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ENVIRONMENTAL FACTORS ASSOCIATED WITH BENTHIC MACROINVERTEBRATE  
COMMUNITIES IN ARCTIC LAKES, NORTHWEST TERRITORIES

By

Rachel Shachar Cohen

Honours BSc Environmental Biology, York University, 2017

THESIS

Submitted to the Department of Biology

Faculty of Science

In partial fulfillment of the requirements for the

Master of Science in Integrative Biology

Wilfrid Laurier University

2019

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## ABSTRACT

Lake water quality and the macroinvertebrate communities in Arctic regions are threatened by increased development and climate change. In order to understand how macroinvertebrate communities may respond to their changing environment, I performed a biological and water quality survey of 46 Arctic lakes located in the Gwich'in Settlement Area and the Inuvialuit Settlement Region of the Northwest Territories. Using these survey data, I performed two interrelated studies that asked: 1) how artificial pit lakes associated with gravel extraction for road development compared with natural lakes in terms of their water quality, morphometry, and macroinvertebrate communities; and 2) how water quality changes associated with permafrost thaw might affect macroinvertebrate communities. For both studies, lake morphometry, water quality, and biological data (macroinvertebrates, and fish presence) were collected. In the first study, gravel pit lakes were four times deeper, two times clearer, and five times smaller in their surface area than natural lakes. Additionally, important nutrients, including phosphorus and nitrogen were significantly lower in gravel pit lakes. Although gravel pit lakes differed in morphometry and nutrients, littoral macroinvertebrate communities did not differ significantly between the two lake types. Therefore, I concluded that despite their recent formation and unnatural morphometry, gravel pit lakes can support invertebrate communities typical of natural lakes in the region. For my second study, I developed multiple regression models to explain variation in macroinvertebrate richness, diversity, abundance, and percent sensitive species among lakes ( $R^2 = 0.44-0.63$ ). The most parsimonious models included variables affected by permafrost thaw, including chlorophyll-*a*, total nitrogen, total phosphorus, pH, conductivity, dissolved organic carbon, turbidity, and Secchi depth. Using these regression models, I showed that for every 5% change in variables associated with permafrost thaw,

macroinvertebrate richness and diversity were predicted to increase at a rate of ~ 0.75% and ~2.5%, while total abundance and percent sensitive species were predicted to decrease by ~5% and ~10%, respectively. These results indicate that while richness and diversity may change little in response to water quality changes associated with permafrost thaw, the structure of communities may shift profoundly due to decreases in abundance and the loss of sensitive species. Taken together, my results suggest that while macroinvertebrate communities may benefit from some aspects of development (the creation of pit lakes), other environmental changes related to permafrost thaw are likely to negatively impact these important members of the lower food web.

## **AUTHORSHIP**

Chapter 2 was published in *Arctic, Antarctic, and Alpine Research*, on which the primary author is Jasmina M. Vucic, and I am the second author, followed by other collaborators from York University contributed to.

**My contributions:** Involved in all water quality and macroinvertebrate data collection and analysis, writing, and manuscript review.

**Data overlap within the study presented in the thesis:** Water quality data overlaps with the contributions of Jasmina M. Vucic and Derek Gray.

**Role of Co-authors:** Jasmina M. Vucic (contributed to zooplankton data (not presented herein), water quality data collection, analysis, writing and manuscript review), Derek Gray (contributed to data collection, analysis, writing and manuscript review), Alyssa D. Murdoch (contributed to fish data collection, produced figure 2.1 and manuscript review), Arnab Shuvo (contributed to fish data collection and manuscript review), Sapna Sharma (contributed to manuscript review).

Chapter 3 was submitted to *Freshwater Science*.

## DEDICATION

Dedicated to the memory of my dad, Eli Cohen (לֵרִי), who always believed in me. Your big smile resonates during milestones like these.

## ACKNOWLEDGEMENTS

### *Dr. Derek Gray*

I would like to acknowledge my supervisor, Dr. Derek Gray, for giving me the opportunity to carry out this exciting research, traveling to the Northwest Territories was truly an amazing experience. Your trust for my involvement and leadership in all aspects (the field, lab, and data analysis) of this multi faceted project means a lot to me. Thank you for encouraging me to seek out opportunities to present this research in different formats to the scientific community and the general public. Your support and guidance throughout my master's degree is truly valued.

### *Dr. Joseph Culp and Dr. Robin Slawson*

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### *Oshri Balilti and my family (Grace and Lenore Cohen)*

Thank you to my partner, my mom, and my sister for always being there to make me laugh and put things into perspective when times got hard. Without your love and encouragement I would not be where I am today.

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## CHAPTER 1: LITERATURE REVIEW

### 1.1 Defining characteristics of natural Arctic lakes

Arctic lakes are typically nutrient-poor oligotrophic systems (total phosphorus  $< 10 \mu\text{g/L}$ ; Namayandeh and Quinlan 2011) found in areas that experience a short growing season and often have limited groundwater flow (Rühland et al. 2003). Primary production in Arctic lakes is limited by low nutrient concentrations and a short growing season (Rühland et al. 2003). Low nutrient concentrations in lakes may be explained by the nutrient poor but organically rich runoff they receive annually from the active layer (surface that melts and refreezes each year) (Burn and Kokelj 2009). Therefore, Arctic lakes often have high organic matter, high colouration, and low ionic concentrations and nutrients (Pienitz et al. 1997; Kokelj and Burn 2003; Burn and Kokelj 2009). The low nutrient and ion concentration found in Arctic lakes is not only a result of the composition of the active layer, but is further limited by low runoff and groundwater flow, resulting in reduced production.

Notwithstanding the above generalizations, Arctic lakes vary in morphometry and receive drainage from heterogeneous landscapes, both characteristics act to modify overall water quality characteristics. A variety of lake sizes and depths can be found in Canada's Arctic, but the majority are shallow with a mean depth that ranges between 0.5 m to 4.5 m (Lesack and Marsh 2010) and a maximum depth that can average  $\sim 3.9$  m (Kokelj et al. 2005). However, water levels can vary according to the time of year, local precipitation, and adjacent river and stream water levels (Lesack and Marsh 2010). It is important to consider lake morphometry because lakes that are shallow and smaller in surface area may shift between water clarity states more readily than

larger, deeper lakes. Shallow lakes can exist in two stable states, being either highly turbid or clear, and these states are determined primarily by nutrient availability and the fish community present (Jeppesen et al. 1999). In their turbid state, shallow lakes have higher dissolved organic carbon levels due to wave action, and more phytoplankton and planktivorous fish (Jeppesen et al. 1999). In contrast, lakes that are in their clear state have more macrophytes, zooplankton, and piscivorous fish (Jeppesen et al. 1999). In comparison with shallow lakes, a majority of deep and large lakes are more likely to be oligotrophic since nutrients are not as concentrated, and mixing is constrained to the surface layer which becomes warmer than the cooler deep water beneath it (Gorham and Boyce 1989, Rühland et al. 2003). This stratification causes nutrients to sink to the bottom of the lake making them less available to plankton and algae found in the upper layer of the lake. In these lakes, the different thermal habitats and ecosystems within the stratified layers of the lake may allow a variety of planktivorous and piscivorous fish to thrive (Jeppesen et al. 2005, Guzzo et al. 2016). Overall, morphometry in addition to the availability of nutrients and organic matter play an important role in determining lake water quality.

Lake water quality is not only influenced by lake morphometry, but also by the properties of the watershed associated with each lake. For example, watersheds may be underlain by a variety of surficial deposits and vegetation, especially if they span the tree line that marks the change from boreal to tundra forests (Kokelj et al. 2009). This heterogeneity may cause lakes to vary in their vulnerability to climate drivers and disturbances occurring regionally. For example, Kokelj et al. (2009) found that total organic carbon and ionic concentrations of lakes could be significantly impacted by the surficial geology of their watersheds. Lakes with lacustrine terrain had higher total organic carbon and dissolved organic carbon levels than those with morainal and glaciofluvial deposits (Kokelj et al. 2009). Furthermore, alkalinity, hardness, TDS (total

dissolved solids), and major ions were found to be higher in lakes characterized by morainal and glaciofluvial deposits as opposed to those surrounded by lacustrine terrain (Kokelj et al. 2009). When considering the boreal-tundra transition, Kokelj et al. (2009) found a weak but positive and significant relationship where total organic carbon, dissolved organic carbon,  $\text{Na}^+$ , and  $\text{Cl}^-$  concentrations increased northward across the boreal-tundra transition and towards the Beaufort Sea. Although previous studies with larger latitude gradients confirmed the  $\text{Na}^+$  and  $\text{Cl}^-$  trend, they found that dissolved organic carbon increased southward in the boreal zone (Pienitz et al. 1997, Rühland et al. 2003). Higher nutrient concentrations such as total phosphorus, total nitrogen, and chlorophyll-*a* levels have been found south of the treeline in boreal dominated areas (Pienitz et al. 1997, Rühland et al. 2003). However, in lakes north of the tree line, permafrost degradation was shown to explain more of the variation in water quality than environmental factors such as surficial geology and proximity to the tree line (Kokelj et al. 2009). These differences are driven by climatic patterns that influence permafrost continuity, ice dynamics, and vegetation. Since Arctic freshwater lake characteristics have been shown to be strongly influenced by ice dynamics and permafrost, they may be especially sensitive to even small changes in climate conditions (Vincent and Laybourn-Parry 2008). Taken together, the dependency of Arctic lake water quality on nutrient availability, lake morphometry, and watershed composition creates significant variability in water quality characteristics among lakes. Therefore, Arctic lakes may be highly responsive to environmental changes brought on by climate change and increased development.

## **1.2 Environmental changes in the Arctic**

As a result of recent warming, lake ecosystems are experiencing dramatic changes (Smol and Douglas 2007). A 2000-year reconstruction of Arctic summer temperatures from 14 Arctic lake sediment cores showed that in the last half-century, warming exceeded what would be expected from earth's natural cycles, and in the past few decades, the Arctic warmed at two to three times the rate of the rest of the world (Prowse et al. 2006, Kaufman 2009, AMAP 2012, Meyer et al. 2015, Cohen et al. 2019). In northern Canada, the mean annual temperature has increased by 2.3°C from 1948 to 2016 resulting in a variety of changes to the environment (Cohen et al. 2019).

Some impacts of climate change include increased lake surface water temperatures (Sharma and Magnuson 2014), as well as increases in precipitation and ground surface temperatures, resulting in intensified permafrost thaw (Kokelj et al. 2013, 2015). Lake surface temperatures worldwide have been warming at an average of 0.34°C per decade from 1985 to 2010 (Schneider and Hook 2010, O'Reilly et al. 2015). The greatest lake surface warming is present at high latitudes (Schneider and Hook 2010) where lakes are seasonally ice covered, air temperature and solar radiation are increasing, and cloud cover is decreasing (O'Reilly et al. 2015). In these regions, the average lake surface warming rate is 0.72°C per decade (Schneider and Hook 2010, O'Reilly et al. 2015). As a result of increasing surface temperatures, a decrease in the duration and thickness of ice cover has been noted in Arctic freshwater ecosystems (Magnuson et al. 2000, Duguay et al. 2006, Paquette et al. 2015), and ultimately this may contribute to increased phytoplankton production (Vincent 2009). Warming decreases ice cover duration causing a decrease in albedo (amount of reflected radiation) that is accompanied by an increase in the absorption of solar radiation due to exposure of the darker water surface for a longer period. The increase in absorbed sunlight due to this phenomenon can create an increase

in phytoplankton production (Vincent 2009). In contrast, snow cover on ice may reduce light availability for photosynthesis, impairing the growth of aquatic mosses (Sand-Jensen et al. 1999) and benthic communities (Wrona et al., 2013). Overall, the amount of time which ice covers lakes versus the time that lake water is exposed plays an important role in shaping lake ecosystems.

Global circulation models have predicted that Arctic regions face increases in precipitation and extreme rainfall events over coming decades (Walsh et al. 2011). These extreme rainfall events along with the rising ground temperatures increase the magnitude of permafrost disturbance (Kokelj et al. 2013, 2015). Permafrost is defined as ground that is frozen at or below 0°C for at least two consecutive years (Zhang et al. 1999) and increasing ground temperatures have been causing this ground to thaw (Burn and Kokelj 2009). The intensification of permafrost thaw has been causing increases in sediment loading, surface runoff, and groundwater flow into lakes (Kokelj et al. 2009; Moquin et al. 2014; Houben et al. 2016). Increased permafrost thaw is also responsible for decreasing lake water levels and lake occurrence (Prowse et al. 2006). Due to the variety of factors that play into lake characteristics, the effects of climate change on lakes are lake specific as they experience differences in evaporation and precipitation rates based on their location and morphometry (Plug et al. 2008).

While the environmental impacts of climate change are expected to be significant on a longer-term scale, the impact of construction and development present a short-term environmental threat that is also important. There is increasing demand for construction and road development to accommodate population growth in northern Canada (Prowse et al. 2009, Gunter 2017). Development of the landscape has been shown to alter water quality and influence biological communities at different levels of the aquatic food web (Dixit et al. 2000, Schindler

and Smol 2006, Laske et al. 2016, Gunter 2017, Busch et al. 2018). For example, differences in water chemistry and diatom communities were noted by Gunter (2017) as a result of calcareous road dust in the Mackenzie Delta Region. Construction may also further exacerbate permafrost thaw through clearing vegetation and increasing ground temperatures (Prowse et al. 2009). However, while the process of construction may destroy habitat, it may also create new opportunities for aquatic organisms. For example, the excavation of materials for highway construction and maintenance creates gravel pits, which often turn into artificial lakes when they fill with rain and groundwater (Gammons et al. 2009, Schultze et al. 2010, Blanchette and Lund 2016, Søndergaard et al. 2018, Vucic et al. 2019). In this thesis, first, I investigate short term impacts of development by comparing the water quality and macroinvertebrate communities of roadside natural lakes and gravel pit lakes. Second, I investigate the potential long-term impacts of changing water quality due to permafrost thaw on macroinvertebrate communities. The following introductory sections will discuss the findings of previous studies on changes in water quality and biological characteristics of lakes that are associated with climate driven permafrost thaw, and discuss previous studies conducted on artificial gravel pit lakes.

### **1.2.1 Defining the impacts of permafrost thaw on lakes**

16% of waterbodies ( $> 0.1 \text{ km}^2$ ) in the Arctic are located in areas that are underlain by permafrost (Lehner and Döll 2004; Vonk et al. 2015). The extent to which permafrost thaw impacts waterbodies may vary according to the continuity of permafrost that differs across Arctic and Antarctic regions. The majority of permafrost in the Northern Hemisphere occurs between  $60^\circ\text{N}$ - $68^\circ\text{N}$  and 37% of Northern Hemisphere permafrost is located in western North America between longitudes of  $60^\circ\text{W}$  and  $165^\circ\text{W}$  (Zhang et al. 1999). The distribution of permafrost



becomes increasingly patchy in lower latitudes of this range keeping with the warmer climates. The changes in permafrost distribution are described by categories of continuous, discontinuous, sporadic, and isolated permafrost (Zhang et al. 1999; Figure 1.1). In the continuous permafrost zone, permafrost covers 90-100% of the available area, while in the discontinuous permafrost zone, the distribution of permafrost is patchy, covering 50-90% of the ground (Zhang et al. 1999). As a result, environments within the continuous permafrost may experience stronger impacts of permafrost thaw, especially since warming in this zone is occurring at a greater rate than in more southern regions (Kaufman 2009).

The impacts of permafrost thaw on lakes are not globally cohesive and vary according to the local soil composition and regional permafrost extent. Specifically, permafrost thaw has been shown to have contrasting impacts on lake occurrence patterns, size (Smith et al. 2005), and water quality (Kokelj et al. 2009) in different regions. For example, in Siberia, where permafrost distribution is continuous, total lake area has increased by 12% and an additional 49 lakes were observed from 1973 to 1998 (Smith et al. 2005). The net growth of lakes in continuous permafrost zones contradicts the pattern seen in discontinuous permafrost zones. In discontinuous zones, there was a net decline in total lake number and area which have outpaced lake gains in more northern continuous permafrost zones overall (Smith et al. 2005).

While permafrost thaw is playing a role in changing the occurrence of lakes, it is also changing the quality of water in existing lakes (Kokelj et al. 2009, Thienpont et al. 2013, Moquin et al. 2014, Houben et al. 2016). Local soil conditions, such as soil composition and permeability, can impact how permafrost thaw influences water quality. One important attribute that determines how water quality may be impacted by permafrost thaw is whether organic or mineral soil is exposed as permafrost degrades (Vonk et al. 2015b). For example, thaw slumping

into lakes in Alaska has resulted in increases of dissolved organic nutrients due to permafrost thaw exposing and delivering organic soils (Abbott et al. 2014). While in other areas within Québec, and the Northwest Territories, slumping increased the delivery of inorganic particles causing decreases in dissolved organic carbon concentrations (Kokelj et al. 2005, Bouchard et al. 2013). Shallow slump impacted lakes in the western Canadian Arctic for example, contain lower total dissolved N and P (Thienpont et al. 2013, Moquin et al. 2014, Houben et al. 2016) which is indicative of the exposed inorganic particles (Vonk et al. 2015b).

In tundra upland lakes east of the Mackenzie Delta region, permafrost degradation was found to be the main driver of water quality degradation (Kokelj et al. 2009). Water quality changes as a result of percent catchment area disturbed by permafrost thaw and thaw slumps (Kokelj et al. 2005; Thienpont et al. 2013; Houben et al., 2016) as well as the activity and presence of thaw slumps (Kokelj et al. 2009; Deison et al. 2012; Moquin et al. 2014) has been widely documented. Slump affected lakes are characterized by greater ion concentrations such as Ca and Mg, lower dissolved organic carbon concentration and colour, as well as increased pH, conductivity, and water clarity in comparison to undisturbed lakes (Kokelj et al. 2005, 2009; Mesquita et al. 2010; Thompson et al. 2012; Houben et al. 2016). The reduction in dissolved organic carbon and increased clarity in the water column has been postulated to occur through adsorption (Thompson et al. 2008). Conglomerates that are formed settle to the lake bottom which clears the water column, enriches sediments, and promotes development of submerged vegetation (Mesquita et al. 2010, Thompson et al. 2012, Thienpont et al. 2013). Thawed sediments and solutes that are entering lakes from thaw slumps are not only causing ionic enrichment but are directly loading trace metals such as uranium, strontium, and lithium (Houben et al. 2016). The higher pH associated with ion rich sediments entering lakes also acts

to decrease Fe, Mn, and Al concentrations in the water column (Houben et al. 2016). This sedimentation is a likely driver of the removal of nutrients such as nitrogen and phosphorus leading to lower chlorophyll-*a* concentrations in thaw slump impacted lakes by as much as two thirds of undisturbed lake chlorophyll-*a* concentrations (Houben et al. 2016). Collectively, these changes result in a reduction in primary productivity of phytoplankton and periphyton and increases in well-developed rooted macrophytes and benthic algae communities (Mesquita et al. 2010; Thompson et al. 2012; Thienpont et al. 2013; Houben et al. 2016). Overall, this suggests that thaw slumps can significantly impact Arctic tundra lakes through increases in submerged macrophytes and development of a benthic habitat which may have effects that cascade throughout the food web.

Since climate change drives permafrost degradation, it may take decades to detect the impacts of permafrost thaw on lakes. However, present day artificial gravel pit lakes may provide some insights into how biological communities are structured in Arctic lakes with elevated ionic concentrations and low nutrient levels. Despite the fact that gravel pit lakes have some morphometric differences from natural lakes, similarities in water chemistry with what would be expected of lakes impacted by permafrost thaw can lead to similarities in levels of primary productivity (Søndergaard et al. 2018).

### **1.2.2 Defining characteristics of gravel pit lakes**

Gravel pit lakes form when abandoned quarries naturally fill with water from connections to adjacent lakes, or through groundwater, rainfall, and snowmelt inputs (Gammons et al. 2009, Mollema and Antonellini 2016, Søndergaard et al. 2018). In many regions, gravel pit lakes have shown significant differences in their physical and chemical parameters from natural lakes

(Boyes 1999, Hindák and Hindáková 2003). In comparison to natural lakes, gravel pit lakes are more oligotrophic and clear (Hindák and Hindáková 2003, Søndergaard et al. 2018). These lakes also tend to be deep with relatively flat bottoms and steep sides due to the nature of gravel extraction (Kalin et al. 2001, Blanchette and Lund 2016, Mollema and Antonellini 2016). This results in a higher depth to surface area ratio of gravel pit lakes (ranging from 10% to 40%) in comparison to natural lakes (less than 5%) (Mollema and Antonellini 2016).

### **1.3 The utility of macroinvertebrate communities in freshwater research**

Physical and chemical changes occurring in Arctic lakes may greatly modify lake biodiversity and food web dynamics. Benthic macroinvertebrates play an important role in controlling nutrient cycling in lakes (Covich et al. 1999). They consume organic detritus, macrophytes, algae and zooplankton and some are preyed on by fish, which makes them an important feature for energy transfer from lower to higher level organisms in aquatic food webs (Covich et al. 1999).

The collection and analysis of macroinvertebrate communities can be approached in a variety of ways that include categorizing them into functional feeding groups, taxonomic groups, and community metrics. Functional feeding groups represent the variety of feeding roles that different macroinvertebrates may have. Feeding groups are classified into collectors which are composed of invertebrates that filter and gather small organic matter, such as degraded algae, from water columns (Cummins 1973). Scrapers include invertebrates that scrape algae from a variety of surfaces such as rocks and plants (Cummins 1973). Shredders, on the other hand, feed on larger pieces of organic matter such as leaves (Cummins 1973). Lastly, predators are species

that feed on other invertebrate species and they therefore indicate that there are sufficient resources in the lake to support a multilevel food web (Cummins 1973). The presence of different macroinvertebrate groups in a given lake can inform on the type of food available, thereby describing the dominant benthic environment. In this respect, macroinvertebrates may also be used as biological indicators to determine lake health either through assigning tolerance indices that account for sensitivity to pollution for certain families or simply through examining richness and abundance (Barbour et al. 1992). Tolerance values on a scale of 0 (organisms very intolerant to organic waste) to 10 (organisms very tolerant of organic wastes) are sometimes used to indicate how resilient macroinvertebrate families are to the presence of organic materials (Hilsenhoff 1987). These values can be used to obtain the biotic index (BI) and a modified family biotic index (FBI) (Hilsenhoff 1988) developed to detect organic pollution in streams, rivers, and lakes. Taxonomically, certain families, genera, or species of macroinvertebrates may be used as indicators for differences in other chemical and physical conditions such as pollution, dissolved oxygen levels, and temperature. For example, Chironomidae populations have been shown to increase in frequency and diversity in response to climate warming and reduced ice cover (Quinlan et al. 2005). In eastern North America, some macroinvertebrate species such as *Chaoborus americanus* and *Graphoderus liberus* have been found among a few others to be robust indicators of fish absence (Schilling et al. 2009). Another set of aquatic macroinvertebrates commonly used to gauge stream, lake, and river pollution are Ephemeroptera, Plecoptera, and Trichoptera (EPT) taxa as they are especially sensitive to reduced dissolved oxygen (DO) levels and other types of pollution (Cairns and Pratt 1993, Jacobsen et al. 2003, Saari et al. 2018). These macroinvertebrates breathe through passive gills which absorb oxygen from the surrounding water (Voshell 2002). This characteristic makes them especially sensitive

to pollution, thus they are normally found in good quality freshwater habitats. A more general way of assessing water quality is using indices such as richness, abundance, evenness, and diversity. This assessment is normally used in conjunction with examining the kinds of species that are present as indicators. If these indices are higher, then the lake may be healthier since it is able to support a wider variety of species, indicating that conditions are habitable even to more sensitive species that may not occur in other lakes (Resh and Grodhaus 1983).

For example, in sub-Arctic lakes, benthic macroinvertebrates were found to be most abundant in mesotrophic lakes (Hayden et al. 2017). In contrast, oligotrophic and eutrophic lakes support fewer benthic macroinvertebrates (Hayden et al. 2017). Arctic freshwaters commonly have low nutrient levels and a short growing season, causing low primary productivity, thus having limited energy to support secondary consumers (Prowse et al. 2006). Therefore, organisms that live in these ecosystems are often adapted to long periods of low temperatures, low food availability, and bed instability due to frequent flooding and ice formation (Milner et al., 2005; Brittain et al., 2009). This results in lower taxonomic richness in Arctic systems where communities are dominated by a small number of species that are highly tolerant to the extreme Arctic conditions. In the case of macroinvertebrates, Diptera and particularly Chironomidae as well as Amphipoda are often the dominating taxa under these kinds of stressful environmental conditions (Milner et al. 2001, Namayandeh and Quinlan 2011). Chironomidae normally account for more than one fifth of all insects in the Arctic region, with increased relative abundance in more severe climatic conditions (Oliver 1968). Since finer identifications were not made in my study, a large amount of variability may be lost in analysis (Jones 2008, Scott et al. 2011). However, several studies suggest that macroinvertebrate communities identified at the genus and species level does not result in clearer patterns than family to order level identifications

(Bowman and Bailey 1997, Mueller et al. 2013). Although Arctic lakes tend to have lower macroinvertebrate richness than temperate lakes, they manage to maintain functional and taxonomical diversity of benthic invertebrate communities, especially in the littoral zone (Johnson and Goedkoop 2002; Wrona et al. 2013). This is because the high water clarity typical of many Arctic lakes allows light penetration and supports benthic primary production even in deep lakes, providing food sources for benthic macroinvertebrates. Although dominant taxa may exist (such as chironomids or amphipods), the littoral zone of many Arctic lakes still support a variety of taxa such as crane fly, caddisfly, mayfly and stonefly larvae (Wrona et al. 2013). Furthermore, lakes that are smaller in surface area and have no connectivity can be fishless, which allows predation sensitive macroinvertebrates to thrive such as beetles and phantom midges (Schilling et al. 2009; Lento et al. 2019).

Given the importance of macroinvertebrates for understanding water quality, the availability of data for northern lakes is surprisingly limited. Benthic macroinvertebrate communities in lakes are understudied in comparison to those in streams and rivers (Lento et al. 2019). According to the 2019 State of the Arctic Freshwater and Biodiversity report, the assessment of macroinvertebrates relative abundance in Arctic lakes is classified as “not undertaken”, while in rivers macroinvertebrate relative abundances are routinely sampled (Lento et al. 2019). Through reporting on macroinvertebrate communities in Arctic lakes within the Northwest Territories, my work aims to contribute to filling this knowledge gap. Specifically, I present research that explores the impacts of gravel pit lakes and potential impacts of permafrost thaw on macroinvertebrate communities on which information is even more limited. Previous research conducted generally about environmental change influencing macroinvertebrates in

lakes, as well as specifically of macroinvertebrates in gravel pit and permafrost impacted lakes is discussed in the following sections (1.3.1-1.3.3).

### **1.3.1 How might macroinvertebrate communities respond to environmental change in the Arctic?**

Considering that Arctic aquatic ecosystems are experiencing stress as a result of climate change, it is likely that that macroinvertebrate community composition and metrics will change in response. Culp et al. (2012) suggested that increased water temperature and longer open-water periods are shifting seasonal phenology which is expected to cause a decrease in cold stenotherms across different levels of the aquatic food web (algae, benthic macroinvertebrates, and fish). Furthermore, species that are cold intolerant may have greater opportunity to expand their range (Culp et al. 2012). This Northward expansion of generalist species that are able to tolerate a wider range of temperatures are expected to occur with climate change increasing the biodiversity of Arctic freshwaters (Culp et al. 2012). However, the increase in productivity and nutrient availability in lakes impacted by climate change could result in increased predation of macroinvertebrates which is expected to limit macroinvertebrate communities through top down control (Diehl 1995, Hayden et al. 2017). Lakes examined by Hayden et al. (2017) that contained the lowest numbers of Chironomidae larvae, had the highest relative abundance of Ruffe (*Gymnocephalus cernua*), a fish that preferentially consumes chironomids. Bottom up controls have also been shown to play an important role in shaping macroinvertebrate communities in Arctic lakes (Namayandeh and Quinlan 2011). Milner and Petts (1994) developed a conceptual model to describe how macroinvertebrate composition would change with decreasing distance to a glacier which is accompanied by decreasing water temperature and habitat stability. This model



showed that diversity declined with decreasing water temperature and bed stability. Furthermore, Diamesinae, a subfamily of Chironomidae, appeared to be the most tolerant organisms to these changes. Therefore, while oligotrophic lakes limit macroinvertebrate communities from the bottom-up (due to extreme environmental conditions), lakes that are eutrophic, resulting from the effects of climate change, may limit macroinvertebrate communities from the top-down (due to increased predation).

Collectively, environmental changes may directly or indirectly affect community compositions at different levels of the freshwater food web. Smol et al. (2005) determined that recent climate warming caused siliceous algal diatoms to undergo important shifts in species composition in high-latitude aquatic ecosystems. In boreal lake areas where forest fires occurred, an increase in shredder invertebrates, such as amphipods, occurred due to their generalist feeding and habitat ecology (Lewis et al. 2014). This was accompanied by an increase in predatory invertebrates (such as Hirudinea, Odonata larvae, and Coleoptera larvae) that feed on amphipods and were therefore responding to the increased prey availability (Lewis et al. 2014). This indicates that macroinvertebrate communities respond to climate change pressures (i.e. Forest fires, permafrost thaw, shorter ice cover duration...) which increase nutrient flow and macrophyte productivity of lakes. Additionally, changing fish communities may also alter macroinvertebrate community since they are slowly transitioning from salmonid to percid to cyprinid dominance as primary production of lakes increases due to the effects of climate change (Hayden et al. 2017). Some warm water fish, such as smallmouth bass, are expected to expand their range and make their way into northern lakes as more suitable thermal habitat becomes available (Sharma et al. 2007). The changes in fish dominance may impact macroinvertebrate communities through their dietary differences.

Overall, considering the great variety of environmental changes occurring in the Arctic region, in comparison to other countries, there is a lack of macroinvertebrate research in Canada's Arctic lakes. While responses of primary producers and fish communities to these environmental changes are widely studied (Smol et al. 2005, Sharma et al. 2007, Wrona et al. 2016) there is currently a knowledge gap in how other trophic levels are affected by these changes especially in Arctic lake ecosystems.

### **1.3.2 Macroinvertebrate communities in gravel pit lakes**

Since important water quality and morphometry differences exist between gravel pit lakes and natural lakes, macroinvertebrate communities should also differ considering their sensitivity to environmental change. Due to low nutrient levels (Gammons et al. 2009) and their young age (Lipseý 1980, Ejsmont-Karabin 1995a, Hindák and Hindáková 2003, Alfonso et al. 2010), gravel pit lakes typically don't support high species diversity in comparison with natural oligotrophic or mesotrophic lakes. The presence of macroinvertebrates in gravel pit lakes is impacted by water quality of the lake in question, benthic diversity in nearby water bodies, as well as dispersal and colonization processes (Beisner et al. 2006, Allen and VanDyke 2011, Audet et al. 2013). In gravel pit lakes especially, macroinvertebrate presence largely depends on whether a littoral habitat with vegetation is established (Gammons et al. 2009).

Macroinvertebrates become common only if littoral zones are established either naturally over time or they can be artificially created to ensure there is habitat available for successful colonization. A diverse invertebrate community was found in East Pit Lake, which was created during coal mine recovery (Sumer et al. 1995), while a uranium mine pit lake in Gunnar which was passively filled from water of a nearby lake contained 22 invertebrate taxa with leeches dominating (Tones 1982). These findings indicate that artificial lakes have the potential to

support diverse and rich macroinvertebrate communities. In contrast, pit lakes can also have a completely absent benthic community due to a combination of meromixis and steep walls that prevent the existence of a littoral zone (BHP 2005). Some pit lakes that have low pH and high toxicity due to metal leaching, may constrain macroinvertebrate communities resulting in lower richness, only allowing only some acid-tolerant species to colonize successfully (Wollmann et al. 2000; BHP 2005; Schultze et al. 2010). However, these acidic pit lakes are not characteristic of gravel pit lakes specifically, and are only present in pit lakes formed from certain mining activities such as coal (Gammons et al. 2009, Schultze et al. 2010) and metals (Blanchette and Lund 2016). Therefore, where gravel mining is responsible for the creation of a gravel pit lake, higher pH levels are expected, and nutrient limitation as well as littoral zone size and biodiversity in nearby lakes should place greater limitations on the macroinvertebrate community.

### **1.3.3 Macroinvertebrate communities in permafrost impacted lakes**

There are a limited number of studies that focus on benthic macroinvertebrate communities in lakes impacted by permafrost thaw. I am only aware of one study, conducted by Moquin et al. (2014) which examines the impact of permafrost thaw disturbance on Arctic lakes. Moquin et al. (2014) found that macroinvertebrate abundance increased in response to permafrost thaw and noted that the macroinvertebrates were likely benefiting from higher concentrations of Ca and Mg in sediments, as well as increases in macrophyte biomass as a result of permafrost thaw increasing nutrient availability in sediments. However, decreases in Chironomidae were observed in response to permafrost thaw (Moquin et al. 2014), due to their sensitivity to sedimentation which was attributed to their feeding and respiration (Gray and Ward

1982), in addition to their burrowing behaviours (Cole 1953, Charbonneau and Hare 1998). Moquin et al. (2014) also found that Bivalvia and Oligochaeta were tolerant to permafrost thaw disturbance. Even more responsive were Ostracoda and Nematoda abundance which were approximately four and ten times greater, respectively, in lakes that were disturbed by thaw slumps (Moquin et al. 2014).

To my knowledge, this study is the only one that investigates the impact of permafrost thaw on benthic macroinvertebrates in lakes. As a result, more research in the area is needed to confirm the impacts of permafrost thaw on macroinvertebrates in lakes. Specifically, research that associates the percentage of disturbed catchment area with macroinvertebrate communities would be useful considering the impacts may vary with increasing permafrost disturbance. I would hypothesize that as a higher percentage of the catchment area is disturbed there would be more dramatic differences observed between permafrost disturbed and undisturbed lakes. To my knowledge, there is also no research that investigates overall community richness, diversity, and looks at sensitive metrics such as % EPT in permafrost impacted lakes. Lastly, Moquin et al. (2014) does not incorporate full community analyses and only focuses on taxa that are likely more responsive to the disturbance.

In this thesis, I therefore aim to fill in some of the abovementioned knowledge gaps by first, adding to literature that investigates associations between environmental variables and macroinvertebrate communities in Arctic lakes. Second, I explored water quality and macroinvertebrate differences found in gravel pit lakes versus natural lakes. Lastly, I investigated how macroinvertebrate communities may respond to water quality changes expected due to permafrost thaw.

## 1.4 The importance of our study site

Our studies were carried out in the Gwich'in Settlement Area (GSA) and the Inuvialuit Settlement Region (ISR) of the Northwest Territories. The vast amount of freshwater that surrounds Gwich'in and Inuvialuit communities is of great importance to their culture and livelihood. Although these communities did little to contribute to climate change, they are on the receiving end of some of its consequences for their land and waterbodies (Trainor et al. 2007). It has been widely documented that due to the impacts of climate change, Inuvialuit communities are experiencing declines in food security and health status, increases in injuries and deaths, and an inability to practice their traditions and cultural activities (White et al. 2007; Ford et al. 2008a, 2008b; Loring and Gerlach 2009). Additionally, settlements, heritage sites, municipal infrastructure, and water supply in northern region are threatened by rising sea levels, coastal erosion and permafrost thaw (Martin et al. 2007, Alessa et al. 2008, Larsen et al. 2008). Although benefits from climate change impacts on these communities were noted as well, the negative impacts are believed to outweigh the positives (ACIA 2005; IPCC 2007). Additionally, even new infrastructure built to mitigate the impacts of climate change may have other unforeseen effects on communities. For example, while the newly built all season Inuvik-Tuktoyaktuk highway may be a good solution to the heavily climate reliant winter seasonal ice road, it also may bring increasing development and tourism which can influence waterbodies and the indigenous communities that rely on them. Collectively, conducting water quality and biological community assessments in our study area not only helps to fill some of the scientific knowledge gaps, but is highly relevant to First Nations communities that live in the area and have a deep cultural connection with their land and waters. Any predicted changes or established differences in disturbed lakes such as gravel pit lakes and permafrost impacted lakes may

ultimately be related to the availability of healthy lakes and fishing opportunities for the communities that live in the region.

In addition to the significance of my work for local communities interested in understanding environmental changes, my study will also fill an important knowledge gap. The lakes in the study area span the Arctic region in the Northwest Territories and by sampling macroinvertebrate communities in these lakes I am filling in an identified knowledge gap for this Focal Ecosystem Component in Canada's Arctic (Lento et al. 2019). The State of the Arctic Freshwater Biodiversity Report rates the existing knowledge gaps of freshwater FECs not only by the frequency and stability of data collection and funding but also by spatial coverage. Macroinvertebrate communities in Canadian Arctic lakes are not routinely sampled and therefore there is poor temporal and spatial coverage for this group. In addition, although our lakes span a latitudinal range of only  $\sim 2.5^\circ$ , the area is heterogeneous in key environmental variables and vegetation that are driven by climatic differences and ultimately may lead to differences in water quality among lakes (Table 1.1; 1.2; Figure 1.2; 1.3). Therefore, although the spatial coverage of my study is relatively small, the variation in environmental conditions of our study areas reflect that which one might expect from a study with a larger spatial extent.

#### **1.4.1 Heterogeneity of study site**

An interconnected system of Arctic rivers, streams, and lakes run through the GSA and ISR. The sampled lakes span the northern half of the Mackenzie Delta ( $68^\circ 56' 23''\text{N}$   $136^\circ 10' 22''\text{W}$ ) stretching from Fort McPherson to Tuktoyaktuk (Figure 1.3). The southernmost lakes in this study were sampled around Fort McPherson, near the confluence of the Peel River ( $67^\circ 0' 0''\text{N}$   $134^\circ 59' 3''\text{W}$ ) with the Mackenzie River. The Peel River joins the Mackenzie just

northeast of Fort McPherson, carrying run-off from northern Yukon (Saskatchewan Watershed Authority, 2003). The Mackenzie River diverges into a few large channels, the largest one heading northeast and emptying into the Beaufort Sea west of Tuktoyaktuk.

The Mackenzie Delta region covers an area of 13,135 km<sup>2</sup> and contains over 49,000 lakes and ponds of which 45,000 are larger than 0.14 ha (Emmerton et al. 2007). Most lakes in this area are shallow with mean depth that range between 0.5 m to 4.5 m, however, depths vary according to the time of year, local precipitation, and adjacent river and stream water levels (Lesack and Marsh 2010). The open water period is generally from June to November with peak water levels during spring break-up in response to snowmelt runoff in more southerly parts of the basin (Lesack and Marsh 2010). This lake-rich environment is one of the most dynamic ecosystems in northern Canada (Squires et al. 2009), providing habitat for a wide variety of wildlife such as moose, black bears, snowshoe hares, caribou, lemming, ptarmigans, foxes and wolves (Bliss et al. 2010).

The Mackenzie River flows through large and thinly populated regions of forest and tundra (Kokelj et al. 2009). For this study, lakes were sampled along this transition area, 23 of which were sampled in August 2017 in the GSA, which is considered a boreal forest region, and 24 of which were sampled northward in the ISR in August 2018 surrounded by the tundra vegetation (Figure 1.2; Table 1.1). Boreal vegetation in the Mackenzie Delta area consists largely of trees such as black and white spruce, as well as some birch and trembling aspen (Bliss et al. 2010). Although the surrounding area was partly forested in the lakes sampled in 2017, the majority was covered by large areas of muskeg, swamps, and many small lakes (Saskatchewan Watershed Authority, 2003). The transitional boreal to tundra zone is characterized by stunted (5-7 m tall) coniferous trees (Bliss et al. 2010). Most commonly, the trees are black and white

spruce, but trembling aspen and paper birch can occur as well (Bliss et al. 2010). In this transitional region, the stunted trees occur in concert with tundra shrubs that include dwarf birch and Labrador tea or alternatively, lichens and mosses (Bliss et al. 2010). In contrast, tundra vegetation is comprised of a mixture of tall and low lying shrub tundra of alder, birch, and willows as well as sedges, lichens, and mosses (Bliss et al. 2010). These categories of tundra vegetation can occur in various combinations that largely depend on how well drained the soils are (Bliss et al. 2010). The treeline that marks this vegetation transition from boreal to tundra has slowly been advancing northward due to warming of surface ground and air temperatures (D'Arrigo et al. 2004). Currently, the transition crosses our study area near the town of Inuvik (Figure 1.2).

Our study area is considered to be in the subarctic climate zone, meaning that it is characterized by long and cold winters with short cool summers (Beck et al. 2018). Specifically, the subarctic climate zone is defined by regions where the coldest month averages below 0°C, and contains only one to three months that average above 10°C making for a short growing season. Notwithstanding the above generalization, there still exists a fair bit of variation in climatic variables measured between the three towns within our study area in terms of temperature, precipitation, and winds (Table 1.2).

Natural, long-term climate patterns in our study area are driven by the Arctic Oscillation (AO) and the Pacific Decadal Oscillation (PDO) (Environment and Natural Resources 2015). These are large annual and decadal fluctuations in ocean circulation and atmospheric pressure that can impact overall climate patterns (Environment and Natural Resources 2015). Therefore, when tracking the impact of anthropogenic driven climate change, these natural fluctuations are important to consider. These oscillations can have direct impact on many climate change



disturbances some of which include permafrost thaw, droughts, and flooding (Environment and Natural Resources 2015).

#### **1.4.2 The impact of road proximity on lakes**

Lakes in this study are proximate to dusty and unpaved highways. Therefore, they are not a true random sample, and water quality as well as macroinvertebrate communities, may be responsive to impacts associated with the lakes' proximity to the highways. Gunter (2017) found that lakes that were less than one kilometer from the Dempster highway in the Northwest Territories had higher alkalinity, conductivity, total dissolved solids, hardness, pH, and increased ion concentrations that include Mg, Ca, SO<sub>4</sub>, and Sr. These effects are comparable to those experienced by lakes exposed to thaw slumps. Gunter (2017) postulated that the few roadside lakes that were not impacted similarly were either protected from dust runoff due to tall shrubbery surrounding lakes that may have trapped some of the dust, or may have experienced dilution from groundwater flow or increased precipitation. Similarly, effects due to climate variation can be lake specific (Plug et al. 2008). A potential confounding factor for including lakes in close proximity to the road is the ability to differentiate whether these concentrations are higher as a result of the road dust, thaw slumping, climate change impacts such as increased evaporation or precipitation, or a mix of these drivers.

## **1.5 Overarching goal and outline of chapters**

The overarching goal of this thesis is to determine how macroinvertebrate communities are shaped by water quality considering the environmental pressures of development and climate change in the Arctic. In Chapter 2, I explore the role of development by comparing gravel pit to natural lakes in terms of their water quality and macroinvertebrate communities. In Chapter 3, I explore the role of climate change by predicting how macroinvertebrate communities may respond to expected changes in water quality as a result of permafrost thaw.

### **1.5.1 The selection of lakes for the following studies**

#### *Chapter 2*

To compare gravel pit and natural lakes, data from 21 lakes sampled in the GSA was used since no gravel pit lakes were visited in the ISR. The 21 lakes were also selected based on there being sufficient zooplankton and benthic macroinvertebrate collections from each lake. Since the paper was a collaboration, lakes that did not have sufficient sample sizes for either of the focal groups (zooplankton or macroinvertebrates) were excluded.

Chapter 2 was published paper in Arctic, Alpine, and Antarctic Research journal.

Citation:

Vucic, J.M., Cohen, R.S., Gray, D.K., Murdoch, A.D., Shuvo, A., and Sharma, S. 2019. Young gravel-pit lakes along Canada's Dempster Highway: How do they compare with natural lakes? Arctic, Antarct. Alp. Res. **51**(1): 25–39. Taylor & Francis. doi:10.1080/15230430.2019.1565854.

For the purpose of this thesis, zooplankton analyses and text were removed from the paper, therefore everything presented is a reflection of my contribution to the paper. All text

included throughout this thesis is my own. For specific roles of co-authors on the paper and overlapping data specifications, refer to page iii.

### *Chapter 3*

For this chapter, I used data from 46 lakes that spanned both GSA and ISR to capture the heterogeneity of the range of lakes sampled in my predictive models. For describing community structure and water quality, I used the entire 46 lake dataset, however, to create strong models for predicting community metrics, I chose to reduce the data set to 35 lakes for which valuable explanatory data were available, including sediment and fish community data. This decision to use a subset of the larger dataset was made based on the results of previous studies that have indicated that both fish communities (Hayden et al. 2015, 2017) and substrate type (Namayandeh and Quinlan 2011; Jones et al. 2012) are important for explaining variation in macroinvertebrate communities.

## Tables

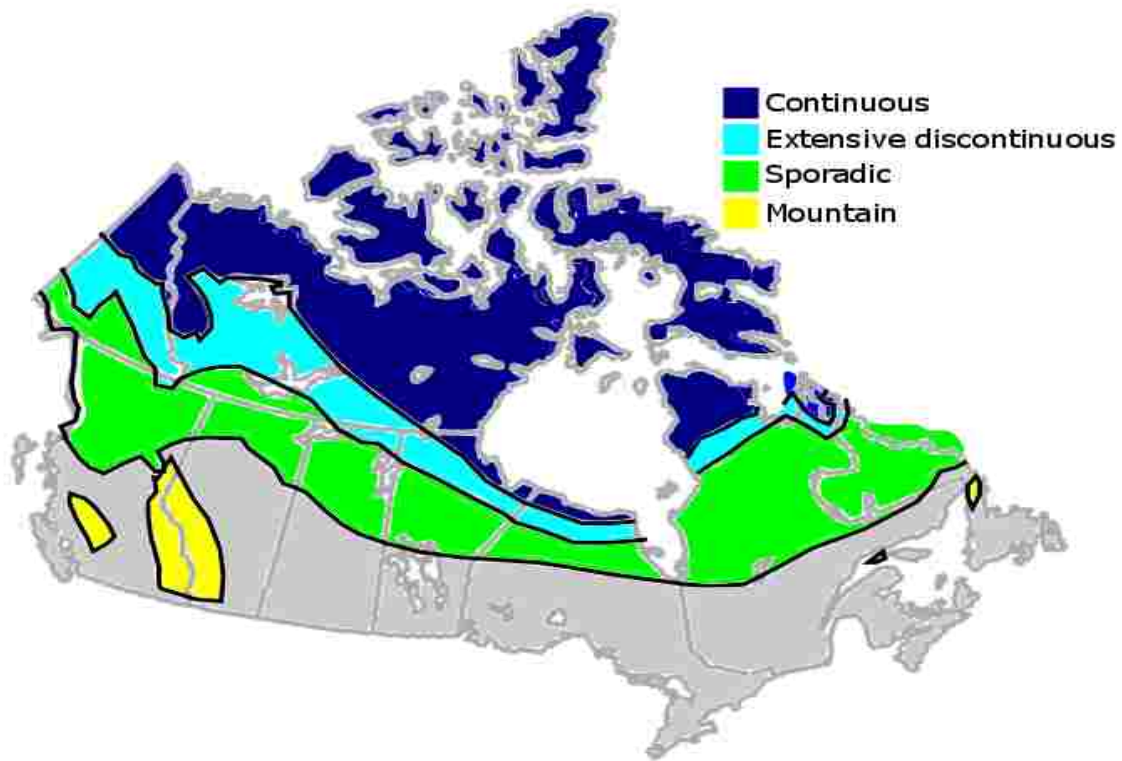
**Table 1.1:** Site description of the Gwich'in Settlement Area (GSA) and the Inuvialuit Settlement Region (ISR).

<b>Location</b>	<b>GSA</b>	<b>ISR</b>
<b>Total number of lakes sampled</b>	23	24
<b>Lake type</b>	6 gravel pit lakes, 17 natural lakes	24 natural lakes
<b>Highway</b>	Dempster	Inuvik-Tuktoyaktuk
<b>Dominant vegetation</b>	Boreal	Tundra
<b>Permafrost</b>	Discontinuous	Continuous

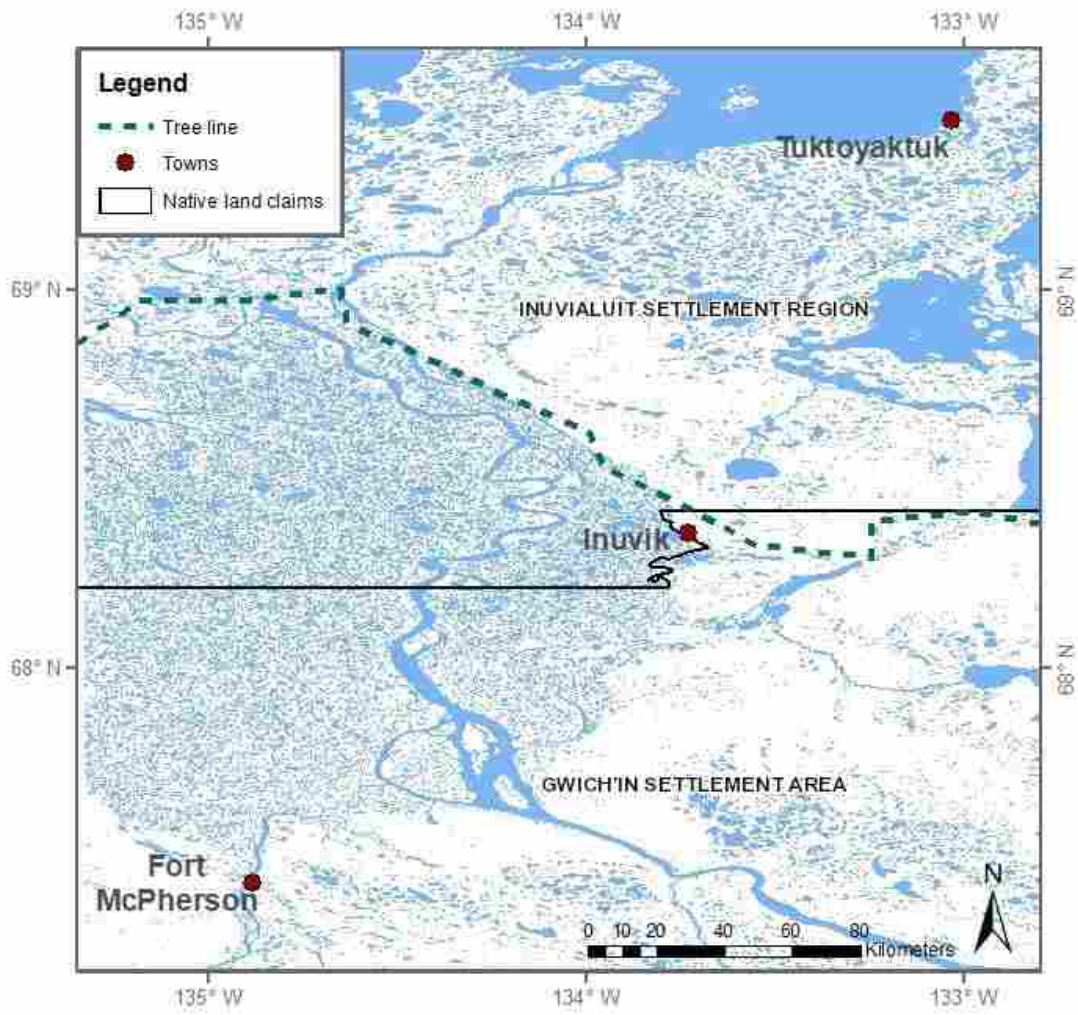
**Table 1.2:** Average yearly climate conditions in Fort McPherson, Inuvik, and Tuktoyaktuk between 1981 to 2010 (Environment and Natural Resources Canada, 2019).

<b>Town</b>	<b>Tuktoyaktuk</b>	<b>Inuvik</b>	<b>Fort McPherson</b>
<b>Location</b>	69°26'34"N 133°01'52"W	68°21'42"N 133°43'50"W	67°26'07"N 134°52'55"W
<b>Daily min to max (°C)</b>	-13.8 to -6.4	-12.9 to -3.5	-11.7 to -2.9
<b>Daily average (°C)</b>	-10.1	-8.2	-7.3
<b>Rainfall (mm)</b>	74.9	114.5	145.9
<b>Snowfall (cm)</b>	103.1	158.6	152.5
<b>Precipitation (mm)</b>	160.7	240.6	297.7
<b>Wind velocity (km/h)</b>	89	65	56

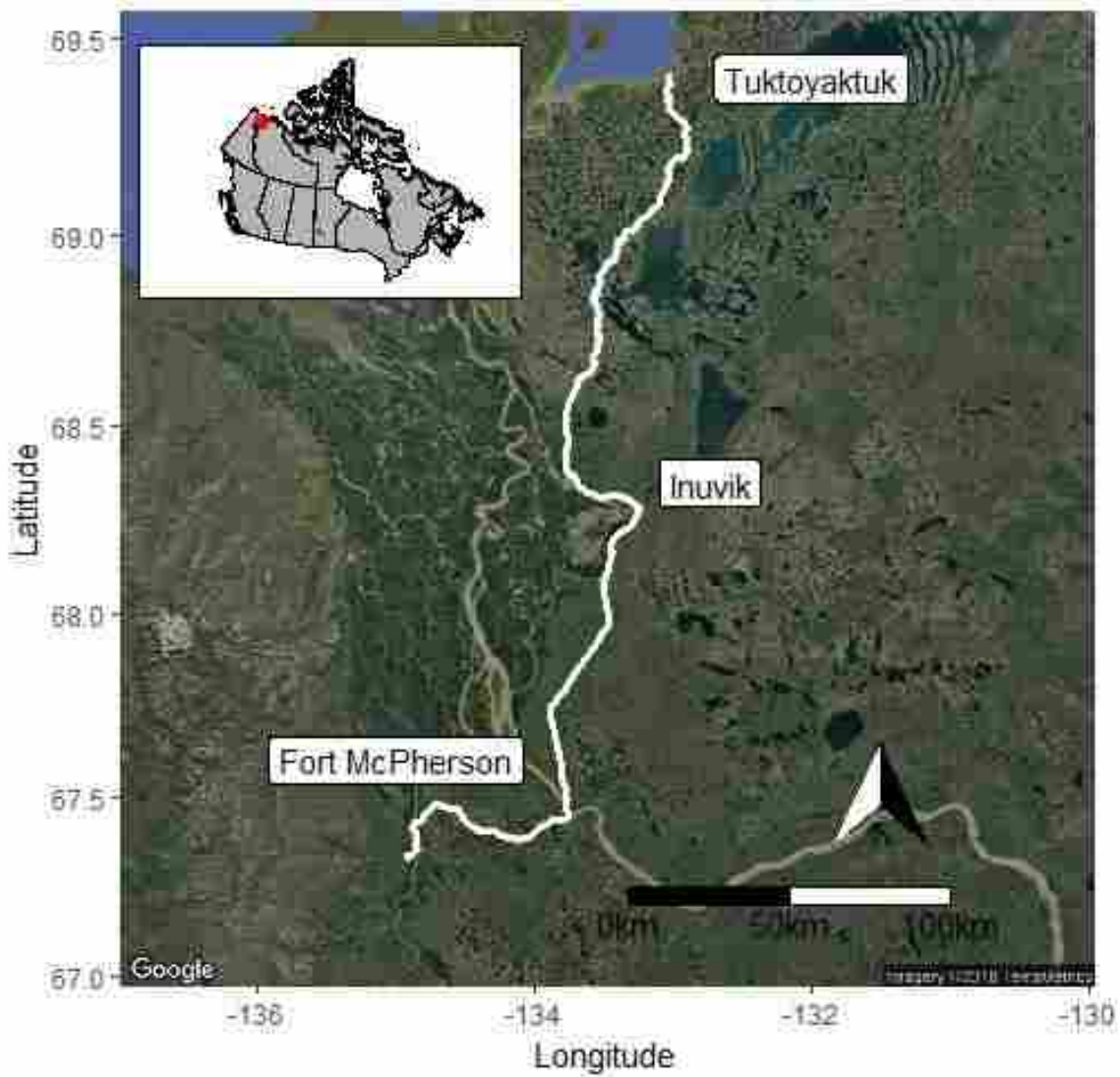
## Figures



**Figure 1.1:** Four permafrost zones found in Canada. The Northwest Territories is impacted by a gradient of varying permafrost continuity that includes continuous permafrost (northernmost), extensive and sporadic discontinuous (southernmost) permafrost (Image adapted from Heginbottom et al.1995).



**Figure 1.2:** The boreal-tundra tree line (green dotted line) spans the middle range of the study area. Boreal vegetation is found between Fort McPherson and Inuvik while tundra vegetation is found between Inuvik and Tuktoyaktuk. The Gwich'in Settlement Area and Inuvialuit Settlement Region are dominated largely by boreal and tundra vegetation within the study area, respectively (Image adapted from Northwest Territories Centre for Geomatics 2011).



**Figure 1.3:** The study area spans Fort McPherson to Tuktoyaktuk. The white line represents the Dempster Highway between Fort McPherson and Inuvik and the Inuvik-Tuktoyaktuk Highway that lakes were sampled along.

## CHAPTER 2:

### **Young gravel pit lakes along Canada's Dempster Highway: How do they compare with natural lakes?**

#### **Abstract**

Gravel pit lakes are a common feature of many human-modified landscapes throughout the world. In Canada's north, they are often formed when gravel is extracted to construct dams, bridges, and highways. Past studies suggest that gravel pit lakes differ from natural lakes in terms of their morphometry, water quality, and biological communities. In this study, we compared gravel pit and natural lakes by sampling lakes between Inuvik and Fort McPherson in the Northwest Territories. We collected lake morphometry, water quality, and biological data (macroinvertebrates, and fish presence), from six gravel pit lakes and fifteen natural lakes. In comparison to natural lakes, gravel pit lakes were four times deeper, two times clearer, and five times smaller in their surface area. In addition, important nutrients, including phosphorus and nitrogen were significantly lower in gravel pit lakes. Despite the differences in morphometry and nutrients, littoral macroinvertebrate communities did not differ significantly between the two lake types. Therefore, I conclude that despite their recent formation and unnatural morphometry, gravel pit lakes along the Dempster Highway can support macroinvertebrate communities typical of natural lakes in the region.

**Key words:** Gravel pit, borrow pit, water chemistry, macroinvertebrates, Northwest Territories, Dempster Highway, Gwich'in Settlement Area



## **Introduction**

Industrial activity and the development of roadways throughout the Northwest Territories require local mining of sand and gravel, leaving behind many abandoned gravel pits (borrow pits). Sand and gravel are extracted for use in construction of buildings, dams, bridges, pipelines, and highways (Bayram and Önsoy 2014, Mollema and Antonellini 2016, Søndergaard et al. 2018). Government records available from the Gwich'in Land and Water Board, reveal that gravel pits in northern Canada are typically used for the purposes of mineral exploration, geological mapping, opening of roads, and highway maintenance. According to these records, there are 18 gravel pits, now lakes, along the Dempster Highway in the Northwest Territories. Due to the construction of the highway during the 1970s, some of the earliest gravel pits opened in the mid-1970s and extraction of material from most pits stopped during the 1990s. However, the demand for gravel mining in the region is expected to increase in order to accommodate future construction associated with a growing population, increased resource development, and tourism. For example, the Inuvik-Tuktoyaktuk highway was completed in November 2017, providing road access to the southern coast of the Arctic Ocean, a region where significant development is anticipated (Kiggiak-EBA Consulting LTD. 2011). Gravel extraction is also anticipated to continue in Canada's north due to the ongoing maintenance of roadways built over permafrost and a dynamic active layer that experiences damaging freeze-thaw cycles.

Gravel pit lakes are formed when an abandoned extraction pit floods naturally through an influx of groundwater, rainfall and snowmelt, or through connections with nearby lakes (Gammons et al. 2009, Mollema and Antonellini 2016, Søndergaard et al. 2018). Although gravel pit lakes are common features of landscapes in many parts of the world, their study has been neglected, and little is known about the development of these lake ecosystems following

extraction activities (Gammons et al. 2009, Mollema and Antonellini 2016). Due to their young age and artificial construction, gravel pit lakes can exhibit differences in important physical and chemical parameters in comparison with natural lakes (Boyes 1999, Hindák and Hindáková 2003). Past studies suggest that most gravel pit lakes are oligotrophic, clear, and exhibit neutral to alkaline pH levels (Hindák and Hindáková 2003, Søndergaard et al. 2018). Their artificial construction can lead to important morphometric differences. Artificial lakes created from mining or gravel extraction activities tend to be deep with relatively flat bottoms and steep sides, creating a high depth:surface area ratio (Kalin et al. 2001, Blanchette and Lund 2016, Mollema and Antonellini 2016). The depth:surface area ratio for gravel pit lakes ranges from 10 to 40%, while natural lakes have a ratio of less than 5% (Mollema and Antonellini 2016). These differences between gravel pit and natural lakes can lead to differences in the types of biological communities that these lakes support. Most gravel pit lakes are unlikely to support a high diversity of species in comparison with natural oligotrophic or mesotrophic lakes owing to low nutrient levels (Gammons et al. 2009). The young age of gravel pit lakes may also contribute to decreased biodiversity since they have less time to accumulate species and proceed through successional cycles exhibited by many older natural lakes (Lipseý 1980; Ejsmont-Karabin 1995; Hindák and Hindáková 2003; Alfonso et al. 2010). The high depth:surface area ratio of gravel pit lakes leaves little room for littoral macrophytes, which act as important habitat for many invertebrates and play a key role as refuges and breeding habitats for fish (Scheffer 1999). As a result, benthic communities in gravel pit lakes may be typical of deep, poorly lit profundal habitats (Gammons et al. 2009). Despite these noted generalities, gravel pit lakes can vary in their physical, geochemical and ecological characteristics in relation to local climate and watershed characteristics (Gammons et al. 2009).

The composition of biological communities in gravel pit lakes will be influenced by the natural biological diversity in nearby water bodies, the physical conditions within each lake, as well as dispersal and colonization processes (Beisner et al. 2006, Allen and VanDyke 2011, Audet et al. 2013). Macroinvertebrates may not be limited by dispersal since a variety of species can colonize via their adult aerial phase (Bilton et al. 2001, Van de Meutter et al. 2007). Exceptions to this generalization are organisms without an aerial phase, such as oligochaetes and amphipods. These groups can disperse to gravel pit lakes using several vectors, including movement through streams, attachment to vertebrates, and through heavy wind and rain events (Mackay 1992). In the Northwest Territories, there are a variety of vertebrate vectors, including the black bear (*Ursus americanus*), grizzly bear (*Ursus arctos*), beaver (*Castor canadensis*), ruddy duck (*Oxyura jamaicensis*), herring gull (*Larus argentatus*), and the common loon (*Gavia immer*). The colonization of fish requires stream connections to natural lakes, or intentional stocking efforts, and will occur slowly without human intervention (Shurin et al. 2009, Søndergaard et al. 2018). In general, past studies show that the distribution of larger organisms, such as fish, are more strongly limited by dispersal, while lower trophic levels, such as macroinvertebrates, zooplankton, and phytoplankton disperse more readily (Beisner et al. 2006). However, dispersal and colonization processes for all taxonomic groups take time to play out (Shurin et al. 2009, Gray and Arnott 2011), therefore, younger gravel pits may have lower levels of biological diversity in comparison to older systems (Lipsey 1980).

To explore the role of gravel pit lakes as habitat for aquatic invertebrate species, we investigated whether there are differences in lake morphometry, water quality, and macroinvertebrate communities between gravel pit lakes and natural lakes. More specifically, this study aims to: (i) Investigate differences in water quality and morphometric characteristics

between six gravel pit lakes and fifteen natural lakes along the Dempster Highway; (ii) Evaluate differences in macroinvertebrate communities between lake types; and (iii) Understand relationships among biological, morphometric, and water quality variables in natural and gravel pit lakes. Based on the few studies that have been conducted in the past, we hypothesized that: (i) Gravel pit lakes will be deeper, clearer, nutrient poor and less productive in comparison to natural lakes (Dodson et al. 2000, Søndergaard et al. 2018); (ii) Macroinvertebrate abundance, richness, and diversity will be lower in gravel pit lakes (Lipseý 1980; Ejsmont-Karabin 1995; Hindák and Hindáková 2003; Alfonso et al. 2010); and (iii) Macroinvertebrate community composition will differ between gravel pit lakes and natural lakes owing to morphometric and water quality differences such as water clarity, nutrient availability, and depth (Blanchette and Lund 2016, Mollema and Antonellini 2016).

## **Methods**

### *Study Area*

This study was conducted along the Dempster Highway running between Fort McPherson and Inuvik within the Gwich'in Settlement Area, Northwest Territories between August 17<sup>th</sup> and September 1<sup>st</sup>, 2017 (Figure 2.1). This study area was chosen due to the accessibility of both gravel pit lakes and natural lakes along the highway. We sampled six gravel pit lakes, and fifteen natural lakes with surface areas less than 100 ha for morphometric, water quality, and biological data (Figure 2.1, Table 2.1). The lakes are located in an area of Boreal forest dominated by coniferous trees, such as black spruce (*Picea mariana*), white spruce (*Picea glauca*) and jack pine (*Pinus banksiana*; Sweetman et al. 2010). While visiting each lake we

recorded qualitative visual observations of the submerged, emergent, and shoreline vegetation present (Table 2.1). The region is underlain by discontinuous permafrost, covering between 50-90% of the total area, and the landscape includes a mix of morainal, glaciofluvial, lacustrine, and alluvial deposits (Kokelj et al. 2009). Recent climate change has had a substantial impact on permafrost (active layer depth), landscape structure, and vegetation (Burn and Kokelj 2009, Lantz et al. 2010). Most of our study lakes were located along remote stretches of highway, and therefore receive drainage primarily from a landscape of coniferous trees, peat hummocks, bogs, and small lakes extending on either side of the road. Based on our observations in the field, only six lakes had a noticeable inflow of water during our July/August fieldwork. Three of the study lakes are located in the town of Inuvik (population ~3200) and two near the hamlet of Fort McPherson (population ~700), which could leave them vulnerable to nutrient pollution (Figure 2.1). The gravel pits along the Dempster are estimated to be approximately 25-30 years old based on closing dates recorded in government records available from the Gwich'in Land and Water Board. Natural lakes in this region could have formed as early as ~30 000 years ago when the Laurentide ice sheet receded until ~13 000 years ago during the Last Glacial Maximum (Dredge and Thorleifson 1987, Hill 1996). Although the construction of the highway may have changed the hydrology for some lakes in the region (Trombulak and Frissell 2000, Kiggiak-EBA Consulting LTD. 2011), an examination of historical maps shows that all the natural lakes we sampled were present on the landscape prior to highway construction (Department of Energy Mines and Resources 1973).

## *Morphometry and Water Quality*

Morphometric variables included surface area, mean depth, and maximum depth. These variables were measured by constructing bathymetric maps of each lake using a Humminbird Helix 5 chartplotter (Johnson Outdoors Marine Electronics, Inc), in combination with Reefmaster bathymetry software (Reefmaster Ltd.). Drainage basin area was determined for each lake with the basin tool in ArcMap version 10.5 (Esri Inc.) using 2 m resolution digital elevation maps (Porter et al. 2018). Water quality variables included Secchi depth (water clarity), turbidity, conductivity, dissolved oxygen, pH, total nitrogen, total phosphorus, total organic carbon, calcium, chlorophyll-*a*, and water temperature (Table 2.1). At the point of maximum depth in each lake, a Manta+ multiparameter probe (Eureka Water Probes) was deployed from the boat to measure turbidity, conductivity, DO, pH, and temperature at 1 m depth from the surface. A Secchi disk was deployed over the shady side of the boat to obtain water clarity measurements. In addition, a 1 L water sample was collected from each site at the deepest point of the lake using a 3 m polyethylene integrated tube sampler that collected a sample throughout the top 3 m of the water column. At the Center for Cold Regions and Water Science at Wilfrid Laurier University, the Perkin Elmer Optima 8000 Inductively Coupled Plasma Optical Emission Spectroscopy (ICP-OES) was used to measure calcium concentrations. The Shimadzu TOC-LCPH Carbon and Nitrogen analyzer (Shimadzu Corp.) was used to measure TN and TOC, as it is capable of measuring a variety of carbon species and total nitrogen in liquid samples. Unfortunately, TP levels were below the detection limit for the ICP-OES (4 µg/L), and so could not be determined from 2017 samples. Low phosphorus levels have also caused difficulty in previous studies conducted in this region (e.g. Scott et al. 2011). Our TN levels from 2017 samples were also implausibly low, possibly due to instrument calibration error. To rectify these issues, we returned

to our study lakes between July 26 – August 5<sup>th</sup>, 2018 and collected shoreline water samples for measurement of TP and TN. Samples for total phosphorus were digested in an autoclave with ammonium persulfate and sulfuric acid following EPA method 365.1. We then followed SEAL method G-103-93 to measure total phosphorus colorimetrically using a SEAL Continuous Segmented Flow Analyzer (SEAL Analytical, Inc.). Estimates of TN concentrations for 2018 samples were obtained as described above. Chlorophyll-*a* data were also obtained by collecting a 250 mL water sample from the shoreline in 2018. Samples were filtered using Fisherbrand G4 glass fiber filters, and chlorophyll-*a* was extracted from the filters using methanol and analyzed using a fluorometer (Turner TD700) at Queens University (Symons et al. 2012).

### *Macroinvertebrate Communities*

Littoral macroinvertebrate samples were collected using a modified version of the Ontario Benthic Biomonitoring Network protocol (Jones et al. 2007). Samples were collected using a 500 µm D-net to kick and sweep macroinvertebrates. Between 1-3 replicate samples were taken along perpendicular transects from the shore. For each replicate, approximately 1 m<sup>2</sup> of the bottom was sampled. The protocol was modified from the standard OBBN in that each replicate was collected for only three minutes, and replicates were not taken from random shoreline locations on the lake. We used a three-minute kick and sweep per replicate rather than a ten-minute collection because the abundance of organic matter on the bottom of most natural lakes quickly clogged the D-net, preventing further sample collection. The inability to sample from random locations along the shoreline stemmed from the boggy terrain, which made it extremely difficult to walk the shoreline without sinking several feet into the peat. Each sample was preserved in 95% ethanol and brought back to the laboratory for identification.

Macroinvertebrates were identified to the order and family level according to the OBBN tally sheet (Jones et al. 2007; Table A1). Macroinvertebrates were collected from all fifteen natural lakes and from five of the six gravel pit lakes.

To determine fish presence and absence in lakes, we used a combination of visual fish observations, surveys with gillnets, and presence/absence of the phantom midge *Chaoborus americanus* (Sweetman and Smol 2006). Fish presence was confirmed using gill nets in nine natural lakes and one gravel pit lake, and by observation in a second gravel pit lake. Fish presence or absence was inferred in an additional eleven lakes based on presence/absence of *Chaoborus americanus*, which are a prevalent species found in northern lakes but not known to co-exist with fish (Sweetman and Smol 2006). Of these eleven lakes, fish presence was likely in three natural lakes and two gravel pit lakes, whereas the remaining lakes were deemed unlikely to support fish. Where fish sampling occurred, methods followed the Ontario Broadscale Monitoring (BSM) protocol which incorporates a standardized study design using large and small mesh gillnets (Sandstrom et al. 2013). Large mesh nets target large-bodied fish generally greater than 20 cm in size, and small mesh gillnets target small-bodied fish under 20 cm. Gillnets were distributed over varying lake strata depths according to the BSM protocol, for a duration of 16-22 h.

To compare species richness and species diversity among lakes, we used indices that correct for differences in sample size (number of individuals identified) among lakes. For richness, we used rarefaction to calculate values that reflect equal taxonomic/sampling effort for each lake (Hurlbert 1971). Rarefaction accounts for differences in sampling effort by resampling abundance data for a particular site hundreds or thousands of times to determine the average number of species identified for a given number of individuals collected (Gotelli and Colwell,



2001). For macroinvertebrate taxa richness, we rarified to 189 individuals for each lake. Rarefaction was conducted using the rarefy function in the Vegan package for R (Oksanen et al. 2016), which is based on the formulation by Hurlbert (1971). Similarly, the diversity index used corrected for differences in taxonomic/sampling effort. Diversity was calculated according to Chao's method for calculating rarified Hill numbers (Chao et al. 2014). We used the estimatedD function in the iNEXT package for R to calculate rarified order 1 Hill numbers representative of the exponential of Shannon's entropy index (Hsieh et al. 2016).

### *Statistical Analyses*

Welch's t-tests were used to test for differences in morphometric, water quality, and biological variables associated with our first two hypotheses. Welch's t-tests are an adaptation of the student's t-test for circumstances where unequal variances and sample sizes are encountered (Welch 1947). Data used for all t-tests was tested for normality by performing Shapiro-Wilks tests. If data were not normally distributed, transformations were applied to meet this assumption. To meet assumptions of normality, turbidity, total organic carbon, conductivity, chlorophyll-*a*, and macroinvertebrate abundance were log transformed, while TN was square-root transformed. Levene's test was used to test for homogeneity of variances (the data for all tests passed this assumption). Bonferroni corrections were used to deal with the problem of inflating type I error when conducting multiple independent t-tests.

To provide additional insight into our first hypothesis regarding physicochemical differences between natural and gravel pit lakes, we performed a principal component analysis (PCA) to visualize differences in morphometric and water quality variables among lakes. A PCA

is a linear indirect gradient analysis that reduces multidimensional data into a set of compound axes (Dytham 2011). The first PCA axis explains the most variation, followed by the second axis, etcetera (Dytham 2011). As a result, the first few PCA axes will typically explain the most variation in a dataset, and sites (lakes) located closer together on an ordination plot will have similar environmental characteristics. Morphometry and water quality variables were standardized to a zero-mean and unit variance using the `decostand` function in the `vegan` library in R. The PCA was conducted using the `prcomp()` function in the `stats` package for R (Borcard et al. 2011). Ordination plots for the first two PCA axes were generated to visualize differences in morphometry and water quality among lakes.

Redundancy analysis (RDA) was used to identify the morphometric and water quality variables that may influence macroinvertebrate community structure. Redundancy analysis is a multivariate method used to extract and summarize variation in a set of response variables that can be explained by a set of predictor variables (McArdle and Anderson 2001). In this case, the response variables were macroinvertebrate taxa abundances by lake and the predictor variables were a corresponding series of spatial (latitude), morphometric (mean depth, maximum depth, lake surface area), biological (fish presence/absence) and water quality variables (DO, turbidity, Secchi depth, pH, temperature, conductivity, calcium, total organic carbon, TP, chlorophyll-*a*, and TN). Lake surface temperatures declined slightly over the course of our sampling period due to changes in air temperature, so the effects of lake temperature were removed prior to analysis by conducting a partial RDA using lake temperatures as a conditioning variable. It was expected that gravel pit lakes would separate from natural lakes on the biplots owing to differences in community composition associated with predictor variables such as water clarity, nutrient availability, and depth. A stepwise variable selection procedure based on Akaike Information

Criterion (AIC) values was used to identify variables that were significantly related to the biological data (Burnham and Anderson 2004). The stepwise selection was implemented using the `ordistep` function in the `vegan` package for R (Oksanen et al. 2016). To test for collinearity among predictor variables, the variance inflation factor (VIF) was calculated using the `vif` function in `vegan` (no variables had a  $VIF > 5$ ; Oksanen et al. 2016).

## Results

### *Morphometry and Water Quality*

There was a significant amount of variation in morphometry and water quality variables among our study lakes (Table 2.1). Gravel pit lakes were significantly deeper, with a mean depth four times greater than that of natural lakes (Tables 2.1, 2.2; Figure 2.2A). Gravel pit lakes also had a smaller surface area, with the mean surface area for gravel pit lakes being five times smaller than natural lakes (Table 2.1). Gravel pit lakes were clearer than natural lakes, having Secchi depths twice as deep as natural lakes and turbidity values one quarter that of natural lakes (Figure 2.2B, C; Table 2.1; 2.2). TN concentrations were twice as high in natural lakes compared to gravel pit lakes and TP was 1.5 times higher in natural lakes (Figure 2.2D, G; Table 2.1; 2.2). However, gravel pit lakes and natural lakes had similar values for pH, water temperature, DO, conductivity, chlorophyll-*a*, total organic carbon, and calcium (Table 2.1; 2.2; Figure 2.2E, F, H). The first two axes of the PCA explained 55.30% of the variation among lakes (Figure 2.3). Gravel pit lakes are found in the upper left quadrant of the ordination plot and are characterized as deep lakes with a small surface area, high water clarity, and lower nutrients (Figure 2.3).

### *Macroinvertebrate Communities*

Macroinvertebrate abundance, richness, and diversity was similar in gravel pit and natural lakes (Figure 2.4; Welch's t-tests  $p > 0.1$  in all cases). The final RDA model for macroinvertebrates included chlorophyll-*a*, fish presence/absence, and mean depth as significant predictors, and the first two axes accounted for 21.24% of variation in communities (Figure 2.5,  $F = 1.59$ ,  $p < 0.05$ , adjusted  $R^2 = 0.08$ ). The RDA hinted that Gastropoda may be positively associated with fish absence, Chironomidae with chlorophyll-*a*, and Hemiptera with mean depth, but for the most part, distinct correlations between macroinvertebrate species and predictor variables were not observed.

### **Discussion**

Gravel pit lakes were markedly different in their morphometry and in several water quality characteristics compared to natural lakes, but surprisingly, macroinvertebrate communities did not differ between lake types. The relatively deep basins and low nutrient, chlorophyll-*a*, and turbidity levels in gravel pit lakes supported our first hypothesis that these lakes would be deep, clear, nutrient poor, and less productive. However, our data provided no support for our two biological hypotheses. Taxa richness, diversity, and abundance for macroinvertebrates were not lower in gravel pit lakes, providing no support for our second hypothesis. Finally, community structure for macroinvertebrates did not differ between lake types, lending no support to our third hypothesis that differences in morphometry and water quality characteristics would lead to differences in community structure.

## *Morphometry and Water Quality*

The values obtained for our morphometric variables were consistent with other studies, as gravel pit lakes were significantly deeper than natural lakes (Mollema et al. 2015, Søndergaard et al. 2018). Gravel pit lakes also had a smaller surface area than natural lakes, consistent with the idea that these artificial lakes typically have a higher depth:surface area ratio (Blanchette and Lund 2016). The reason that most gravel pits conform to this structure is that deep pits allow for a large extraction volume while minimizing cost and disturbance to terrestrial landscapes (Blanchette and Lund 2016). Low levels of turbidity and high Secchi depths for gravel pits are likely the result of interactions among morphometry, nutrients, and organic carbon. Shallow lakes are often turbid due to wave action causing resuspension of bottom sediments, resulting in minerogenic turbidity (Bloesch 1995). Although we have no direct measurements of sediment resuspension for these lakes, the depth of gravel pit lakes in our study (mean=6.40 m) likely means that resuspension of bottom sediments through wave action is less frequent than for the natural lakes (mean depth=1.62 m). Water clarity is also influenced by biological production in a lake. Chlorophyll-*a* concentrations were lower in gravel pits in comparison to natural lakes (although not after Bonferroni correction) and gravel pit lakes had significantly lower total nitrogen and total phosphorus concentrations than natural lakes. These differences indicate that gravel pit lakes are relatively unproductive in comparison with natural lakes (Brylinsky and Mann 1973, Smith 1982). Finally, total organic carbon levels were lower in gravel pit lakes (although not after Bonferroni correction), suggesting that water colouration due to dissolved organic substances was also lower in these lakes. Decreasing terrestrial biomass has been associated with decreases in lake total organic carbon levels, so we suspect that lower total

organic carbon levels may be related to the clearing of vegetation along the shoreline of the lakes in concert with development of the gravel pits (Pienitz et al. 1997; Rühland et al. 2003).

The water quality measurements for the 21 lakes in our study generally conformed well with previous studies in the region. The pH of lakes in this region was found to range between 6.9-7.6 in previous studies (Swadling et al. 2000; Kokelj et al. 2009; Houben et al. 2016), which falls into the range for our 21 lakes (6.1-8.5). Total organic carbon levels measured in 39 lakes by Kokelj et al. (2009) averaged 16.1 mg/L, falling in between our recorded concentrations for natural and gravel pit lakes, which had mean total organic carbon concentrations of 22.2 and 15.3 mg/L, respectively. The mean chlorophyll- *a* concentration in natural lakes was 1.25 µg/L and in gravel pit lakes was 0.38 µg/L, which fell within the range measured by Houben et al. (2016) where concentrations ranged from 0.20µg/L to 19.60 µg/L. Our calcium levels had a slightly higher range compared to Houben et al. (2016), Kokelj et al. (2009), and Swadling et al. (2000). We measured Ca levels between 8.1-52.5 mg/L, while the aforementioned studies found mean concentrations ranging between 8.6-31.4 mg/L. Conductivity was slightly elevated compared to previous studies by Houben et al. (2016) and Kokelj et al. (2009), who found mean conductivity levels of 108.8 µS/cm and 259.1 µS/cm, respectively. The slightly higher range for calcium, and the elevation of conductivity compared to previous studies may be attributed to the fact that all sites were located along the Dempster Highway, a significant source of calcareous dust (Gunter 2017). Our total nitrogen levels, which ranged from 0.13 to 0.98 mg/L, were similar to those concentrations measured by Houben et al. (2016) where concentrations ranged from 0.13 to 0.73 mg/L and Swadling et al. (2000), whose total nitrogen concentrations ranged from 0.25 mg/L to 1.58 mg/L. Our total phosphorus levels, which ranged from 22.97 to 85.56 µg/L, were also

similar to those concentrations measured by Houben et al. (2016) where concentrations ranged from 6.40 to 67.90  $\mu\text{g/L}$ .

### *Macroinvertebrate Communities*

We expected macroinvertebrate communities to differ between gravel pit and natural lakes owing to the relatively young age of the former, and differences in morphometric and water quality variables. However, our analyses did not find a significant difference in richness, diversity, or abundance between lake types. The relatively old age of these gravel pits may suggest that enough time has passed for most macroinvertebrate species to colonize these systems, leaving no difference in diversity metrics. This idea is supported by previous studies that have demonstrated rapid colonization of new habitats by benthic invertebrates (Voshell and Simmons 1984, Layton and Voshell 1991, Bass 1992). The taxonomic resolution used for macroinvertebrates may also offer an explanation, as this group was identified to the order and family level, which perhaps was too coarse to reveal differences in richness or diversity between lake types (Resh and Unzicker 1975, Jones 2008). However, some studies refute this and show that identifying below the genus level does not contribute more than coarser family to order level identifications of macroinvertebrates (Bowman and Bailey 1997, Mueller et al. 2013). Our ordination did not reveal differences in the structure of macroinvertebrate communities between natural and gravel pit lakes. In our RDA, chlorophyll-*a*, fish presence/absence, and mean depth were selected as significant predictors of community structure for macroinvertebrates. Chlorophyll-*a* levels and mean depth did differ significantly between gravel pits and natural lakes, but the low percentage of variation explained by the model (21.2%), suggests that macroinvertebrates are likely structured by variables that we did not measure.

### *Future Directions*

While we believe that our study design allowed us to test our hypotheses, there are some obvious limitations. Accessing a large number of lakes in isolated northern environments is difficult, and therefore we were only able to assemble a dataset of fifteen natural lakes and six gravel pit lakes which were accessible by the highway. Given this relatively small sample size, we considered running a power analysis to identify if biological differences between our lake categories (gravel pit vs. natural) did exist, but were not statistically different due to low power. However, there did not appear to be obvious differences in means for most variables (e.g. richness) that would suggest a difference was present, but not detected due to low power. Nonetheless, future work comparing littoral macroinvertebrate communities between younger gravel pit lakes than those examined in this study (<25 years old) may result in statistically significant differences. Our study was also limited in that we chose to focus on littoral macroinvertebrates. It is possible that future studies exploring differences in profundal macroinvertebrate communities could find a difference between gravel pits and natural lakes, especially given differences in depth between these two lake types. Finally, the redundancy analysis for our macroinvertebrates explained only 21% of variation in those communities. Although this level of explained variation is common in many studies (e.g. Tolonen et al. 2018), some studies have been able to explain in excess of 40% of the variation in macroinvertebrate communities (e.g. dos Santos et al. 2016). This suggests that future work measuring additional predictor variables that are relevant for littoral macroinvertebrates communities could be fruitful (e.g. sediment types).



### *How should we view gravel pits in the context of environmental management?*

Gravel extraction has several potential negative impacts, including the destruction of terrestrial habitats and the exposure of groundwater to pollution and evaporative losses (Mollema and Antonellini 2016, Søndergaard et al. 2018). In northern permafrost-laden areas specifically, cutting into the ground to extract gravel could lead to a change in the air-surface temperature balance, promoting slumping and erosion in adjacent areas (Kiggiak-EBA Consulting LTD. 2011). However, the results of this study and others suggest that the end result of gravel extraction is not entirely negative. In this study, gravel pit lakes were found to provide an adequate simulation of natural lakes for littoral macroinvertebrates. This is consistent with other studies that suggest gravel pit lakes can have ecological value by providing habitat for aquatic species, increasing biodiversity (Ejsmont-Karabin 1995; Gammons et al. 2009; Alfonso et al. 2010). In addition to their ecological value, gravel pit lakes can be used for recreational purposes including boating, fishing and swimming (Søndergaard et al. 2018). In some parts of the world expected to experience climate-change related shortages of freshwater supplies, gravel pit lakes may even increase the availability of surface water (Fang et al. 2010).

### *Conclusions*

In summary, gravel pit lakes differed in key morphometric and water quality parameters in comparison with natural lakes, however, littoral macroinvertebrate communities were similar. This similarity in macroinvertebrate abundance, richness, and diversity between gravel pit and natural lakes has also been noted for zooplankton communities sampled from the same lakes (Vucic et al. 2019). Since no differences in macroinvertebrate or zooplankton communities were

observed, this suggests that enough time may have passed for invertebrates that inhabit littoral (Voshell and Simmons 1984, Layton and Voshell 1991, Bass 1992) and pelagic (Ejsmont-Karabin 1995b, Alfonso et al. 2010) zones of the lakes to colonize. Our results suggest that gravel pit lakes along the Dempster Highway provide habitat that is of similar quality to natural lakes. The increasing pressure of northern development brings with it both economic growth and the potential for negative environmental effects. However, anthropogenic by-products, such as gravel pit lakes, may also yield unexpected positive effects for freshwater resources and the people that depend on them.

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## Tables

Table 2.1. Morphometric, water quality, and visually estimated vegetation characteristics of natural lakes and gravel pit lakes sampled along the Dempster Highway in August 2017. S.D. = standard deviation.

	Natural lakes				Gravel pit lakes			
	Mean	Min	Max	Standard Deviation	Mean	Min	Max	Standard Deviation
Latitude	67.80	67.34	68.35	0.44	67.78	67.38	68.04	0.25
Longitude	-133.91	-134.91	-133.28	0.58	-133.75	-134.15	-133.47	0.26
Temp (°C)	14.06	9.67	16.91	2.27	14.60	12.48	15.84	1.20
pH	6.92	6.10	8.28	0.62	7.81	6.62	8.54	0.80
Conductivity (µS/cm)	259.10	71.70	896.90	190.00	526.65	108.80	1084.00	360.54
DO (mg/L)	9.63	8.75	11.35	0.95	9.89	9.06	10.32	0.44
Turbidity (NTU)	4.33	0.34	13.22	4.13	0.98	0.57	1.72	0.45
Area (ha)	17.06	0.44	89.61	24.82	2.57	1.70	3.41	0.61
Volume (m <sup>3</sup> x 10000)	23.70	0.99	181.00	42.10	7.42	2.54	19.30	6.37
Shoreline Length (km)	1.80	0.26	5.58	1.64	0.61	0.49	0.69	0.07
Drainage basin area (ha)	3143.35	4.92	13824.30	4303.13	3604.63	4.68	13824.30	5214.96
Mean Depth (m)	1.62	0.80	2.60	0.51	6.40	3.50	10.00	2.19
Max Depth (m)	3.75	1.50	6.10	1.66	11.93	6.90	19.00	4.83
Secchi Depth (m)	1.91	0.47	3.65	0.97	4.09	1.26	7.59	2.04
Ca (mg/L)	26.57	8.08	51.03	11.24	30.53	13.11	52.53	17.02
Chlorophyll- <i>a</i> (µg/L)	1.25	0.18	4.97	1.38	0.38	0.08	0.94	0.33

TOC (mg/L)	22.20	11.61	40.39	8.03	15.28	9.30	22.95	5.96
TN (mg/L)	0.55	0.98	0.18	0.07	0.26	0.13	0.42	0.14
TP (µg/L)	56.28	34.24	85.56	16.05	35.24	22.97	49.26	9.71
Percent of lake bottom with submerged vegetation†	13.36	0.00	45.00	15.14	7.50	0.00	20.00	8.66
Percent of lake surface with emergent vegetation†	6.07	0.00	20.00	6.56	7.50	5.00	10.00	2.89
Percent of lake surface with floating vegetation†	4.64	0.00	45.00	12.00	1.25	0.00	5.00	2.50
Percent of lake surface with vegetation cover†	16.93	0.00	50.00	13.61	16.25	10.00	30.00	9.46
Percent shoreline consisting of trees†	23.60	0.00	51.33	23.93	5.85	2.25	8.10	2.03
Percent shoreline consisting of shrubs†	11.18	0.00	64.17	16.39	1.26	0.00	2.70	1.01
Percent shoreline consisting of grass†	21.77	0.00	64.17	25.73	1.08	0.00	1.80	0.63
Total riparian vegetation cover (%)†	64.17	5.00	100.00	41.82	9.00	1.00	16.00	7.55

†Visual estimates, not quantitative measures

Table 2.2. Results of Welch's t-tests comparing selected water quality and physical variables. T-tests were conducted only for variables associated with our three hypotheses. The Bonferroni p-value is corrected for eight tests. df = degrees of freedom.

	<b>t</b>	<b>df</b>	<b>p-value</b>	<b>Bonferroni p</b>
<b>Turbidity</b>	3.261	22.310	0.004	0.028
<b>Total Nitrogen</b>	4.714	17.696	0.000	0.001
<b>Mean Depth</b>	-5.400	5.172	0.003	0.021
<b>Total Organic Carbon</b>	2.537	7.697	0.036	0.288
<b>Conductivity</b>	-2.018	6.745	0.085	0.679
<b>Secchi depth</b>	-3.213	9.760	0.010	0.077
<b>Total phosphorus</b>	3.446	12.074	0.005	0.038
<b>Chlorophyll-<i>a</i></b>	2.261	9.040	0.050	0.400

## Figures

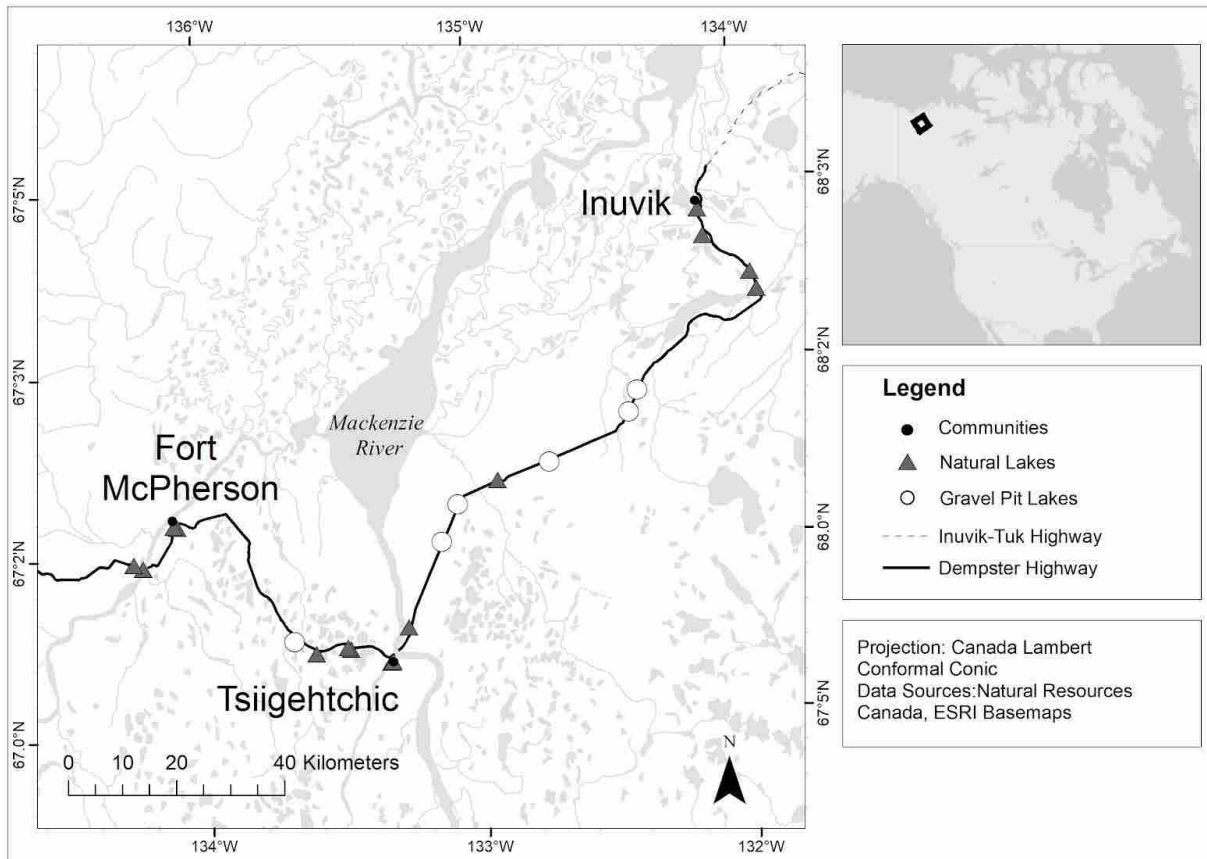


Figure 2.1. Map of lakes sampled along the Dempster Highway between Fort McPherson and Inuvik, Northwest Territories.

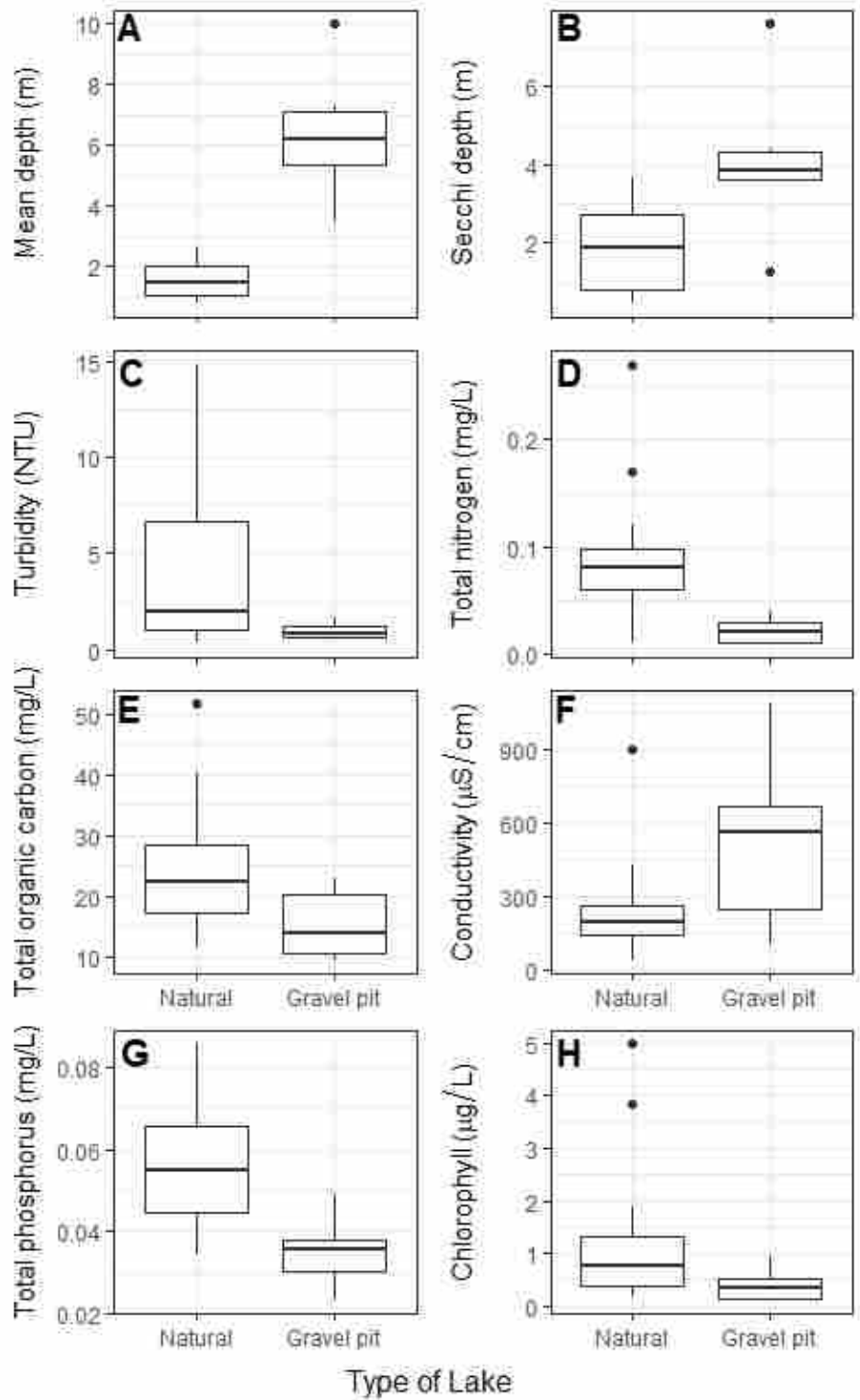


Figure 2.2. Comparison of selected morphometric and water quality variables between natural and gravel pit lakes. Bolded line=median, lower end of box=first quartile, upper end of box=third quartile, whiskers=range of data, dots=outliers.

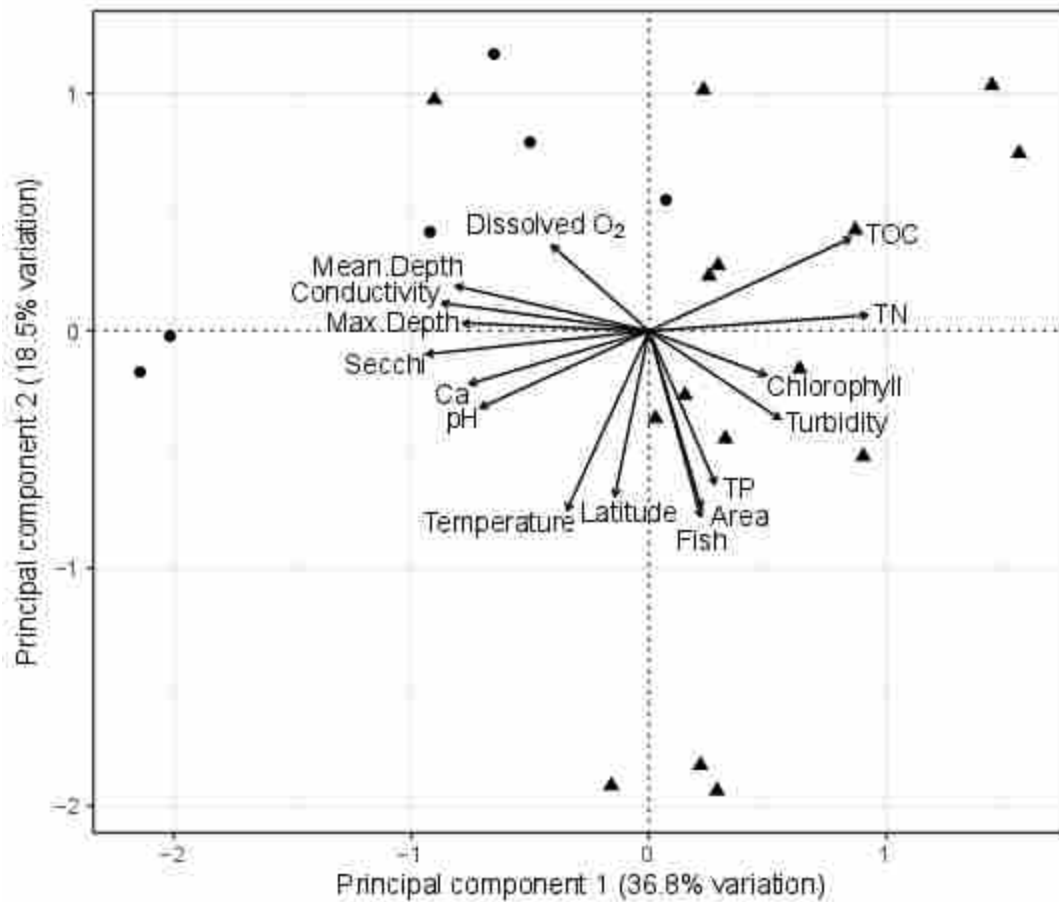


Figure 2.3. Principal component analysis (PCA) conducted with morphometry and water quality data for each of our 21 study lakes. Circles represent gravel pit lakes and triangles represent natural lakes. Sites that are closer together tend to have similar morphometry and water quality than sites that are farther apart. The angle between the arrows reflects the correlation between predictor variables. Gravel pits tend to cluster in the upper left quadrant of the PCA, indicating that they are deeper, clearer (high Secchi depth, low turbidity), smaller in area, and have low nutrient concentrations.



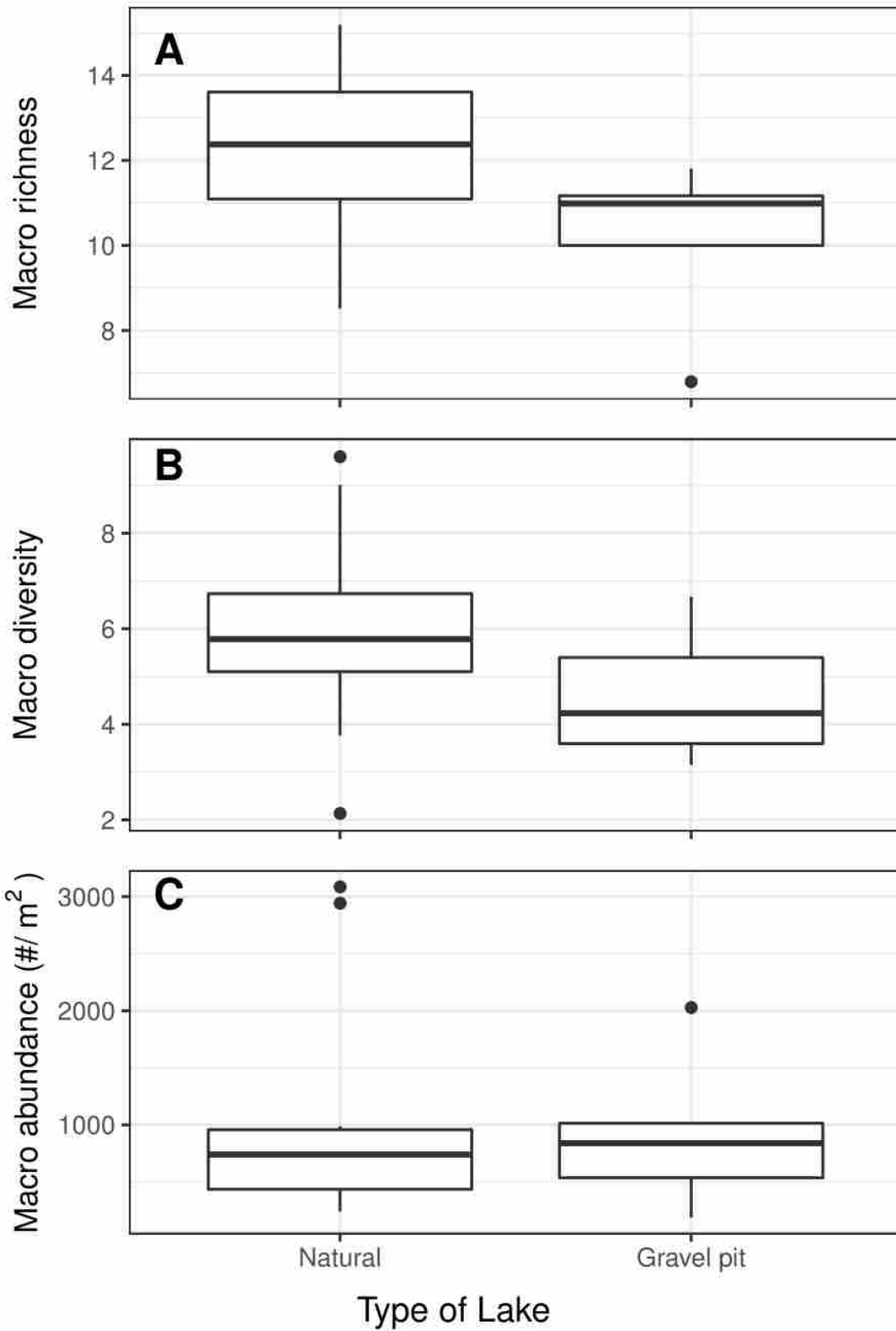


Figure 2.4. Comparison of rarefied species richness (A), Hill diversity (B), and abundance (C) of macroinvertebrates in natural lakes and gravel pit lakes.

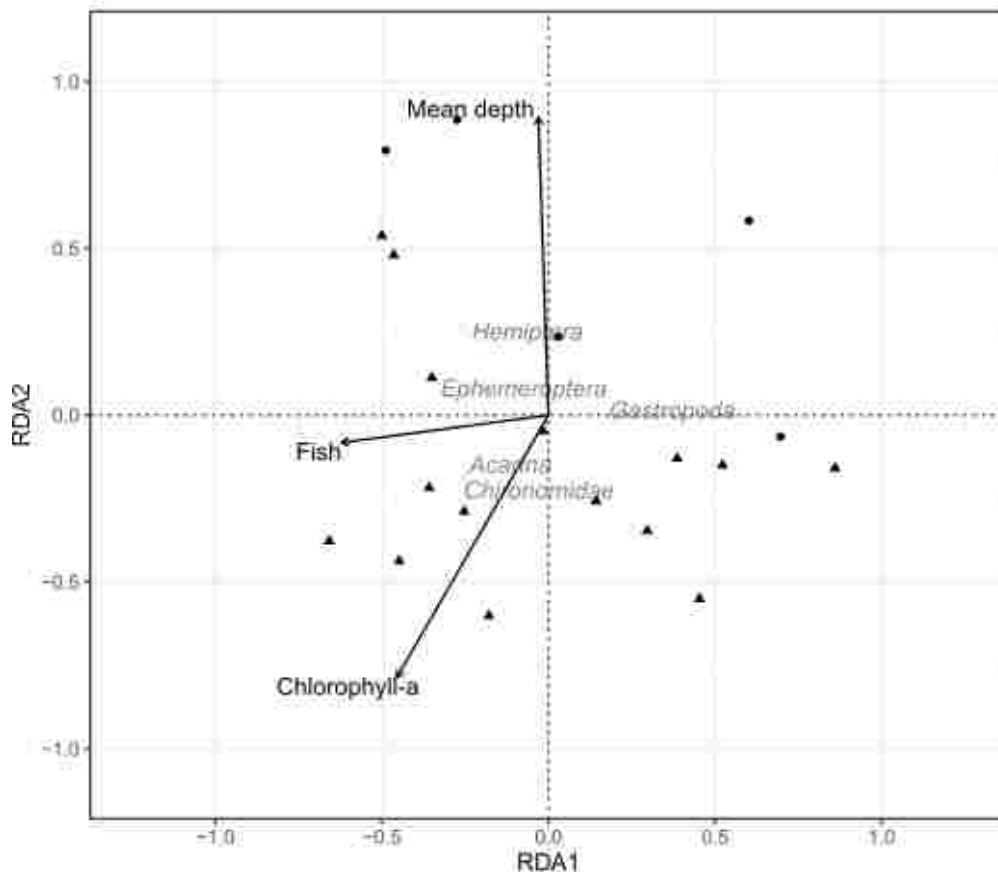


Figure 2.5. Results of redundancy analysis displaying predictor variables (morphometry and water quality) with macroinvertebrate abundances as response variables. Circles represent gravel pit lakes, triangles represent natural lakes. Taxa are represented by their grey text labels. Morphology and water quality variables are represented by arrows. Sites that are closer together in the ordination plot have similar macroinvertebrate community composition than sites that are further apart.

## CHAPTER 3:

### **Changes in water quality due to permafrost thaw may affect littoral macroinvertebrate community composition in Arctic lakes**

#### **Abstract**

The intensification of permafrost thaw in Arctic regions is altering lake water quality, presenting a need for an analysis of associated changes in biological communities. In this study, we characterised water quality and macroinvertebrate community composition in 46 Arctic lakes in the Northwest Territories. We then used the resulting dataset to build multiple linear regression models to describe how water quality variables were related to four community metrics: richness, diversity, abundance, and proportion of sensitive species in each community (Ephemeroptera, Plecoptera, Trichoptera or EPT). Using our models, along with data from the literature, we then predicted how community metrics may respond to changes in water quality expected due to permafrost thaw. The most parsimonious models included between 1-5 variables expected to be influenced by permafrost thaw (e.g. calcium, turbidity) and explained between 44-63% of the variation in community metrics. Our models predicted small increases in richness and diversity in response to water quality changes related to permafrost thaw, but abundance and % EPT were predicted to decline by ~7% and ~20% for every 10% change in permafrost thaw-related variables. Given the magnitude of the predicted changes in community composition and abundance, organisms at other trophic levels that depend on macroinvertebrates, such as fish and water birds, could be affected.

**Key words:** Macroinvertebrates, permafrost, lakes, Arctic, Mackenzie delta, climate change, Gwich'in Settlement Area, Inuvialuit Settlement Region.

## **Introduction**

Studies of long-term temperature change in the Arctic show that in the last half-century, warming exceeded expectations based on earth's natural cycles, and in the past few decades, the Arctic has warmed at two to three times the rate of the rest of the world (Prowse et al. 2006, Kaufman 2009, AMAP 2012, Meyer et al. 2015). Due to rising temperatures, soil that was normally frozen year-round (permafrost) is beginning to thaw (Zhang et al. 1999). Ongoing warming in the north is expected to change the coverage and distribution of permafrost, leading to significant impacts on infrastructure, vegetation, freshwaters, and the organisms that live in northern habitats (Wrona et al. 2006, AMAP 2012, Ford et al. 2015). Studies show that the distribution of permafrost is already shifting in many regions by disappearing entirely from its southern limit and becoming discontinuously distributed where it was previously continuous (AMAP 2012). The total area occupied by permafrost is expected to decline by 11, 18, and 23% by 2030, 2050, and 2080, respectively (ACIA 2005). In Canada, climate models project that by 2100, the top 2-3 m of permafrost will thaw in 16-20% of regions underlain by permafrost (AMAP 2012).

In many areas, permafrost thaw results in the deepening of the layer of soil that thaws and refreezes annually (the active layer), but along lake and stream margins, permafrost degradation can lead to the collapse and subsequent erosion of shoreline soils, creating features called shoreline retrogressive thaw slumps (hereafter referred to as thaw slumps; Kokelj et al. 2009, 2013). As permafrost thaws, water quality in nearby lakes and streams can be significantly altered (Kokelj et al. 2009). Permafrost in the western Canadian Arctic contains elevated levels of solutes, including calcium, magnesium, sodium, and phosphorus (Keller et al. 2007; Burn and Kokelj 2009). The deepening of the active layer can allow for weathering of these minerals and

their movement into freshwater habitats (Keller et al. 2007). Lakes and streams affected by thaw slumps are impacted not only by elevated levels of solutes, but by increased sediment loads, surface runoff, and groundwater flow (Prowse et al. 2006, Wrona et al. 2016). The nutrient runoff received by lakes from thaw slumps and permafrost thaw results in lower dissolved organic carbon concentration and colour, while increasing water ion concentrations (such as Ca and Mg), pH, conductivity, and water clarity (Kokelj et al. 2005; Burn and Kokelj 2009; Mesquita et al. 2010; Thompson et al. 2012; Houben et al. 2016). Thawed sediments and solutes that enter lakes from permafrost thaw cause not only ionic enrichment, but increases in trace metals such as uranium, strontium, and lithium (Houben et al. 2016). In contrast, the higher pH associated with ion rich sediments entering lakes acts to decrease ions such as Fe, Mn, and Al concentrations in the water column (Houben et al. 2016). This sedimentation is a likely driver of the removal of nutrients such as nitrogen and phosphorus leading to a decrease in chlorophyll-a concentrations in thaw slump impacted lakes by as much as two thirds compared to undisturbed lakes (Houben et al. 2016). Collectively, these changes result in a reduction in primary productivity of phytoplankton and periphyton and increases in well-developed rooted macrophytes and benthic algae communities (Mesquita et al. 2010; Thompson et al. 2012; Thienpont et al. 2013; Houben et al. 2016). Overall, this suggests that thaw slumps can significantly impact food webs in Arctic tundra lakes through increases in submerged macrophytes and development of a benthic habitat which may have effects that cascade through the food web. Permafrost thaw impacts on lakes have been shown to increase with the percent catchment area impacted by thermokarst activity (Kokelj et al. 2005, 2009; Houben et al. 2016). However, disturbance of as little as 2% of a catchment can influence lake water chemistry and quality (Kokelj et al. 2005).

Benthic macroinvertebrate communities may be especially sensitive to the effects of permafrost thaw, as they respond to changes in conductivity, water hardness, and sedimentation rates (Duan et al. 2009; Pyron et al. 2009; Blaen et al. 2014; Savić et al. 2017; Brown et al. 2018). To our knowledge, there are has only been a single study that has directly investigated the impacts of permafrost disturbance on macroinvertebrates in lakes (Moquin et al. 2014). Moquin et al. (2014) found that macroinvertebrates abundance was higher in lakes affected by thaw slumps, probably due to higher concentrations of Ca and Mg in sediments and increased macrophyte biomass. They also found differences in community structure between control and thaw slump-impacted lakes, with lower Chironomidae and much higher abundances of Ostracoda and Nematoda in thaw slump lakes (Moquin et al. 2014). While Moquin et al. (2014) performed a very comprehensive survey of macroinvertebrates within each of their study lakes, this necessitated a trade-off with the number of total lakes they could assess, which included only three control and five thaw slumps-impacted lakes. In addition, since their dataset did not include any lakes affected by permafrost thaw without thaw slumps, it is unlikely that their data are representative of lakes not directly influenced by thaw slumps. As a result, studies are needed to evaluate how macroinvertebrates might respond to more subtle changes in water quality caused by permafrost thaw without thaw slumps.

For this study we conducted a survey of physiochemical and biological parameters for 46 lakes in Canada's western Arctic. We used the resulting dataset to develop models that explain variation in macroinvertebrate community structure among lakes. These models were then used to predict how macroinvertebrate communities may respond to changes in water quality as a result of permafrost thaw. Our model results predict that richness and diversity of

macroinvertebrates will increase, while abundance and % EPT will decrease significantly in response to water quality changes associated with permafrost thaw.

## **Methods**

### *Study site*

The study was carried out in the Northwest Territories within the Gwich'in Settlement Area (GSA) and Inuvialuit settlement region (ISR). These low-Arctic regions contain an interconnected system of rivers, streams, and lakes which provide hunting and fishing ground for the Gwich'in and Inuvialuit indigenous communities that live in the GSA and ISR respectively.

In this study, lakes were sampled along the Dempster and Inuvik-Tuktoyaktuk highways between Fort McPherson and Tuktoyaktuk, spanning the northern half of the Mackenzie Delta (Figure 3.1). The Mackenzie Delta region covers an area of 13,135 km<sup>2</sup> and contains over 49,000 lakes and ponds (Emmerton et al. 2007). Most lakes in this area are small (<2 ha) and shallow with mean depth that range between 0.5 m to 4.5 m; however, depths vary according to the time of year, local precipitation, and adjacent river and stream water levels (Lesack and Marsh 2010). This lake-rich environment is one of the most dynamic ecosystems in northern Canada (Squires et al. 2009), providing habitat for a wide variety of wildlife. Lakes and rivers in this region flow northeast, through large and thinly populated regions of forest and tundra, and they empty into the Beaufort Sea west of Tuktoyaktuk (Kokelj et al. 2009).

Our study lakes were located along the Boreal to Tundra transition area. Nineteen of the lakes were sampled in August 2017 in the Boreal forest region within the GSA, and 27 of the lakes were sampled in August 2018 in the ISR where Tundra vegetation dominates (Figure 3.1).

The boreal-dominated GSA is underlain by discontinuous (“patchy”) permafrost while the Tundra of the ISR is located in an area of continuous permafrost (Kokelj et al. 2009) (Figure 3.1).

### *Biological data*

Macroinvertebrate samples were collected using a modified version of the Ontario Benthic Biomonitoring Network protocol (OBBN). Following the protocol, three replicates of samples were collected using a 500 µm D-net to kick and sweep macroinvertebrates. The modifications to the original OBBN protocol were that each replicate was collected over three minutes, and replicates were taken along parallel transects from the shore until 1 m depth was reached. Replicates were not taken in different parts of the lake as in the conventional OBBN protocol due to inaccessibility of different parts of the shoreline. The boggy terrain often made it difficult to access lake shorelines and walking the shoreline of some lakes was sometimes impossible without sinking into the peat. A three-minute kick and sweep per replicate rather than the ten minute one was a decision made based on the abundance of organic matter on the lake bottom that quickly clogged the D-net, preventing further sample collection. Each sample was preserved in 95% ethanol and brought back to the laboratory for identification. Using a 500 µm sieve and a dissecting microscope, macroinvertebrates were identified to the order and family level in the laboratory according to the OBBN tally sheet (Jones et al. 2007; Table A1). Quality assurance and quality control was performed on taxonomic accuracy and sorting efficiency (Figure A1) following the Canadian Aquatic Biomonitoring Network (CABIN) protocol (Ministry of Science & Information Branch, 2009). Full samples were counted and identified from the 19 lakes collected in 2017 from the GSA, while subsampling by weight was used in the



27 lakes sampled the next year in the ISR. In these set of samples, the total weight of each sample was recorded, and a small subsample that accounts for at least 10% of the sample was taken. If at least 100 individuals were not counted in the first subsample, an additional subsample was taken. This was repeated until at least 100 individuals were identified. The weights of subsamples were recorded to allow for proper estimation of the macroinvertebrate population within the entire sample.

Fish community data was collected in both sampling years. In 2017, gillnetting was executed according to the Ontario Broadscale Monitoring (BsM) protocol (Sandstrom et al. 2013). In 2018, the BsM protocol was modified and nets were checked every 45-60 minutes and deployed an average of 11 hours in small to medium lakes (<5 km<sup>2</sup>) and 37 hours in larger lakes (>5 km<sup>2</sup>). The sampling method was changed to address community concerns regarding the more lethal method of the BsM protocol where gillnets are left overnight (16-22 hours). As a result of difference in sampling between field seasons, the presence and absence of fish species was used instead of catch per unit effort. In our statistical analysis we used the presence and absence data for the most abundant fish that were caught, including lake whitefish (*Coregonus clupeaformis*), northern pike (*Esox lucius*) and least cisco (*Coregonus sardinella*). We also used overall fish presence and absence which was determined using gillnetting as described above. Where gillnetting was not performed, the presence of the phantom midge *Chaoborus americanus* was used as an indicator for fish absence (Schilling et al. 2009). The absence of fish was inferred in 9 of the 46 lakes using *C. americanus*, lake whitefish was present in 9 lakes, least cisco in 14 lakes, and northern pike in 19 lakes.

### *Water quality and chemistry data*

A variety of water quality and chemistry parameters were collected in lakes where macroinvertebrates were sampled (Table 3.1). Water clarity was obtained by measuring Secchi depth at the deepest point of the lake by lowering the Secchi disk over the shady side of the boat. Near shore, A Eureka Manta multi-parameter probe was used to take water quality measurements that included pH, conductivity, turbidity, and water temperature. Additionally, a nearshore water sample was collected for use in measuring total suspended solids (TSS), chlorophyll-*a*, total phosphorus, total nitrogen, dissolved organic carbon, and calcium. The standard operating procedure to determine total suspended solid concentrations was followed according to method 2540 D (American Public Health Association et al. 2012). Chlorophyll-*a* concentrations were obtained by filtering 250 mL of the water sample through Fisherbrand G4 glass fiber filters. Methanol was then used to extract the chlorophyll-*a* from the filters which was measured using a fluorometer (Turner TD700) (Symons et al. 2012). A Perkin Elmer Optima 8000 Inductively Coupled Plasma Optical Emission Spectroscopy (ICP-OES) was used to measure Ca concentrations in the shoreline water samples. Dissolved organic carbon and total nitrogen concentrations were measured using the Shimadzu TOC-LCPH carbon and nitrogen analyzer (Shimadzu Corp.). Total phosphorus was obtained by first digesting a portion of the sample in an autoclave using ammonium persulfate and sulfuric acid according to EPA method 365.1. Then, a SEAL Continuous Segmented Flow Analyzer (SEAL Analytical, Inc.) was used to measure total phosphorus colorimetrically.

In addition to the described water quality parameters, we collected sediments which have been shown to be important in determining the structure of macroinvertebrate communities in lakes (De Sousa et al. 2008; Namayandeh and Quinlan 2011). We determined sediment size

distribution by drying sediment samples at 105 °C for 8 hours and then using a sieve shaker for ten minutes per sample to separate grain sizes using seven different sieve sizes (4 mm, 2 mm, 1 mm, 500 µm, 250 µm, 125 µm, 63µm). In our analyses we chose to include only % fines (<2mm), and % silts and clays (<63 µm) due to a strong negative correlation between larger sediments and smaller sediments which was leading to problems with collinearity of predictors in our models. We then took 5 g of sediment that was <2 mm for each sample, and using the standard operating procedure for loss on ignition, we calculated % organic matter in the sediment and % CaCO<sub>3</sub> by burning the sediment in the muffle furnace at 550°C for four hours and then 1000°C for 2 hours, respectively (Santisteban et al. 2004).

#### *Physical data*

Mean depth and the surface area were determined by constructing a bathymetric map of each lake using a Humminbird® Helix 5 chart plotter (Johnson Outdoors Marine Electronics, Inc.) with Reefmaster bathymetry software (Reefmaster Ltd.). Catchment area for each lake was obtained using 2 m resolution digital elevation maps (Porter et al. 2018) and the watershed tool in ArcMap version 10.5 (Esri Inc.).

#### *Water quality and community composition analysis*

A principal component analysis (PCA) was run for both water quality variables and macroinvertebrate community data. The linearity assumption of the PCA was tested using a detrended correspondence analysis (DCA). This method determines gradient lengths which can be used to decide if the data may be better evaluated by linear (PCA) or unimodal ordination

(correspondence analysis). The decorana function from the “vegan” package in R (Oksanen 2019) was used to determine gradient lengths which are represented by the axis length in this function’s output (Borcard et al. 2011). Gradient lengths  $<4$  indicated that both water quality and species data were suitable for a PCA (Borcard et al. 2011). All water quality variables were transformed, standardized, and examined with histograms to achieve a normal distribution for each (Table A2) and the PCAs were created using the “prcomp” function in R (R Development Core Team, 2018). To reduce problems associated with rare species, macroinvertebrate abundances were Hellinger-transformed and species present in fewer than 5% of sampled lakes were removed prior to conducting the species PCA (Legendre and Gallagher 2001). A cluster analysis was used to further understand variability of the macroinvertebrate communities in the sampled lakes. This method categorized lakes into groups based on the similarity of their macroinvertebrate community structures (Dytham 2011). We used a k-means cluster analysis as implemented in the k-means function from the “stats” package in R (R Core Team 2019). To choose k, the number of clusters, the “elbow method” was used, which plots the within group sum of squared errors for the model against the number of clusters (Kodinariya and Makwana 2013). From interpreting the resulting plot, three groups were chosen since adding additional groups resulted in only small improvements to the within group sum of squares (Figure A2). To investigate associations between macroinvertebrate community structure recovered in the PCA, we ran Pearson correlations between the predictor variables and the community PCA axis scores using the rcorr function in the Hmisc package for R (Harrell and Dupont 2019).

### *Community metrics*

We considered using a variety of common metrics to describe the structure of macroinvertebrate communities in our study lakes, however many of these metrics were correlated with one another (Figure A3). Rather than using metrics with duplicate information, we selected a subset of four variables that were not strongly correlated with one another: Hill's diversity, richness, % Ephemeroptera/Plecoptera/Trichoptera (EPT), and total abundance (Figure A3). The % EPT metric is frequently used because these benthic invertebrates are sensitive to depletion of dissolved oxygen and to a variety of pollutants (Cairns and Pratt 1993, Jacobsen et al. 2003, Saari et al. 2018). Therefore, they are normally found in good quality freshwater habitats.

In calculating our measures of diversity and richness, we used methods to correct for differences in sampling effort among lakes. For species richness, we used rarefaction, which calculates the expected number of species given a fixed sample size across lakes (Gotelli and Colwell 2001). The rarefy function from the 'Vegan' package in R was used to obtain the expected species richness based on 239 individuals per lake (Oksanen 2019), as that was the lowest number of individuals counted for a single lake. Similarly, diversity was also corrected for differences in sampling effort by calculating rarified Hill numbers according to Chao's method (Chao et al. 2014). The estimateD function was used in the iNEXT package in R to calculate order 1 Hill numbers that represent an exponential of Shannon's entropy index (Hsieh et al. 2016).

Total abundance of macroinvertebrates per lake was calculated by summing up the total number of individuals collected from each lake. For macroinvertebrate counts based on subsamples, the subsample was used to estimate the total number in the entire sample, which was

representative of total abundance. % EPT was calculated by summing up the abundances of all individuals belonging to Ephemeroptera, Plecoptera, and Trichoptera in each lake and dividing by the total abundance of macroinvertebrates in each lake.

#### *Accounting for missing data*

Although all explanatory variables were collected to the best of our ability in the 46 lakes where macroinvertebrates were sampled, we were only able to obtain a dataset with 35 lakes that contained both fish community data and sediment data. The larger 46 lake dataset had fish community data but was missing sediment data for some lakes. When examining overall macroinvertebrate community structure and water quality, we used our 46-lake dataset to maximize the number of lakes in our sample. However, since sediment and/or fish community data may play an important role in explaining different community metrics, we used the 35-lake dataset when building our predictive models for richness, Hill diversity, total abundance, and % EPT.

#### *Model development and predictions*

Multiple linear regressions were performed on total abundance, % EPT, diversity, and richness using the 35-lake data set (including all explanatory variables). The final regression models were selected using the `glmulti` function in R which performs exhaustive screening of models and ranks the best models according to an information criterion (Calcagno 2019). We used a modification of the Akaike Information Criterion, AIC-c which is intended to avoid overfitting if the number of predictors is large compared to the size of the sample (Burnham and

Anderson 2004). The `gvlma` function in R was used to test that our models met the assumptions of a multiple linear regression as described in Peña and Slate (2006). Diversity was log transformed to improve the linear relationship while total abundance and %EPT were both cube root transformed in order meet assumptions, and improve the linear relationship, respectively. The variance inflation factor (VIF) was calculated for each model to ensure there was little to no collinearity (VIF < 4 for all variables included in the final models).

The linear models we developed for each community metric (richness, diversity, abundance, % EPT) were used to predict future changes in those metrics by altering values for permafrost related variables that were included in the regression models in 5% intervals. The values were altered up or down according to their expected direction of change found in previous studies (Table 3.2). For example, Ca was included in the model for Hill Diversity, and this variable has been shown to increase with permafrost thaw. Therefore, we increased calcium levels for each of the lakes in our dataset in 5% intervals and used our model to predict values for Hill Diversity given this increase. We limited the percent increase or decrease of the permafrost thaw-related variables such that mean values used in predictions did not fall outside the range found in our dataset. For example, total nitrogen is expected to decrease as a result of permafrost thaw, and the lowest value for total nitrogen in our dataset was ~0.20 mg/L, so the mean total nitrogen levels used for our predictions were lowered in 5% intervals until that level was reached.

## Results

### *Water quality*

The 46 lakes included in our study exhibited a wide range in their physiochemical properties (Table 3.1). Lake surface area ranged from 0.004 km<sup>2</sup> to 82.90 km<sup>2</sup> with catchment areas between 0.01 km<sup>2</sup> to 126.18 km<sup>2</sup>. Mean depth of our study lakes varied between 0.80 m and 10.00 m. Variables expected to be influenced by permafrost thaw (Table 3.2) also exhibited wide ranges, including pH (6.7-9.8), conductivity (58-873 µS/cm), Secchi depth (0.46-7.59 m), Ca (7.06-59.48 mg/L), total phosphorus (22.98-173.81 µg/L), total nitrogen (0.099-0.988 mg/L), and chlorophyll-*a* (0.084-24.19 µg/L) (Tables 3.1, 3.2).

The PCA of environmental variables explained 46% of the variation among our study lakes (Figure 3.2). The results of our PCA with water quality parameters showed that lakes sampled within the GSA, the more southern region of the study, had lower PCA 1 scores and were characterized by higher temperature, conductivity, dissolved organic carbon and pH (Figure 3.2). Artificial gravel pit lakes sampled in the GSA tended to have much lower PCA 1 scores because they were deep with high conductivity and calcium levels (Figure 3.2). In contrast, the northern lakes in our dataset sampled in the ISR had higher PCA 1 score and were characterized by their larger surface area, fish presence, turbidity, and chlorophyll-*a* (Figure 3.2).

### *Community structure*

The PCA of the macroinvertebrate communities explained 45.6% of the variation in community structure among our study lakes (Figure 3.3). Our cluster analysis grouped our study lakes into three clusters based on the dominant organisms found within them: Chironomidae,



Amphipoda and Gastropoda (Figure 3.3). Generally, lakes with abundant Chironomidae and Amphipoda were clustered on opposite ends of the first PCA axis, while lakes with Gastropoda was found on the positive end of the second axis (Figure 3.3). The first axis was found to be negatively related to Cisco presence, conductivity, and pH ( $p < 0.01$ ; Figure 3.4A). Axis 2 was found to be negatively related to lake turbidity, catchment and surface area, chlorophyll-*a*, and latitude ( $p < 0.01$ ; Figure 3.4B). The same axis was also positively related to temperature, conductivity, Ca, total phosphorus, and dissolved organic carbon ( $p < 0.01$ ; Figure 3.4B).

### *Community metrics*

The rarefied richness for macroinvertebrates ranged from ~8.1 to ~16.5 with a mean of ~12.0 taxa per lake (Table 3.3). The regression model for richness included chlorophyll-*a*, dissolved organic carbon, total nitrogen, whitefish presence, and % silts and clays (Table 3.4). Collectively, these variables explained 52.8% of the variation in richness ( $p < 0.001$ ; Table 3.4). In response to expected declines in chlorophyll-*a*, dissolved organic carbon, and total nitrogen from permafrost thaw (Table 3.2), richness is predicted to increase by ~1.5% for every 10% decrease in these three variables (Figure 3.5).

Hill's diversity varied from ~2.4 to ~10.5, with a mean of ~5.3 in our study lakes (Table 3.3). The regression model for diversity included dissolved organic carbon, mean depth, % fine sediment (<2 mm in size), and whitefish presence (Table 3.4). Together, these predictors accounted for 44.0% of the variation in diversity ( $p \sim 0.001$ ; Table 3.4). In response to an expected decrease in dissolved organic carbon due to permafrost thaw (Table 3.2), diversity is predicted to increase by ~5% for every 10% decrease in dissolved organic carbon (Figure 3.5).

On average, we found ~738 macroinvertebrates per square meter, but total abundance ranged from ~80 to ~2161 individuals m<sup>-2</sup> (Table 3.3). The regression model for total abundance included chlorophyll-*a*, mean depth, Secchi depth, whitefish presence, and % fine sediment (Table 3.4). This model explained 62.4% of the variation in total abundance (P<0.001; Table 3.4). Using this model, we predicted that an expected decline in chlorophyll-*a*, and an increase in Secchi depth (Table 3.2), could lead to a 10% decrease in abundance for every 10% change in these permafrost thaw-related variables (Figure 3.5).

% EPT varied in our lakes from ~0.2% to ~15.3% with a mean of ~5.2% (Table 3.3). The variables included in the regression model for % EPT were temperature, pH, conductivity, turbidity, chlorophyll-*a*, total phosphorus, and whitefish presence (Table 3.4). This model explained 62.8% of the variation in % EPT (p<0.001; Table 3.4). Due to the expected decrease in chlorophyll-*a*, dissolved organic carbon, turbidity, and total phosphorus, as well as an increase in conductivity (Table 3.2), our model predicts that % EPT will decrease by ~20% for every 10% decrease in these permafrost thaw-related variables (Figure 3.5).

## **Discussion**

Using data from our lake survey, we were able to build models that explained 44% to 63% of the variation in macroinvertebrate richness, diversity, abundance and % EPT in small Arctic lakes. Importantly, over half of the variables selected in our multiple linear regression models for these metrics have been shown to be affected by permafrost thaw (Table 3.4; 3.5). According to our models, overall macroinvertebrate richness will change very little in response to the combined effects of decreased chlorophyll-*a*, dissolved organic carbon, and total nitrogen,

while diversity is expected to increase moderately in response to declining dissolved organic carbon levels (~5% for every 10% decline in dissolved organic carbon). More significant changes are expected for macroinvertebrate abundance and % EPT, with abundance declining ~10% for every 10% change in chlorophyll-a and Secchi depth, and % EPT declining by ~20% for every 10% change in conductivity, chlorophyll-a, turbidity, and total phosphorus. Our prediction of a decline in abundance is in contradiction with the findings of Moquin et al. (2014) who recorded increased abundance of macroinvertebrates in five lakes affected by thaw slumps relative to three undisturbed sites. Moquin et al. (2014) suggested that the increased abundance of macroinvertebrates in lakes impacted by thaw slumps was related to increases in Ca and organic matter in sediments. While both sediment calcium and organic matter were included as possible variables in our multiple regressions, they did not show a significant association with abundance in our lakes. For % EPT, we are unaware of any studies that have examined changes in relation to permafrost degradation. However, the relationship between % EPT and the variables included in our model, such as conductivity and turbidity, have been found in other studies looking at the impacts of disturbance (Móra et al. 2011; Savić et al. 2017).

Our models show that abundance is heavily positively related to chlorophyll-*a* and negatively related with Secchi depth. This is in contrast to the negative relationship of % EPT and richness with chlorophyll-*a* and the negative relationship of macroinvertebrate richness and diversity with DOC. These results suggest that lakes we sampled may be reflecting alternate stable states as this is common for shallow northern lakes containing intermediate phosphorus levels (Jeppesen et al. 1990, Scheffer 1990, Scheffer et al. 1993). Our models suggest that in the clear state, macroinvertebrate richness, % EPT, and overall diversity thrive while in the turbid state, one dominant macroinvertebrate such as an amphipod or chironomid succeeds increasing

overall macroinvertebrate abundance. It may be that alternate stable states are affecting our model predictions by masking some of the true long term variation in overall lake water quality. Therefore, long term monitoring on these roadside lakes may be necessary to confirm they are alternating between two stable states.

#### *Potential responses of community structure to permafrost thaw*

Macroinvertebrate community structure showed clear gradients in community composition between those dominated by chironomids, amphipods, or gastropods. Interestingly, these gradients in community structure were related to many variables that are affected by permafrost thaw. Along the first axis, the transition from communities dominated by amphipods to those dominated by chironomids was correlated with lower levels of pH, conductivity, and cisco presence (Figure 3.3; Figure 3.4A). Therefore, expected increases in pH and conductivity due to permafrost thaw are likely to cause a shift towards amphipod and nematode dominated communities (Table 3.2; Figure 3.3; 3.4A). Declines in chironomids in thaw slump lakes were also noted by Moquin et al. (2014), however, in their study, these declines were attributed to decreases in organic carbon in water and sediments. Minerogenic inputs from permafrost thaw can increase conductivity and pH, while at the same time decreasing sediment organic carbon by covering natural lake sediment (Deison et al. 2012). Therefore, chironomids may be susceptible to permafrost thaw through changes both to their general habitat (water chemistry) and their food availability (they are largely detritivores).

Along the second PCA axis, the transition between gastropod-dominated communities and those dominated by either amphipods or chironomids was also related to a variety of

variables that are expected to change in response to permafrost thaw (Figure 3.3; 3.4B; Table 3.2). Scores along the second axis were positively correlated with higher conductivity and Ca levels (Figure 3.3; 3.4B), meaning that gastropod-dominated communities tended to be found in lakes with higher conductivity and Ca, while amphipod and chironomid-dominated communities often existed in lakes with high turbidity and chlorophyll-*a*. According to Houben et al. (2016) and Kokelj et al. (2005), permafrost thaw is expected to decrease lake chlorophyll-*a* levels by ~1.3x and turbidity by ~1.5x, while conductivity and calcium levels are expected to increase by ~4.8x and ~5.5x, respectively. Our PCA (Figure 3.3) and Pearson correlations (Figure 3.4B) indicate that these changes could lead to more gastropod-dominated communities. Although dissolved organic carbon levels are expected to decrease by ~1.5x, suggesting a shift toward amphipod or chironomid dominated communities, the magnitude of the expected changes in calcium and conductivity are much higher than those for dissolved organic carbon, chlorophyll-*a*, and turbidity, meaning that an overall shift toward higher axis 2 scores is more likely. These results share some commonalities with those of Moquin et al. (2014), but there are also some important differences. Moquin et al. (2014) did find that the relative abundance of chironomids was lower in lakes affected by thaw slumps, but in their study ostracods and nematodes made up for the loss of chironomids rather than gastropods. This may simply be a result of the differing importance of gastropods between lakes in our dataset and those sampled by Moquin et al. (2014), as gastropods made up between 0-44% (mean 5.4%) of the abundance of macroinvertebrates in our lakes, while gastropods were rare in the lakes sampled by Moquin et al. (2014).

### *Water quality of lakes in the study area*

Water quality parameters in our study lakes generally appeared to be representative of lakes within our region of study, with some exceptions. Our average pH of 8.0 was slightly higher than the average observed in other studies in the area which ranged from 6.9 to 7.9 (Pienitz et al. 1997; Rühland et al. 2003; Kokelj et al. 2009; Houben et al. 2016; Table A3). The average conductivity and calcium values and ranges of our lakes were similar to those found by Pienitz et al. (1997) and Kokelj et al. (2009) (Table A3). In contrast, our values were much higher than those reported by Houben et al. (2016) and Rühland et al. (2003). This is likely because the lakes investigated in our study were in close proximity to the road (Gunter 2017), receiving ions such as Ca and Mg, therefore raising the conductivity. Pienitz et al. (1997) sampled a number of brackish lakes near the Beaufort Sea coast and Kokelj et al. (2009) sampled lakes that were disturbed by permafrost thaw, likely explaining the higher conductivity and ion concentrations in their studies. Our Secchi depth average and range were higher than that found in Houben et al. (2016) for natural lakes. This is likely because our data set includes gravel pit lakes which have been shown to be two times clearer than natural lakes (Vucic et al. 2019). Chlorophyll-*a* concentrations in our study averaged 4.86 µg/L and ranged from 0.08 to 24.20 µg/L, similar to the average of 4.53 and a range of 0.60 to 19.60 µg/L found by Houben et al. (2016). The lower end of our range for chlorophyll-*a* is also due to the inclusion of gravel pit lakes in our data set which were shown to contain three times less chlorophyll-*a* than natural lakes (Vucic et al. 2019). The total nitrogen average of 0.45 mg/L falls within the 0.43-0.55 mg/L range of average total nitrogen found in multiple studies conducted in similar and overlapping study areas (Pienitz et al. 1997; Rühland et al. 2003; Houben et al. 2016). The mean total phosphorus value of 66.15 µg/L also falls within the higher end of the 6.40-67.90 µg/L

range found in Houben et al. (2016), although the range of our total phosphorus values is wider, this is likely due to the inclusion of lakes adjacent to the towns of Inuvik and Fort McPherson.

The ordination resulting from our principal component analysis with our water quality variables showed that lakes clearly separated into those located in the boreal-dominated Gwich'in Settlement Area versus those in the tundra-dominated Inuvialuit Settlement Region (Figure 3.2). This separation of lakes along the boreal-tundra transition has also been found in previous studies where more southern lakes have elevated total nitrogen, pH, temperature, conductivity and calcium levels (Pienitz et al. 1997, Swadling et al. 2000, Rühland et al. 2003). One explanation for this pattern is that lakes located in the northern continuous permafrost zone experience less groundwater flow, resulting in less cations running into the lakes in comparison with southern lakes found in the discontinuous permafrost zone (Rühland et al. 2003). It is interesting to consider that permafrost thaw may alter lake chemistry not only through the leaching of dissolved solutes, but also through changes to the flow of groundwater into lakes (Yoshikawa and Hinzman 2003).

#### *Model quality and study limitations*

The accuracy of our projections for future change in macroinvertebrate communities depend on the quality of models constructed with our dataset. We made efforts to avoid overfitting and data dredging by using AIC<sub>C</sub> during model selection (Cavanaugh 1997), and by excluding variables from the model building process unless they had been found to have relationships with our selected community metrics in previous studies. For example, while we had data on chemical variables other than Calcium (i.e. Fe, K, Mn, Sr, Li), they were not included as potential variables in our models because we could not find literature that reported

any associations with species richness. In addition, we checked to ensure that the direction of the relationships between our predictor and response variables matched those reported in the literature. Fortunately, the relationships identified in our models were supported by previous findings in the literature (Table 3.5), giving us confidence that spurious relationships were not driving our models.

It is important to keep in mind that our models were limited by the availability of predictors that were measured for each lake, and by the availability of information in the literature about potential environmental changes associated with permafrost thaw. For example, it is likely that thaw slumps affect the distribution of sediment sizes in affected lakes (Kokelj et al. 2013, 2015; Moquin and Wrona 2015), but we did not consider changes in sediment sizes in our projections since we could not find studies that have looked at differences in lake sediment size distribution between lakes that have been affected by permafrost thaw and those that have not. Information on the abundance and composition of macrophytes might also have been helpful since previous studies have shown that macrophytes can shape macroinvertebrate community structure (Stoffels et al. 2005, Savić et al. 2017), and previous studies have shown that macrophyte abundance and composition can change in response to water quality changes associated with permafrost thaw (Mesquita et al. 2010). Our projections of future change were also limited in that we assumed that all variables affected by permafrost thaw would change simultaneously and at the same rate. While this assumption was made for the sake of simplicity in our models, and to avoid criticisms of arbitrarily choosing the rate of change for each variable, it is likely that some variables such as conductivity and calcium will experience much greater changes than others, such as dissolved organic carbon (Kokelj et al. 2005; Houben et al. 2016). The advantage of modifying variables in 5% intervals, is that our results allowed for a better



consideration of how low to moderate permafrost degradation (i.e. deepening of the active layer) might impact lakes rather than focusing on lakes experiencing a high level of impact from thaw slumps.

### *Conclusions and future directions*

Overall, our results suggest that macroinvertebrate diversity may increase moderately, while total abundance, and % EPT are predicted to decrease in response to change associated with permafrost thaw. Changes in lake water quality related to permafrost thaw may also favour gastropods rather than chironomids and amphipods, leading to more lakes with macroinvertebrate communities dominated by snails. Given the expected decrease in macroinvertebrate abundance, there may be impacts on other members of lake food webs, such as fish. More research on the impacts of permafrost thaw on macroinvertebrates would be helpful, specifically looking at how different degrees of permafrost degradation in a catchment can affect communities (thaw slumps vs. active layer deepening). In addition, given the small number of lakes included in our dataset, additional data on more lakes in our study region would be helpful for validating the models we built.

## **Acknowledgements**

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## Tables

Table 3.1. Environmental variables of lakes sampled in the GSA and ISR in August 2017 and 2018, respectively. *N*= number of lakes, *SD*=standard deviation. DO=dissolved oxygen, TSS= total suspended solids, DOC=dissolved organic carbon, TN=total nitrogen, TP=total phosphorus, OM= organic matter.

<b>Variable</b>	<b>N</b>	<b>Mean</b>	<b>Min</b>	<b>Max</b>	<b>SD</b>
Latitude	46	68.473	67.331	69.367	0.668
Longitude	46	-133.543	-134.913	-132.888	0.469
Temperature (°C)	46	14.024	4.680	19.940	4.368
pH	46	8.025	6.770	9.780	0.720
Conductivity (µS/cm)	46	209.122	58.000	873.000	176.567
DO (mg/L)	46	10.556	8.460	13.800	1.106
Turbidity (NTU)	46	31.357	0.040	406.800	71.435
TSS (mg/L)	46	0.019	0.000	0.248	0.039
Chlorophyll- <i>a</i> (µg/L)	46	4.868	0.084	24.190	5.416
DOC (mg/L)	46	20.247	0.264	176.100	25.388
TN (mg/L)	46	0.454	0.099	0.988	0.157
Ca <sup>2+</sup> (mg/L)	46	22.115	7.059	59.485	11.859
TP (µg/L)	46	66.151	22.976	173.815	30.170
Surface area (km <sup>2</sup> )	46	2.612	0.004	82.900	12.313
Catchment area (ha)	46	8.745	0.010	126.181	20.196
Mean depth (m)	46	2.042	0.800	10.000	1.610
Secchi depth (m)	46	1.996	0.460	7.590	1.249
% OM	41	19.481	1.022	74.100	23.926
% CaCO <sub>3</sub>	41	2.896	0.000	15.643	3.324
% fine sediment (<2mm)	41	59.319	1.931	98.365	24.124
% silts and clays (< 63 µm)	41	5.947	0.028	24.387	5.526

Table 3.2. Direction of expected change of water quality and chemistry parameters in lakes in response to permafrost thaw determined from the listed supporting literature.

<b>Parameter</b>	<b>Direction of change</b>	<b>Supporting literature</b>
DOC	-	Houben et al. 2016 Kokelj et al. 2005 Moquin et al. 2014 Thompson et al. 2012
Chlorophyll- <i>a</i>	-	Houben et al. 2016 Thompson et al. 2012
TN	-	Houben et al. 2016 Thompson et al. 2012
TP	-	Houben et al. 2016 Moquin et al. 2014 Thienpont et al. 2013 Thompson et al. 2012
Secchi depth	+	Houben et al. 2016
Turbidity	-	Kokelj et al. 2005 Moquin et al. 20014 Thienpont et al. 2013
Conductivity	+	Houben et al. 2016 Kokelj et al. 2005 Moquin et al. 2014 Thienpoint et al. 2013
pH	+	Houben et al. 2016 Kokelj et al. 2005 Thienpont et al. 2013

Table 3.3. Summary of macroinvertebrate metrics used in this study. Means are calculated from the full set of 46 lakes sampled in the GSA and ISR in August 2017 and 2018 respectively.

*SD*=standard deviation. EPT= Ephemeroptera, Plecoptera, and Trichoptera.

<b>Metric</b>	<b>Mean</b>	<b>Min</b>	<b>Max</b>	<b>SD</b>
Richness	12.009	8.065	16.521	1.957
Diversity	5.332	2.374	10.472	1.778
Individuals/m <sup>2</sup>	738.404	79.667	2160.795	581.506
% EPT	5.283	0.154	15.296	3.876

Table 3.4. Multiple linear regression models on the macroinvertebrate richness, diversity, abundance, and % EPT.

<b>Metric</b>	<b>Variable</b>	<b>Estimate</b>	<b>SE</b>	<b>t-value</b>	<b>p-value</b>
<b>Richness</b> Multiple R <sup>2</sup> =0.5281 Adjusted R <sup>2</sup> =0.4468 p-value=3.660X10 <sup>-4</sup>	(Intercept)	12.766	2.227	5.731	3.34E-06
	Chlorophyll-a	-1.307	0.551	-2.372	0.0245
	Dissolved organic carbon	-4.485	2.497	-1.796	0.0829
	Total nitrogen	13.991	4.461	3.136	0.00390
	% silts and clays	-1.15	0.421	-2.729	0.0107
	Whitefish presence	2.766	0.606	4.565	8.47E-05
<b>Diversity</b> <i>*Log</i> Multiple R <sup>2</sup> =0.440 Adjusted R <sup>2</sup> =0.366 p-value=0.0012	(Intercept)	1.186	0.175	6.769	1.66E-07
	Dissolved organic carbon	-0.292	0.127	-2.303	0.0284
	Mean depth	-0.079	0.033	-2.418	0.0219
	% sediment <2mm	-0.002	0.001	-2.471	0.0194
	Whitefish presence	0.150	0.046	3.297	0.00252
<b>Total abundance</b> <i>*Cube rooted</i> Multiple R <sup>2</sup> =0.6248 Adjusted R <sup>2</sup> =0.5601 p-value=1.650x10 <sup>-5</sup>	(Intercept)	20.121	3.689	5.455	7.17E-06
	Chlorophyll-a	3.538	0.991	3.569	0.00127
	Mean depth	2.803	0.904	3.101	0.00427
	Secchi depth	-7.32	2.682	-2.729	0.0107
	% sediment <2mm	-0.035	0.018	-1.888	0.0691
	Whitefish presence	-2.435	1.078	-2.259	0.0316
<b>% EPT</b> <i>*Cube rooted</i> Multiple R <sup>2</sup> =0.628 Adjusted R <sup>2</sup> =0.532 p-value=1.489x10 <sup>-4</sup>	(Intercept)	0.876	1.041	0.842	0.407
	Temperature	0.610	0.207	2.942	0.00661
	pH	0.345	0.112	3.082	0.00469
	Conductivity	-1.294	0.406	-3.184	0.00364
	Turbidity	0.088	0.049	1.781	0.0861
	Chlorophyll-a	-0.684	0.161	-4.256	0.000224
	Total phosphorus	0.728	0.255	2.854	0.00820
	Whitefish presence	0.430	0.132	3.244	0.00313

Table 3.5. Multiple linear regression model variables and their relationship to richness, diversity, abundance and % EPT in our models. Supporting literature for the relationships of these variables with the given metrics are detailed. \*=permafrost thaw related variable.

Variable	Richness	Diversity	Abundance	% EPT	Supporting literature	Supporting literature findings
Chlorophyll- a*	-		+	-	Quinn and Hickey 1990	Negative correlation of chlorophyll- <i>a</i> to % EPT and richness.
					Brodersen et al. 1998	Negative correlation of chlorophyll- <i>a</i> to richness and abundance.
					Beaty et al. 2006; Lewis and Mccutchan 2010	Positive relationship of chlorophyll- <i>a</i> with abundance.
					Chun et al. 2017	Negative correlation of EPT richness with chlorophyll- <i>a</i> .
DOC*	-	-		-	Çağlar and Albayrak 2012	Richness and diversity negatively related to TOC.
					Moquin et al. 2014	DOC explained significant amount of variation in community structure.
TN*	+			+	Brodersen et al. 1998	Positive relationship of TN with richness.
					Nyakeya et al. 2009	% EPT and richness negatively correlated with TN.
					Chun et al. 2017	Negative correlation of EPT richness with TN.
Whitefish presence	+	+	-	+	Pothoven and Nalepa 2006	Medium whitefish in Lake Huron show preference for Chironomidae.
					Schilling et al. 2009	Fishless lakes have higher macroinvertebrate abundance.
					Hayden et al. 2015	Whitefish influence macroinvertebrate community composition and density.

% Silts and clays (<63 µm)	-				Beaty et al. 2006; Çağlar and Albayrak 2012	Richness is negatively related to mud substrate.
% Fine sediment (<2mm)		-	-		Beaty et al. 2006; Çağlar and Albayrak 2012	Diversity and abundance are negatively related to mud substrate.
Mean depth		-	+		Brodersen et al. 1998	Positive relationship of abundance and diversity with mean depth.
					Ntislidou et al. 2018	Negative relationship of mean depth with diversity.
Turbidity*				+	Nyakeya et al. 2009	% EPT negatively correlated to turbidity.
Secchi depth*			-		Brodersen et al. 1998	Negative relationship of Secchi depth with abundance.
Conductivity*				-	Nyakeya et al. 2009	% EPT negatively correlated to conductivity.
					Móra et al. 2011; Savić et al. 2017	Important for structuring EPT assemblages.
TP*				+	Nyakeya et al. 2009	% EPT negatively correlated to TP.
					Chun et al. 2017	Negative correlation of EPT richness with TP.
pH*				+	Nyakeya et al. 2009	% EPT positively correlated to pH.
					Móra et al. 2011; Savić et al. 2017	pH is important for structuring EPT assemblage.
Temperature				+	Móra et al. 2011; Savić et al. 2017	Temperature is important for structuring EPT assemblage.



## Figures

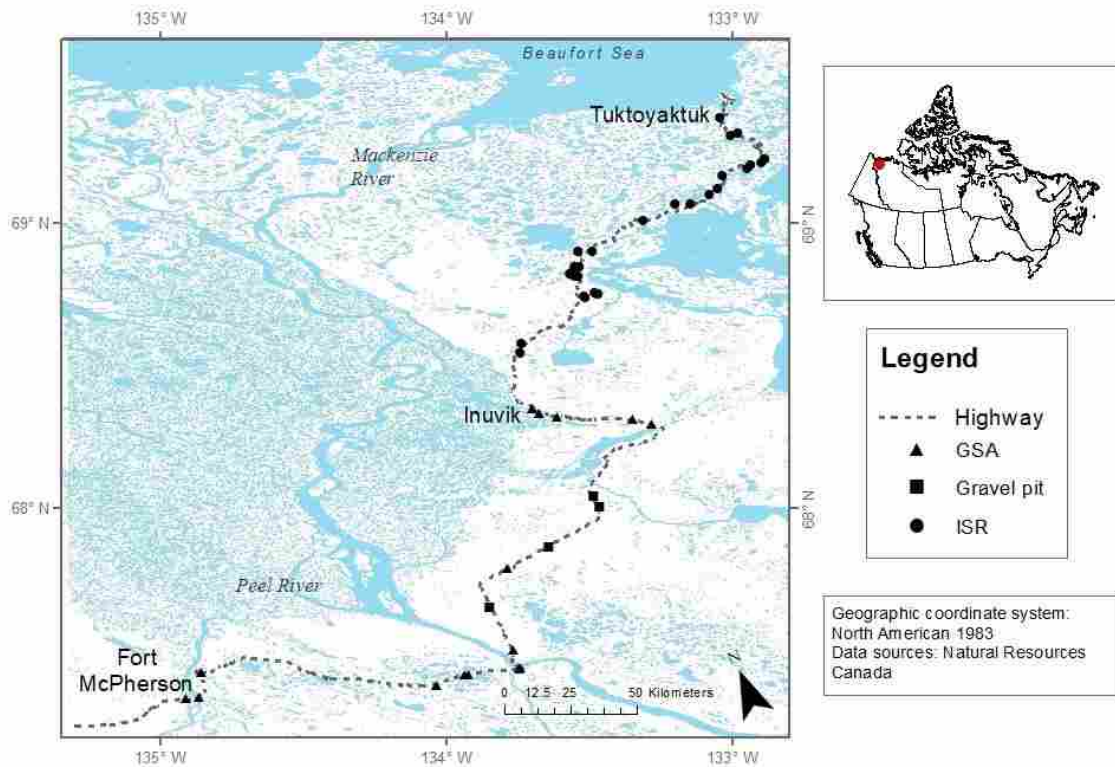


Figure 3.1. Map of the lakes (represented by shapes) sampled during 2017 in the Gwich'in Settlement Area (GSA) and during 2018 in Inuvialuit Settlement Region (ISR) along the Dempster Highway between Fort McPherson and Inuvik and newly built Inuvik-Tuktoyaktuk Highway, respectively. Gravel pit lakes sampled during 2017 in the GSA are represented by squares.

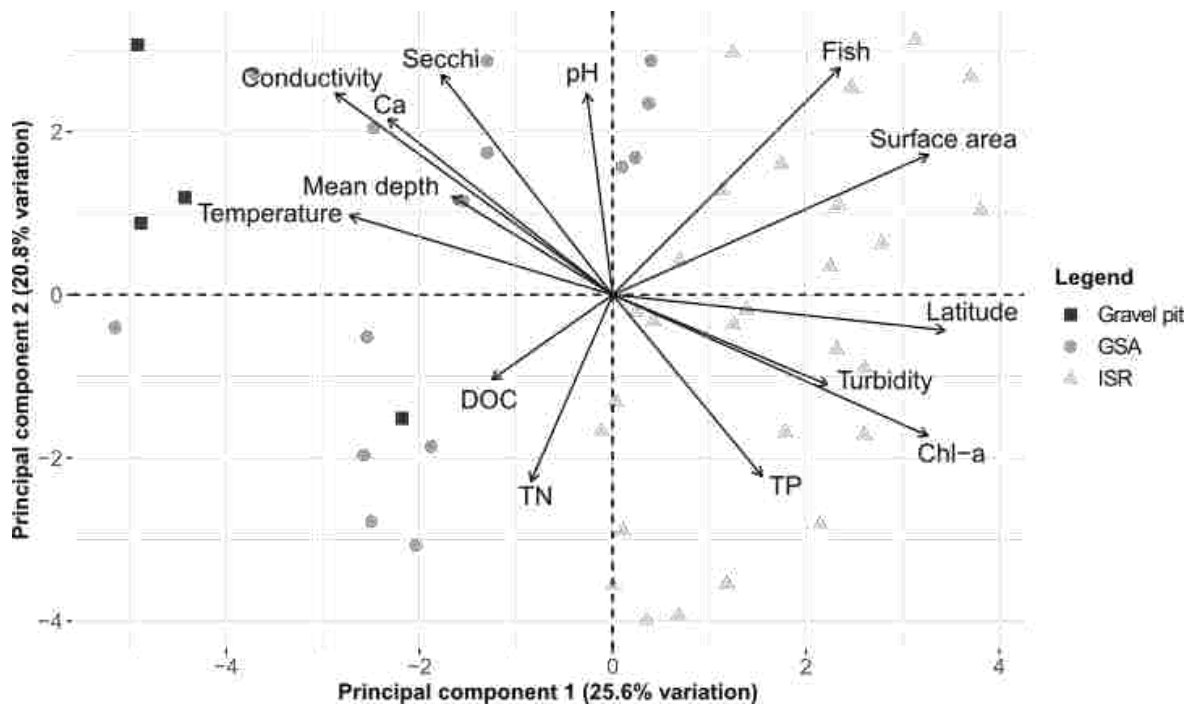


Figure 3.2. Principal component analysis (PCA) conducted on environmental variables collected for the 46 lakes in our study. GSA = natural lakes sampled along the Dempster Highway in the Gwich'in Settlement Area during August 2017. ISR = natural lakes sampled along the Inuvik-Tuk highway in the Inuvialuit Settlement Region during August 2018. Gravel pit lakes were sampled in the GSA area.

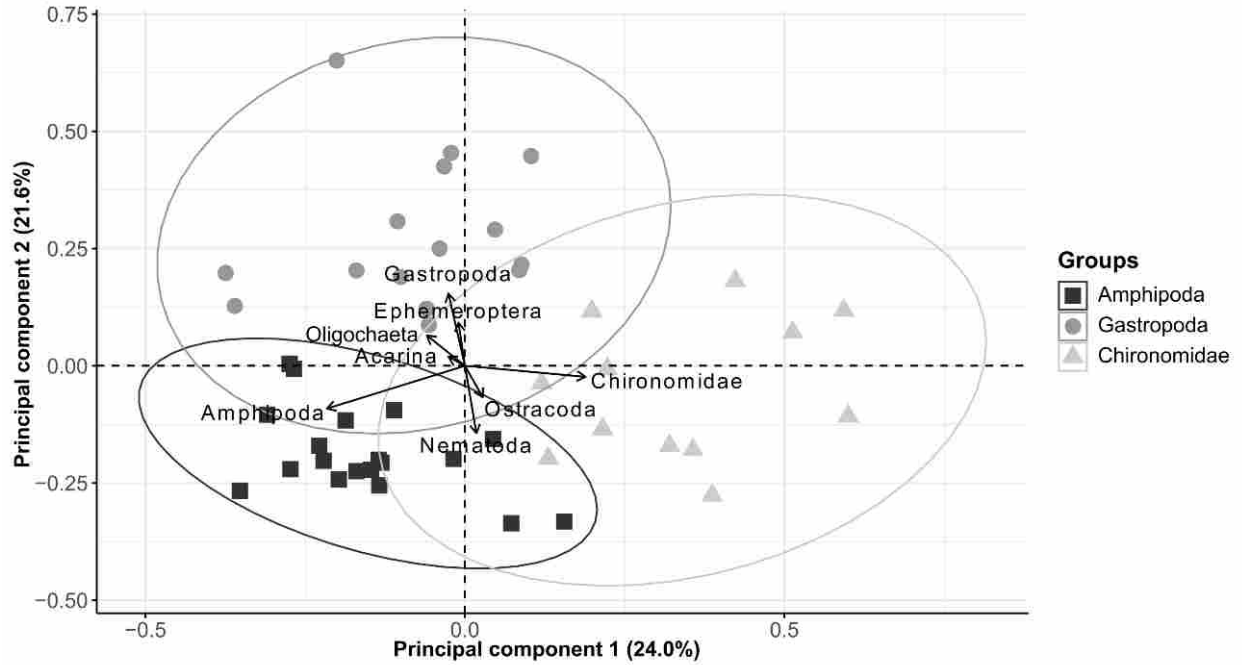


Figure 3.3. PCA analysis of macroinvertebrate communities for 46 lakes in the GSA and ISR.

Lakes were grouped into 3 clusters using a k-means cluster analysis where the following macroinvertebrates dominated: Chironomidae, Amphipoda, and Gastropoda.

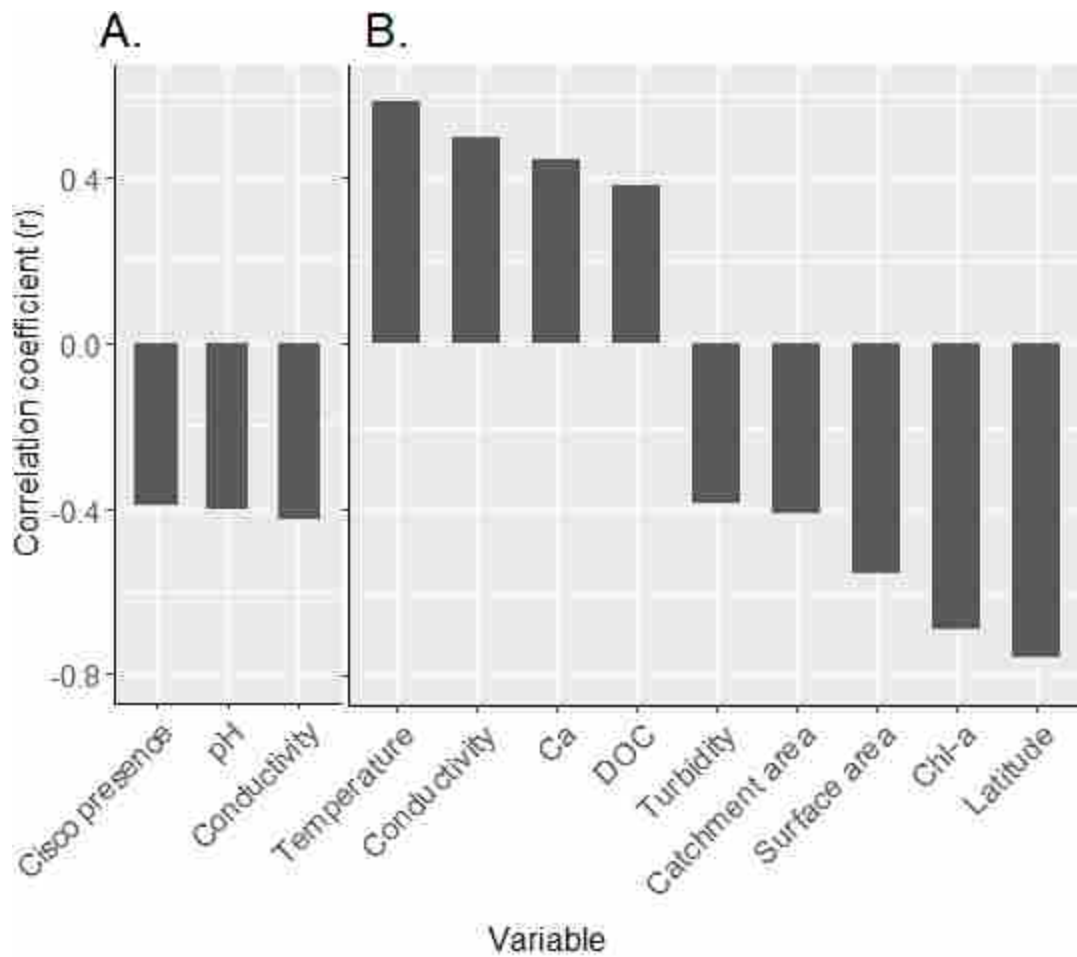


Figure 3.4. Correlation coefficient (r) shown for explanatory variables ( $p < 0.01$ ) that account for the variation of macroinvertebrates along principal component 1 (A) and principal component 2 (B) of the PCA shown in figure 3.3.

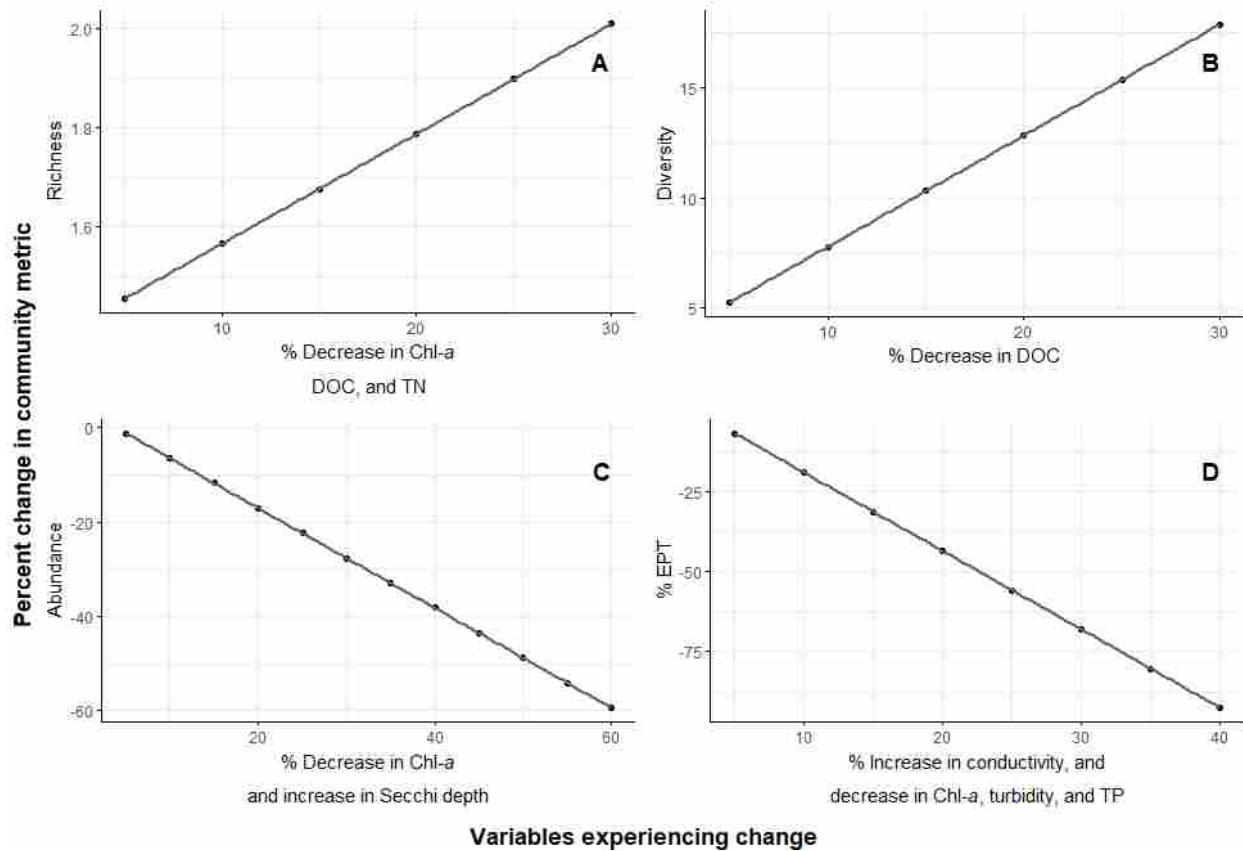


Figure 3.5. The percent change in macroinvertebrate richness (A), diversity (B), abundance (C), and % EPT (D) as a response to percentage changes in variables influenced by permafrost thaw. Note that the variables chosen for each community metric correspond to those included in the multiple regression model.

## CHAPTER 4: DISCUSSION AND SYNTHESIS

### 4.1 Variation of lake water quality in the study area

Overall, water quality in roadside lakes was compared to water quality in roadside gravel pit lakes in chapter 2 and was assessed on a broader spatial scale in chapter 3. The water quality measurements for both of our studies generally conformed well to previous studies on gravel pit lakes and natural lakes in the region. Respective comparisons were drawn in the discussion section of chapter two and three. Within the GSA, I report that gravel pit lakes are deeper and have a smaller surface area than natural lakes. This morphometry is due to the deep extraction of gravel from the ground over a small surface area (an average of 2.57 ha in our study) in order to minimize cost and disturbance to terrestrial landscapes (Blanchette and Lund 2016). Gravel pit lakes were found to be clearer with increased pH, conductivity, and ionic concentration but with less nutrient availability than natural lakes. Interestingly, the water quality differences observed between gravel pit lakes and natural lakes are similar to changes in water quality described for permafrost impacted lakes in our region (Kokelj et al. 2009; Moquin et al. 2014; Houben et al. 2016). Although these disturbances are quite different in nature, there are two possible commonalities between them that could account for their water quality similarities. The first is that both are a form of landscape disturbance. For the construction of gravel pits, the top layer of the landscape is stripped in order to dig up the gravel, while for permafrost thaw, runoff from previously frozen ground beneath the active layer is entering lakes. Both of these disturbances operate below the topmost layer of ground, which may be one of the causes for their similar water quality. A second commonality between gravel pit lakes and permafrost impacted lakes is that both may be influenced by increases in groundwater flow. Gravel pit lakes are often filled by groundwater which influences their water quality (Søndergaard et al. 2018), similarly, natural

lakes in watersheds experiencing permafrost thaw are likely receiving more groundwater along with the inputs from permafrost thaw (Williams and van Everdingen 1973; Larson et al. 2017).

One major difference between gravel pit lakes and natural lakes that may be impacted by permafrost thaw is their morphometry. While gravel pit lakes are deep (average mean depth ~ 6 m) with smaller surface areas, the majority of natural lakes are shallow (average mean depth < 1.6 m) with more variability in their surface areas. Morphometry of both natural and artificial lakes plays a large role in controlling their water quality attributes. Shallow lakes are often turbid due to wave action causing resuspension of bottom sediments, resulting in minerogenic turbidity (Bloesch 1995). Therefore, it is unlikely that the deeper gravel pit lakes are experiencing enough sediment resuspension to affect their turbidity. There are many natural southern lakes that group out along with gravel pit lakes and contain similar morphometric and water quality variables (Figure 3.2). This is likely due to increased groundwater flow in the GSA where permafrost is discontinuous, and ground temperatures are higher, leaching more organic carbon for some and increasing pH and ion concentrations in others (Pienitz et al. 1997; Rühland et al. 2003). In Chapter 3, lake environmental variables collected north of the GSA demonstrate the importance of depth in regulating water quality. On the PCA of water quality presented in this chapter, there is a group of lakes in the ISR opposite to some of the gravel pit lakes (Figure 3.2). These lakes are shallow with high turbidity and increased chlorophyll-a levels. In these lakes, wave resuspension likely increases turbidity, and phytoplankton growth is likely a larger contributor to productivity than macrophytes due to poor light penetration to the lake bottom. The dominance of phytoplankton in shallow turbid lakes represents a clear contrast with gravel pit and permafrost-impacted lakes that are often dominated by rooted macrophytes (Mesquita et al. 2010, Søndergaard et al. 2018). Ultimately, depth was likely an important variable regulating

nutrient concentrations and vegetation types in these study lakes (Jeppesen et al. 1997, Lim et al. 2001).

In addition to depth, surface area and catchment area were also likely important morphometric variables that influenced the water quality and biology of my study lakes. Many of the larger lakes in my dataset contained fish and had low levels of dissolved organic carbon and nutrients that may act to deplete oxygen availability for fish. The positive relationship of fish presence in larger lakes (Haynes et al. 2014, Henriksson et al. 2015) with higher connectivity (Roux et al. 2016, Laske et al. 2016) and dissolved oxygen (Saksgard and Hesthagen 1995, Eick and Thiel 2014) is widely recognized. In contrast, there are lakes that may be too small (Henriksson et al. 2015) with too much organic matter to support healthy fish communities (Saksgard and Hesthagen 1995). Ultimately, morphometry and watershed size play an important role in regulating lake water quality conditions such as nutrient and oxygen availability, thus supporting specific biological communities in the study area. The range in water quality within my study area allowed me to produce models to describe macroinvertebrate communities which capture the variability of the environmental features of the selected lakes.

#### **4.2 Association of macroinvertebrate communities with environmental disturbance**

Our findings indicate that water quality can have an important influence on benthic macroinvertebrates in northern lakes. The unique properties of artificial lakes (gravel pit lakes) and the changes in water quality caused by permafrost thaw may lead to differences in macroinvertebrate community structure in comparison with natural, undisturbed lakes. However, while community composition may differ, summary metrics such as species richness and



diversity may be less affected. These findings are supported by the notion that community structure may be more sensitive to disturbance (Hartmann and Widmer 2006).

#### **4.2.1 Changes in macroinvertebrate community structure**

The similarity in water quality between gravel pit lakes and those impacted by permafrost thaw suggest that these two lake types may support similar macroinvertebrate communities. The RDA in chapter 2 describing differences between gravel pit lakes and natural lakes, hinted that Gastropoda may be positively associated with fish absence, and Hemiptera with mean depth, while Chironomidae and Acarina show a slight positive association with chlorophyll-a and fish presence (Figure 2.5). Although for the most part, distinct correlations between macroinvertebrate species and predictor variables were not observed. These associations which are weakly displayed in the RDA have been supported by other literature. The abundance of Gastropoda in permanent lake habitats has been shown to be negatively related to the presence of predators (Lodge et al. 1987). Specifically, fish can reach high densities and feeding rates, reducing snail occurrence in habitats where they would normally be found based on environmental conditions (Lodge et al. 1987). Densities of Hemiptera have been noted to be positively related to deeper waters, especially in their adult aquatic phase (Streams and Shubeck 1982, DeWalt et al. 2010). This taxa seeks out deep water for overwintering, where they also thrive because if the water is well oxygenated, they do not need to surface for air (DeWalt et al. 2010). Additionally, they may have greater success catching their prey in deep water since it makes escape and shelter in vegetation more difficult for their prey (Streams and Shubeck 1982).

In contrast to Hemiptera and Gastropoda being weakly associated with deep and fishless lakes, Chironomidae and Acarina show a weak positive association with fish presence,

chlorophyll-*a*, and lakes that are shallower in the RDA (Figure 2.5). These taxa may be more successful in lakes that are more turbid, shallow, and contain more phytoplankton (high chlorophyll-*a*) due to wave action as previously described. Lakes with abundant phytoplankton have been shown to have higher densities of Chironomidae that graze on periphytic algae (Tarkowska-Kukuryk 2013). It is likely that the position of Acarina on the RDA reflects its parasitic relationship with one of its common hosts, Chironomidae (Smith and Oliver 1976, Stryjecki et al. 2016).

Although, the associations of macroinvertebrate communities in the GSA with variables are weak, I find strong correlations between macroinvertebrate community structure (Figure 3.3) and a variety of permafrost related variables (Figure 3.4) in 46 lakes sampled in the GSA and ISR. This means that in response to permafrost degradation, strong changes in macroinvertebrate community structure may occur.

Along PC1, a transition from a community dominated by Chironomidae to other community types can be explained by increases in pH, conductivity, and cisco presence (Figure 3.3; Figure 3.4). The negative correlation of Chironomidae with cisco presence might be reflective of the negative selection that cisco larvae can have on Chironomidae (Eckert et al. 2018). Tolerance of Chironomidae to water chemistry variables such as low pH and conductivity is a little more difficult to justify with a taxonomic resolution of family level. Chironomini, a tribe of Chironomidae has been found to be negatively correlated to pH and conductivity in streams that span the latitudinal range of our study area (Scott et al. 2011). This may suggest that the Chironomini constitute a majority of the Chironomidae family sampled in our lakes. However, it is difficult to generalize the effects of pH and conductivity on all Chironomidae

given that this family of dipterans has a broad range of tolerance for different environmental conditions (Carew et al. 2007; Hill et al. 2016; Serra et al. 2016) .

Along PC2, a transition between a Gastropoda dominated community to an Amphipoda dominated community is also related to a variety of parameters that are expected to change in response to permafrost thaw (Figure 3.3; 3.4; Table 3.2). As far as the permafrost related variables, Gastropoda dominated communities were significantly correlated with higher conductivity and Ca concentrations (Figure 3.3; 3.4). Conductivity has been previously correlated with gastropod communities (Pyron et al. 2009), however this is not a typical finding (Lodge et al. 1987). This variable may be coming through in sites such as ours with little to no groundwater input, therefore increasing anthropogenic influences and overall salinity (Pyron et al. 2009). Lakes dominated by Gastropoda also contain high calcium concentrations. The calcium levels in our study average ~22 mg/L allowing a range of calciphile gastropod species (requiring calcium levels of 20 mg/L at least) and noncalciphile gastropod species (that can exploit lower calcium levels of about ~5.2 mg/L) species to coexist (Boycott 1936; Lodge et al. 1987; Briers 2003). In contrast, Amphipoda and Chironomidae dominated communities were found where there is high turbidity and chlorophyll-*a*. Here, higher chlorophyll-*a* concentrations paired with turbidity may be indicative of particulate organic matter and detritus from phytoplankton which amphipods and chironomids may feed on. Amphipods have been shown to respond positively to increases in phytoplankton (Jorgenson et al. 1992) which is represented largely by chlorophyll-*a* (Søndergaard et al. 2017). The positive correlation between chlorophyll-*a* and amphipods has been found in several studies (Subida et al. 2005, Corcoran et al. 2009). Similarly, detritivorous chironomids may also be responding to an increase in food source, and

have been shown to be positively related to chlorophyll-*a* concentrations (Saether 1979, Herren et al. 2017).

An interesting feature to note is that PC2 is highly correlated with latitude and temperature suggesting that differences in permafrost distribution, boreal-tundra vegetation, and general thermal tolerances may play an important role in distinguishing the gastropod dominated communities from the amphipod and chironomid dominated communities (Figure 3.3; 3.4). Specifically, Gastropoda is more abundant in lower latitudes where temperature is higher and the land is underlain by discontinuous permafrost supporting Boreal vegetation. Therefore, these lakes may be receiving higher groundwater flow than more northern lakes. In contrast, Chironomidae and Amphipoda are more abundant in northern lakes which are colder and located on lands characterized by continuous permafrost and tundra which are likely limiting groundwater flow into the lakes.

Taken together, it seems that increases in permafrost thaw may shift communities towards gastropod dominant ones due to increases in groundwater flow associated with the loss of continuous permafrost (Pienitz et al. 1997, Rühland et al. 2003). The water quality changes that result from permafrost thaw may cause shifts to gastropod dominated communities which parallels their slight positive association in gravel pit lakes that are impacted by increased interactions with groundwater and surface disturbance.

#### **4.2.2 Changes in macroinvertebrate community metrics**

Macroinvertebrate community metrics responded differently when comparing the impact of gravel pit lakes versus the projected impact of permafrost thaw. Specifically,

macroinvertebrate community indices were not significantly different between natural and gravel pit lakes but are projected by our models to change in response to permafrost thaw. This might be related to the significant differences in morphometric characteristics between gravel pit and natural lakes, which may have masked some of the potential differences caused by differing water chemistry. However, it is also possible that macroinvertebrate communities did differ in appreciable ways between gravel pit lakes and natural lakes. In gravel pit lakes, macroinvertebrate richness and diversity were slightly lower and abundance was slightly higher ( $p > 0.05$ ). This may indicate that with more sampling and increased statistical power, I may have detected a statistically significant difference.

When projecting changes in macroinvertebrate indices due to water quality change associated with permafrost thaw, richness and diversity were predicted to increase slightly while abundance was predicted to decrease (Figure 3.5). These responses to permafrost thaw might have been driven by the decline in overall abundance which was represented largely by the permafrost thaw sensitive taxa Chironomidae (Moquin et al. 2014; Chin et al. 2016). The decline in Chironomidae may allow macroinvertebrate communities to become more even, resulting in increased diversity. Lastly, although richness is predicted to increase, the change is negligible at ~1.6% for a 10% change in permafrost related variables. This indicates that richness does not respond strongly to the overall changes predicted by the important permafrost related variables in its model. The lack of response to change may be due to the coarse taxonomic resolution of my study. A stronger pattern may be observed with finer taxonomy (Jones 2008, Cañedo-Argüelles et al. 2012), especially with taxa such as Chironomidae which are so widely distributed in the Arctic region (Scott et al. 2011; Cañedo-Argüelles et al. 2012).

In comparison to the rest of the metrics, % EPT showed the most dramatic decrease in response to changes in water quality expected from permafrost thaw (Figure 3.5). These are representative of taxa that are sensitive to anthropogenic and climate related environmental degradation (Móra et al. 2011, Holmes et al. 2016, Savić et al. 2017). The large decreases predicted in % EPT within my study may still be an underestimate of their response to this disturbance since I was conservative in the amount of change considered in my models (increments of 5%). In lakes with shoreline retrogressive thaw slumps, the impacts of permafrost related variables such as conductivity on % EPT could be even greater considering conductivity can increase by ~343% (Moquin et al. 2014). Therefore, the large decline in % EPT found in my study reaffirms the utility of these species as indicators of healthy aquatic systems, and specifically their usefulness for any future studies investigating the impacts of permafrost thaw in lakes.

### 4.3 Synthesis

The overarching goal of my thesis was to determine which environmental variables were associated with macroinvertebrate community structure in Canadian Arctic lakes located in the Northwest Territories. This question was explored under the umbrella of development and climate change that are expected to influence waterbodies and thus the biological communities that are within them. The influence of development was explored in context of gravel pit lakes, while the impact of climate change was explored in context of expected water quality changes associated with permafrost thaw.

Taken together, I found water quality differences between gravel pit and natural lakes, but no macroinvertebrate community differences, meaning that they seem to offer quality aquatic habitat for macroinvertebrates. I also found that in response to water quality changes associated with permafrost thaw, community structure are predicted to shift to be gastropod dominated, with fewer sensitive species (% EPT), and overall lower abundance. In contrast, macroinvertebrate richness and diversity are expected to slightly increase in response to the impacts of permafrost thaw. It is difficult to tell whether communities in permafrost thaw impacted lakes will differ significantly from non impacted lakes considering water quality changes are similar to those observed for gravel pit lakes. However, the ability of communities to thrive in permafrost impacted lakes will likely depend on the duration and degree of disturbance (i.e. percent catchment area, or permafrost depth), as well as on individual lake properties such as size, connectivity, and proximity to other lakes.

### **4.3.1 Contributions to the field**

This research helps fill in the knowledge gap of macroinvertebrate communities in Arctic lakes identified by the 2019 State of the Arctic Freshwater and Biodiversity report (Lento et al. 2019). More specifically, by investigating how macroinvertebrates may respond to development and climate change disturbance, this project may be helpful for environmental policy-makers and project managers. Through comparisons of water quality and macroinvertebrate communities in gravel pit lakes, I conclude that this habitat is supportive for biological communities. Therefore, as development continues to increase in the Arctic and the need for construction grows (Schindler and Smol 2006, Prowse et al. 2011), policy-makers and resource managers may consider our results in the context of balancing concerns about the destruction of terrestrial habitat with the benefits of creating new aquatic habitat that is capable of supporting a diversity of aquatic species. Similarly, the models developed in chapter 3 may be applied in decision-making about water uses that may impair water quality. The models could provide a mechanism to assess potential biological changes when discharges from industry may change conductivity levels, for example. Lastly, this study provides much baseline water quality and macroinvertebrate community data which may be used in the future to assess how these lakes change in response to environmental disturbances.

### **4.3.2 Remaining gaps and future directions**

Although it was determined that gravel pit lakes in the Arctic can be quality habitat, I only sampled littoral macroinvertebrate communities and comparisons may still need to be conducted for organisms in the profundal zone. Furthermore, several studies demonstrated that



macroinvertebrates can colonize new habitats within two and a half to three years (Voshell and Simmons 1984, Bass 1992). This suggests that future research comparing macroinvertebrate communities between natural lakes and younger gravel pit lakes than our study investigated may be more fruitful. While the conclusion that gravel pit lakes offer good quality habitat for invertebrate communities is in agreement with some previous literature (Ejsmont-Karabin 1995; Gammons et al. 2009; Alfonso et al. 2010), our predictions of permafrost effects on lake macroinvertebrate communities do not match exactly with the one previous study on this topic (Moquin et al. 2014). Therefore, there is a need for further studies to assess the validity of these results. This is especially important considering that permafrost degradation is accelerating in the western Canadian Arctic (Segal et al. 2016) and more specifically in the Mackenzie Delta Region (Lantz and Kokelj 2008). Additionally, the models developed to assess the potential effects of permafrost thaw were quite conservative in several ways. First, they were limited in that they did not account for variation in the magnitude of change among permafrost variables. By changing the permafrost related variables by 5% at a time, it was assumed that all variables would change at the same time and with the same magnitude. This has been shown to not be the case, since variables in permafrost impacted lakes tend to vary by different degrees. For example, conductivity has been shown to increase by ~343% in permafrost impacted lakes, while Ca increased by ~488% (Moquin et al. 2014). Another limitation of my projections is that potential changes in sediment and fish communities were not included, although these are important in explaining macroinvertebrate community metrics and they are variables that may change in response to permafrost thaw. These variables were not included in projections because they have not previously been compared between permafrost impacted and non impacted lakes. Therefore, a good next step would be for studies to compare these important variables under

permafrost disturbance conditions so that they may be used in predictive models. Lastly, it is not yet determined how macroinvertebrate communities may change in response to different degrees of permafrost thaw. Moquin et al. (2014) did test this to a degree by comparing disturbed to undisturbed lakes, and then within disturbed lakes they compared the area adjacent to the slump and area opposite to the slump. However, more studies may be done that look at a gradient of macroinvertebrate responses with differences in % catchment area disturbed, depth of permafrost thaw disturbance, or variation in thaw slump activity.

#### **4.3.3 How is this project integrative?**

My thesis work is part of a larger project that is looking at other components of the food web in Arctic lakes. For the same lakes sampled in this project, my colleague, Jasmina Vucic (Wilfrid Laurier, MSc) investigated zooplankton communities, and Alyssa Murdoch (York University, PhD candidate) sampled fish communities. With this data, ultimately, we will be able to get an overall understanding of how these trophic levels interact with each other and their environment. This project integrates biology with other sciences through the collection of environmental variables that include water quality, sediment data, and catchment area. Chemistry techniques were used in analyzing water quality. Sediment data was analyzed with guidance of the Geography laboratory coordinator at Laurier. Lastly GIS was used to calculate catchment area and produce maps for this project which is also generally overlapping with Geography. In addition to collaborations and the integration of other scientific fields, in executing this project, efforts were made to involve the Gwich'in and Inuvialuit First Nations locals in different aspects of the research. Local help for executing field work was hired from the Hunters and Trappers Committee of the GSA and the ISR. Additionally, presentations about the research that were

open to the public were provided at the Aurora Research Institute to encourage open communication and transparency. Therefore, this project is integrative first, through collaborations with various students whose data will ultimately be merged to produce a larger and more cohesive explanation of the Arctic lakes that were sampled. Second, it is integrative in some techniques used from other branches of science to provide a holistic description of my study site and the environment preferred by macroinvertebrate communities. Lastly, through efforts to involve the local First Nations communities, science communication and local support was a big component for the success and execution of the project.

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## APPENDIX

### Tables

Table A1. Level of identification used for each macroinvertebrate taxa found in the samples (Jones et al. 2007).

<b>Level of identification</b>	<b>Macroinvertebrate taxon</b>
Phylum	Nematoda (round worms)
Class	Gastropoda (snails)
	Ostracoda (seed shrimp)
Subclass	Oligochaeta (aquatic worms)
	Hirudinea (leeches)
	Acarina (water mites)
Order	Coleoptera (beetles)
	Amphipoda (scuds)
	Hemiptera (true bugs)
	Ephemeroptera (mayflies)
	Plecoptera (stoneflies)
	Trichoptera (caddisflies)
	Mysida (opossum shrimps)
Suborder	Anisoptera (dragonflies)
	Zygoptera (damselflies)
Family	Pelecypoda (clams)
	Diptera (true flies)
	Megaloptera (alderflies, dobsonflies, fishflies)

Table A2. Transformations performed on explanatory variables used in Chapter 3. Variables that are used in some data sets and not others are annotated.

<b>Parameter</b>	<b>Transformation</b>
Temperature	$\ln(x + 1)$
Conductivity, surface area, chlorophyll- <i>a</i> , total phosphorus	$\log x$
Turbidity, calcium, catchment area	$\ln x$
Dissolved organic carbon	$\log(x + 1)$
Mean depth, % organic matter <sup>†</sup>	$\log_2 x$
Total suspended solids, secchi depth, % CaCO <sub>3</sub> <sup>†</sup> , % silt and clay <sup>†</sup>	$\sqrt[3]{x}$
% Fines <sup>†</sup> , pike presence, whitefish presence, cisco presence, fish presence, pH, latitude, total nitrogen, dissolved oxygen	<i>No transformation applied</i>

<sup>†</sup>sediment parameter included only in 35 lake data set

Table A3. Water quality variables in chapter 3 compared to other studies. Means are in white, ranges are coloured in grey.

<b>Variable</b>	Value in this study	Houben et al. (2016)	Kokelj et al. (2009)	Pienitz et al. (1997)	Rühland et al. (2003)
Location	Boreal-Tundra lakes along Dempster and Inuvik-Tuk highway, NWT	Upland tundra lakes, Mackenzie Delta Region, NWT	upland lakes across the subarctic boreal forest-tundra transition in the Mackenzie Delta region	Southern Yukon-Tuktoyaktuk Peninsula	From Yellowknife-Bathurst Inlet in the central Canadian Subarctic
<i>N</i>	46	38	73	59	56
Ca (mg/L)	22.11	8.66	31.4	19.58	6.84
	7.06-59.49	2.68-26.7	-	3.52-50.30	0.3-37.00
Chlorophyll- <i>a</i> (µg/L)	4.86	4.53	-	2.1	3.0
	0.084-24.2	0.6-19.60	-	0.1-20.4	0.6-17.3
Conductivity (µS/cm)	209	87.10	257.7	159.7	68.9
	58-873	31-220.80	-	24-1500	2.5-478.5
DOC (mg/L)	20.25	17.53	-	12.3	29.9
	0.26-176.1	9.6-36.4	-	3.1-35.1	1.3-332.0
pH	8.025	6.99	7.6	7.9	7.2
	6.7-9.8	6.04-8.02	-	5.9-9.3	6.2-8.3
TN (mg/L)	0.454	0.519	-	0.5589	0.435
	0.099-0.99	0.353-0.734	-	0.123-1.585	0.135-1.96
TP (µg/L)	66.15	29.93	-	15.5	12.1
	22.98-173.81	10.6-67.9	-	3.0-55.1	2.7-48.6
Secchi depth (m)	1.996	0.85	-	3.4	-
	0.46-7.59	0.5-1.73	-	0.7-11.5	-

## Figures

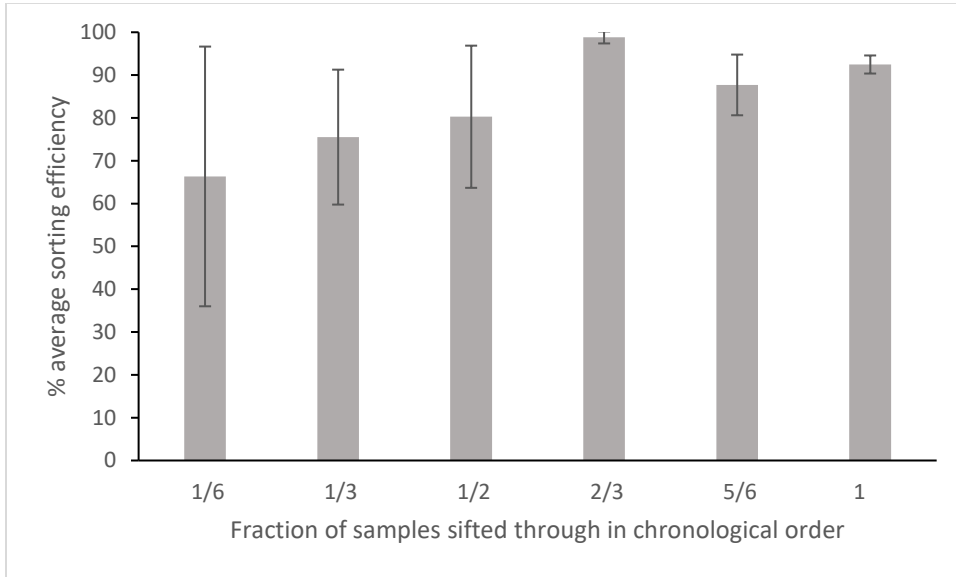


Figure A1. The % average sorting efficiency every 1/6<sup>th</sup> of all samples. Sorting efficiencies were calculated for 10% randomly selected samples in each round of samples.

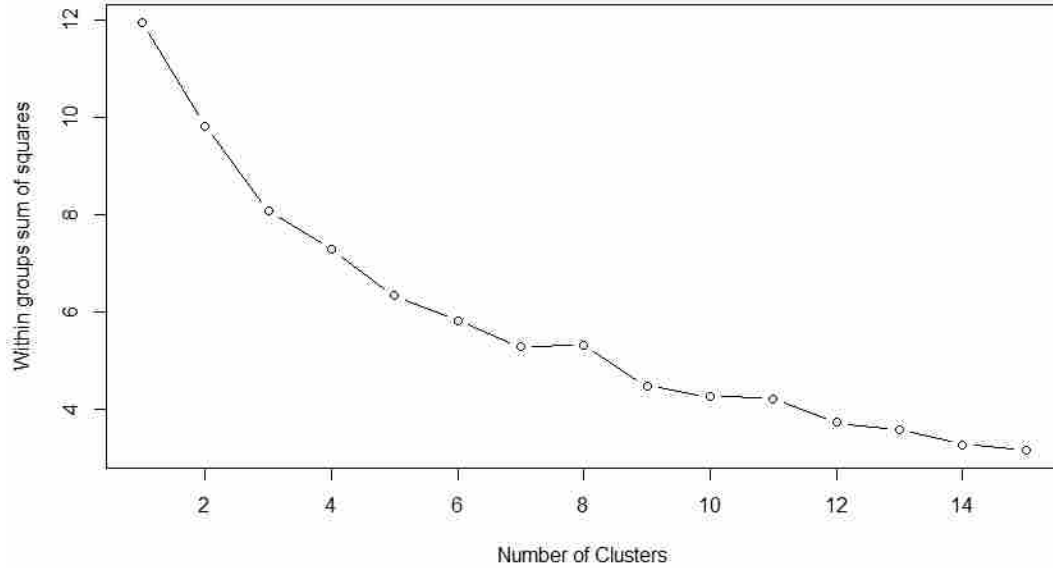


Figure A2. Elbow method used to determine that  $k=3$  for the k-means cluster analysis used in chapter 3.

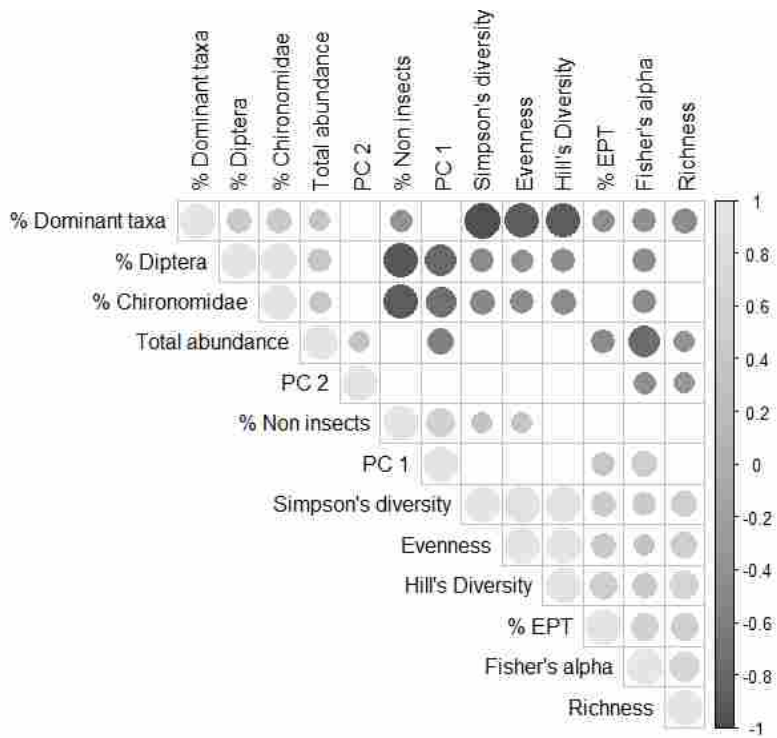


Figure A3. Pearson correlation matrix of macroinvertebrate indices used to choose which indices to investigate in chapter 3.