.539	0.219
OCF46-08	-26.42971	0.67	-19.604	0.954
OCF46-09	-24.18247	0.33	-22.924	0.462
OCF46-10	-24.07582	0.5	-18.719	0.671
OCF46-11	-24.13306	0.41	-20.640	0.687
OCF46-12	-24.77528	0.27	-22.284	0.703
OCF46-13	-24.94173	0.23	-22.296	0.532
OCF46-14	-24.09557	0.23	-21.478	0.415
OCF46-16	-21.60702	0.31	-20.284	0.352
OCF46-17	-22.01789	0.36	-17.771	0.498
OCF46-18	-21.61492	0.31	-19.526	0.364
OCF46-19	-22.50443	0.19	-19.897	0.437
OCF48-08	-24.31902	0.16	-23.974	0.144
OCF48-09	-25.76986	0.21	-24.125	0.131
OCF48-10	-24.42506	0.22	-22.929	0.347
OCF48-11	-24.11341	0.16	-23.910	0.142
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OCF48-13	-23.67081	0.06	-23.764	0.047

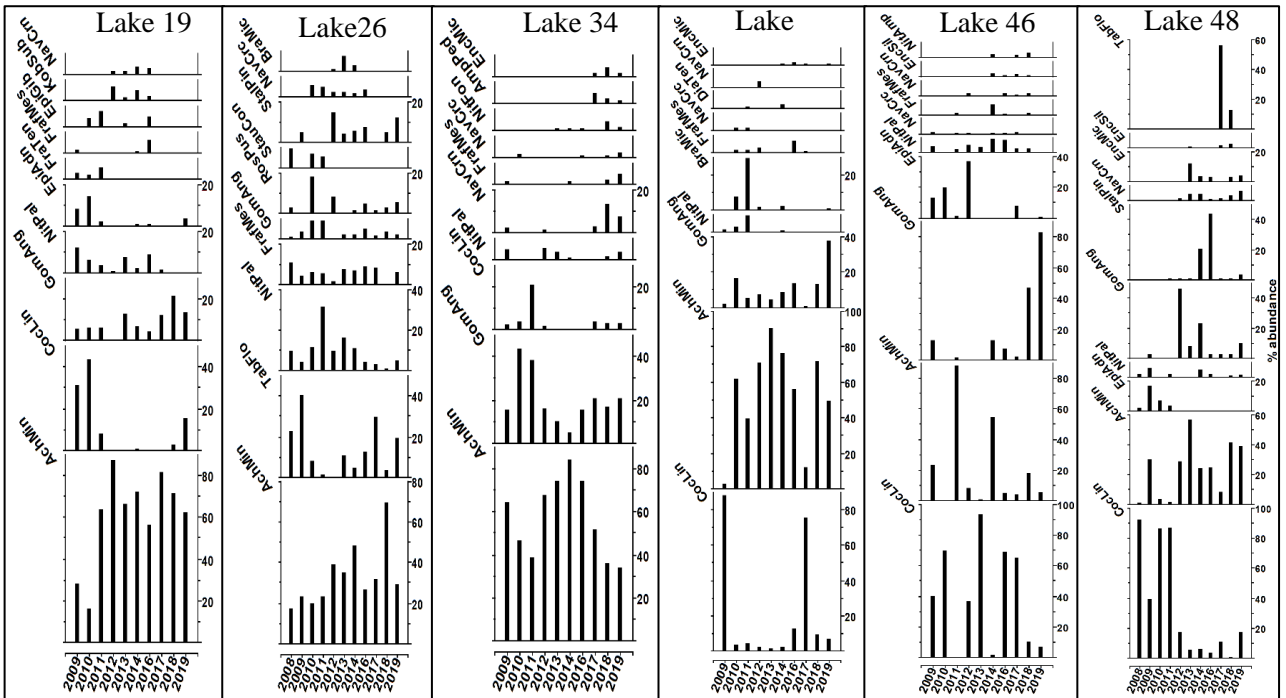
OCF48-14	-23.95483	0.15	-23.692	0.071
OCF48-16	-23.45079	0.12	-23.526	0.055
OCF48-17	-24.1816	0.08	-23.456	0.062
OCF48-18	-23.76611	0.08	-23.522	0.050
OCF48-19	-23.83274	0.1	-23.640	0.062
OCF49-08	-22.45705	0.56	-21.478	0.778
OCF49-09	-23.03548	0.56	-21.560	0.558
OCF49-10	-21.87027	0.51	-19.835	0.652
OCF49-11	-20.46787	0.44	-21.474	0.896
OCF49-12	-24.46623	0.62	-21.681	0.653
OCF49-13	-22.38074	0.44	-22.683	0.767
OCF49-14	-22.28877	0.43	-21.499	0.578
OCF49-16	-21.47522	0.4	-20.579	0.517
OCF49-17	-21.32569	0.45	-19.187	0.581
OCF49-18	-20.31248	0.45	-18.959	0.549
OCF49-19	-20.90482	0.4	-19.566	0.517
OCF55-08	-25.46839	0.14	-25.513	0.227
OCF55-09	-25.77126	0.12	-24.393	0.150
OCF55-10	-25.72262	0.23	-23.507	0.201
OCF55-11	-25.6883	0.07	-25.129	0.147
OCF55-12	-26.69347	0.13	-24.651	0.114
OCF55-13	-26.32624	0.09	-25.591	0.127
OCF55-14	-25.24514	0.14	-24.236	0.157
OCF55-16	-24.32957	0.09	-23.398	0.129
OCF55-17	-24.02957	0.09	-22.803	0.128
OCF55-18	-22.63282	0.12	-21.851	0.139
OCF55-19			-23.435	0.137
OCF58-08			-23.573	0.780
OCF58-09	-22.52173	0.44	-23.054	0.579
OCF58-10	-23.89706	0.66	-22.181	0.576
OCF58-11	-22.70235	0.41	-24.166	0.696
OCF58-12	-26.64494	0.68	-23.364	0.589
OCF58-13	-22.4259	0.4	-22.668	0.602
OCF58-14	-22.37895	0.43	-22.333	0.561
OCF58-16	-22.72121	0.36	-21.802	0.441
OCF58-17	-22.28757	0.39	-20.870	0.492
OCF58-18	-21.02255	0.43	-20.246	0.477
OCF58-19	-21.17384	0.37	-20.480	0.506

Appendix F:

a: Rainfall dominated lakes



b: Intermediate lakes



c: Snowmelt dominated lakes

Horizontal bar graphs showing the percent abundances of the most common diatom taxa accrued on artificial substrate periphyton samplers retrieved from the 14 selected OCF lakes during the long-term period which extended from 2008 to 2019.

panel a = rainfall-dominated lakes.
 panel b = intermediate lakes.
 panel c = snowmelt-dominated lakes.

