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Factors Influencing Zooplankton Community Structure in Small Arctic Lakes, Northwest Territories

By

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Abstract

The Canadian Arctic has been warming at an unprecedented rate, causing significant changes to the environment. At the same time, continued development in the north has increased the demand for gravel extraction used to construct and maintain infrastructure such as highways. The development of roadways and gradual loss of permafrost in Canada's north has led to changes in water quality, including increased calcium, conductivity, and nutrients. In addition, gravel extraction has led to the formation of artificial gravel pit lakes. Research has yet to determine how physical and chemical changes associated with development and permafrost thaw might impact zooplankton, and no studies have been conducted to examine the water quality of the region's gravel pit lakes, or the diversity of biota living within them.

To examine how water quality and invertebrate communities differed between natural and gravel pit lakes, I collected baseline water chemistry data, bathymetry, and zooplankton samples from 15 natural and 6 gravel pit lakes along the Dempster Highway between Fort McPherson and Inuvik. In comparison to natural lakes, gravel pit lakes were deeper, clearer, and significantly lower in nutrients. Despite these differences, pelagic zooplankton did not differ significantly between lake types, suggesting that gravel pit lakes offer quality habitat for local invertebrate species.

To examine how zooplankton respond to water quality changes caused by permafrost thaw, I surveyed additional lakes between Inuvik and Tuktoyaktuk, increasing the size of my dataset to 37 lakes. I then used my dataset to develop models used to predict how changes in water quality could affect zooplankton. My models showed that zooplankton abundance, evenness and diversity were related to conductivity, turbidity, calcium, and nutrient levels, and that water quality changes could lead to a significant increase in zooplankton abundance (1.6-3.6-fold) but decreases in evenness (1.1-1.4-fold) and diversity (1.2-1.7-fold). The magnitude of these changes raises concerns about cascading effects potentially influencing other members of the food web, such as fish.

Taken together, my results suggest that while some stressors may have unexpected positive benefits for northern biodiversity (creation of gravel pit lakes), others may negatively influence diversity in small Arctic lakes (permafrost thaw).

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CHAPTER 1: Literature Review

1.1 Introduction

The Northwest Territories is warming at an unprecedented rate which is causing changes to the natural environment (Frey & McClelland, 2009; Kokelj et al., 2009; Houben et al., 2016). The coupled effects of climate change and increased development in the Canadian Arctic may impact freshwater zooplankton communities. Critical to the functioning of freshwater ecosystems, zooplankton allow for the transfer of energy from primary producers to larger organisms such as macroinvertebrates and fish (Richardson, 2008). Concern arises through the changes in abiotic and biotic factors driven by climate and development that have the potential to alter the structure of zooplankton communities and cause shifts in species composition (Gray & Arnott, 2011). To predict the potential impacts of current and future environmental stressors in the Canadian Arctic, it is essential to understand the physical, chemical, and biological variables that structure zooplankton communities (Gray & Arnott, 2011).

1.2 Zooplankton Ecology

Zooplankton are heterotrophic, microscopic, multicellular organisms that are dominated by crustaceans and some gelatinous animals (Suthers & Rissik, 2009). Small organisms including bacteria, phytoplankton and zooplankton are abundant in aquatic systems, and play a large role in sustaining ecosystem services (Suthers & Rissik, 2009). Planktonic organisms range in size from 0.2 μm to 2 m, however the groups focused on throughout this thesis include the mesoplankton and microplankton (Suthers & Rissik, 2009). Mesoplankton (0.2-20 mm) include copepods and cladocerans while microplankton (0.2-2.0 mm) include rotifers and nauplii (early stages of crustaceans such as copepods) (Suthers & Rissik, 2009). Copepods are one of the most abundant multicellular organisms on earth and comprise approximately 95% of zooplankton abundance and biomass across all aquatic ecosystems (Richardson, 2008). In freshwaters, cladoceran zooplankton, such as *Daphnia*, are often found in equal abundance with copepods. Changes in abiotic conditions have the potential to alter the structure of zooplankton communities and cause shifts in species composition (Allen et al., 1999; Bos et al., 1996; Dodson et al., 2009; Gannon & Stemberger, 2006; Gray & Arnott, 2009; MacLeod et al., 2018; Soto & Rios, 2006; Swadling et al., 2000). For example, many zooplankton species are poikilothermic, therefore changes in temperature, coupled with species-specific physiological tolerances, may cause changes in community metrics such as species richness or diversity (Gray & Arnott, 2011; Richardson, 2008). Zooplankton communities represent an ideal study system for examining the impacts of environmental stressors on biological communities as they are abundant, diverse, easy to collect and play a vital role in aquatic ecosystems.

1.2.1 Role in Aquatic Systems

Zooplankton are ubiquitous animals as they can be found in rivers, streams, lakes, reservoirs, ponds and wetlands (Suthers & Rissik, 2009). Some zooplankton are termed holoplankton as they spend their entire life cycle in the water column while others, such as larval insects, only spend parts of their life cycle entirely underwater (Suthers & Rissik, 2009). Many zooplankton are grazers in aquatic food webs, allowing for the transfer of energy from primary producers to larger organisms such as macroinvertebrates and fish (Balcer et al., 1984; MacLeod et al., 2018; Ricci & Balsamo, 2000). Zooplankton can also be classified as filter-feeders and predators (Radwan, 1980; Suthers & Rissik, 2009). No matter their functional feeding group, zooplankton provide a link to transfer organic carbon from phytoplankton to fish and excrete faecal pellets that provide nutrients to the water column (Radwan, 1980; Suthers & Rissik, 2009). As a result, they play an important role in recycling nutrients and energy back into the food web (Radwan, 1980). Due to their intermediate position in the food web, changes in zooplankton community composition may impact higher trophic levels (Loria, 2017; MacLeod et al., 2018). Zooplankton also play a role in regulating water clarity and the standing stock of primary producers in freshwaters through top-down control of phytoplankton (Loria, 2017; Sommer & Sommer, 2006), and are in turn regulated by planktivorous fish species (Luecke et al., 1990).

In the limnetic region of the water column, zooplankton are often sparse with several high-density clusters (Folt & Burns, 1999). This pattern of spatial heterogeneity is driven by four potential mechanisms including diel vertical migration (DVM), predator avoidance, finding food and mating (Folt & Burns, 1999). DVM is the pattern of zooplankton rising to the surface at night where they feed on phytoplankton and migrating to greater depths during the day (Folt & Burns, 1999; Suthers & Rissik, 2009). DVM is triggered by changes in light intensity, and is likely an adaptation to avoid predators (Suthers & Rissik, 2009). Other mechanisms of predator avoidance include increased swim speeds and halt of movement which in turn effect aggregation and spacing (Folt & Burns, 1999). Zooplankton also gather in areas of high food concentrations as they migrate towards chemical exudates to locate their food (Folt & Burns, 1999). The last mechanism related to zooplankton aggregation is mate finding. For some zooplankton, mating is dependant on chance encounters, however, the majority of zooplankton locate mates using chemoreception or mechanoreception (Folt & Burns, 1999). Chemoreception refers to the detection of water-born pheromone trails left by potential mates, while mechanoreception is a species-specific mating behaviour where individuals follow fluid disturbance patterns unique to individual species (Folt & Burns, 1999).

1.2.2 Anatomy

The anatomy of zooplankton differs between copepods, cladocerans and rotifers. Copepods are easily differentiated from other zooplankton due to their elongated thorax and segmented rear appendages (Loria, 2017). There are three orders of copepods including calanoids, cyclopoids and harpacticoids, which are easily distinguished based on the length of the antennules, size of the metasome and urosome, as well as the structure of the fifth legs (Loria, 2017; Witty, 2004). The size of the antennae varies between orders of copepods consisting of eight to twenty-five segments; their primary use is for locomotion as well as chemo- and mechanoreception (Balcer et al., 1984). The metasome of copepods includes the head and thoracic segments (Balcer et al., 1984). The head is enclosed by a carapace which consists of a small eyespot, a mouth and maxillipeds used for feeding (Balcer et al., 1984). Along the second to sixth thoracic segments are five pairs of swimming legs, with the fifth pair being a key feature for taxonomy due to the shape of the claw and position of the lateral spine (Balcer et al., 1984). The urosome holds both the genital and abdominal segments (Balcer et al., 1984). Following these segments are two caudal rami and their caudal setae where the length and position of the setae are useful in species identification (Balcer et al., 1984).

In contrast to copepods, cladocerans have a long, round, laterally flattened body shape and non-segmented thorax (Balcer et al., 1984; Suthers & Rissik, 2009). This group of zooplankton also possess projections such as long spines, hair, and wings which increase drag and reduce sinking (Suthers & Rissik, 2009). Unlike copepods, the head of cladocerans is not enclosed in a carapace but, there is a head shield for protection (Balcer et al., 1984). The head holds a single compound eye and, in some species, a light sensitive organ called the ocellus; since this feature is not present in all individuals it is helpful for species identification (Balcer et al., 1984). The size of the rostrum, or beak, is also a distinguishing feature of cladocerans (Balcer et al., 1984). Cladocerans have two sets of antennules, the first attached to the ventral surface of the head and the second to the sides of the head which are primarily used for swimming (Balcer et al., 1984). The body of cladocerans is protected by the carapace, a hard-shell structure which acts as a defense mechanism (Balcer et al., 1984). In addition, four to six pairs of appendages extend from the thorax and this area holds the intestines, brood chamber and abdomen. Key components of cladoceran taxonomic structure are found in the abdomen including the abdominal processes, post-abdominal claw and pectin (Balcer et al., 1984; Witty, 2004).

Rotifers are elongated, transparent, soft bodied organisms that are unsegmented and bilaterally symmetrical (Ricci & Balsamo, 2000; Stemberger, 1995). Their body is comprised of a head, elongated trunk and terminal foot (Ricci & Balsamo, 2000; Stemberger, 1995). The head, also known as the corona, has an apical ciliated region and the trunk contains the digestive, excretory and reproductive organs (Ricci & Balsamo, 2000).The foot is present in some species, however it may be less distinct in individuals which live their entire life in the pelagic zone (Ricci & Balsamo, 2000). When present, the foot terminates in an adhesive disk or toes allowing for attachment (Ricci & Balsamo, 2000).

1.2.3 Development and Reproduction

The lifecycle differs between copepods, cladocerans and rotifers. Copepods develop by moulting into six larval stages (naupliar) followed by five juvenile stages (copepodite) until they reach their final adult stage (Allan, 2002; Suthers & Rissik, 2009). Throughout the moulting stages, segments of the thorax also develop (Suthers & Rissik, 2009). The time it takes to proceed through the copepod lifecycle is variable with development on average taking four to six weeks from egg to adult (Balcer et al., 1984; Suthers & Rissik, 2009). However, development time is significantly influenced by temperature and food availability, therefore, some species grow and mature rapidly producing several generations per year while in other scenarios it may require a year for a copepod to reach maturity (Balcer et al., 1984; Suthers & Rissik, 2009). All copepods reproduce sexually, with a spermatophore being transferred from the male to female (Balcer et al., 1984; Suthers & Rissik, 2009). Most eggs are held in one (calanoids) or two (cyclopoids) egg sacs attached to the genital segment in females, however some species release their eggs directly into the water column prior to hatching (Balcer et al., 1984).

Unlike copepods, cladocera develop without an independent larval stage, meaning that juveniles have the same appearance as adults (Allan, 2002). Early development occurs in a brood pouch and juveniles are released when relatively developed (Allan, 2002). Often, cladocerans complete five to six life stages, termed instars, before maturing into an adult (Allan, 2002). Cladocera reproduce sexually and through parthenogenesis (Allan, 2002). When environmental conditions are favourable, cladocera reproduce asexually, however if environmental conditions deteriorate (overcrowding, lack of food, oxygen depletion) sexual reproduction is preferred (Allan, 2002).

Like cladocerans, rotifers reproduce both sexually and parthenogenetically (Allan, 2002; Stelzer, 2005). The rotifer lifecycle can be divided into three stages after hatching including a pre-reproductive phase, a reproductive phase and a post-reproductive phase (Stelzer, 2005). The pre-reproductive phase involves somatic development while the reproductive phase involves the sequential production of offspring (Stelzer, 2005). The post-reproductive phase is rarely seen in the natural environment; however, it can be found in laboratory cultures (Stelzer, 2005). The lifespan of a rotifer differs pending on the species, some produce a lot of offspring in a short time with a short lifespan, while others live longer and reproduce slower (Stelzer, 2005). The lifespan of a rotifer can range from a few days to a month (Kaneko & Yoshinaga, 2017) with the mean lifespan being eight days (Thorp & Rogers, 2014).

1.3 Metrics to Measure Change

A biological community is defined as a naturally occurring group of species found together in time and space (Mittelbach & McGill, 2019). The structure of a community refers to the composition of species present, as well as the relative abundances of those species. Community structure can be influenced by abiotic factors, species interactions, dispersal, disturbance and chance events (Shurin, 2000). There are two general categories of metrics describing community structure: univariate and multivariate. Univariate metrics include species richness, evenness, and diversity, while multivariate metrics use various types of ordination methods. Univariate metrics describe communities and allow us to compare different regions, taxa and trophic levels (Morris et al., 2014). Species richness refers to the number of unique species present in the community, while species evenness refers to the relative abundance or density of each species (Morris et al., 2014). A community with an even distribution of species would have a similar number of each species, while an uneven community is dominated by one or a few species. Diversity indices take into account both species richness and evenness (Morris et al., 2014). One of the most popular indices is the Shannon-Wiener diversity index [1] where p_i represents the proportion of the entire population made up of species i and S represents the number of species encountered (Peet, 1974).

[1] $H' = -\sum_{i=1}^{s} p_i \ln p_i$

To describe community evenness, Pielou J's (J) index [2] can be calculated where H' is Shannon-Weiner diversity and S represents the total number of species in the community. J assumes a value between 0 and 1, with 1 being complete evenness (Peet, 1974).

$$[2]\quad J = \frac{H\prime}{\ln{(S)}}$$

Multivariate ordination techniques, including principal component analysis (PCA) and Nonmetric Multidimensional Scaling (NMDS), allow for a visualization of the differences in structure between communities (Gray & Arnott, 2009). The resulting ordination plots display differences in the structure of communities in two-dimensional space, with points located closer together having community structures that are more similar than points located further apart (Dytham, 2015).

1.4 Factors Affecting the Structure of Zooplankton Communities

The structure of zooplankton communities is influenced by both local and regional processes (Swadling et al., 2000). At a local scale, biotic and abiotic factors, including pH, ionic concentrations, productivity and predatory-prey relationships can influence structure (Swadling et al., 2000). On a regional scale, colonization and dispersal trends become important (Swadling et al., 2000). High dispersal rates for zooplankton can result in the homogenization of communities across the landscape, while low dispersal rates can produce clumped species distributions and spatial autocorrelation (Shurin et al., 2009). In northern regions, both dispersal and environmental conditions may limit zooplankton diversity because of low productivity and extended periods with ice cover that allow for little movement of individuals among lakes (Swadling et al., 2000). However, the variables identified as having an important influence on zooplankton structure and diversity have varied significantly among studies, and very few studies have been conducted on northern lakes (Aranguren-Riaño et al., 2011). Richardson (2008), found that temperature played a major role in aquatic systems, as temperature influences water column stability, reproductive and metabolic rates, and primary production. As a result, temperature can impact the abundance, size, diversity and trophic efficiency of zooplankton (Richardson, 2008). Sweetman et al. (2010) and Moore (1978) found similar results when they examined the composition of zooplankton communities in Canadian Arctic and subarctic lakes. Sweetman et al. (2010) found that water temperature, dissolved organic carbon (DOC) and total phosphorous (TP) were the environmental variables that significantly influenced the structure of cladoceran communities. In contrast, Moore (1978) found that variations in temperature, surface area, maximum water depth, pH and ionic composition were unimportant in controlling communities. On the other hand, a study done in Alaskan arctic lakes by O'Brien et al. (2004) found that zooplankton communities were influenced most by lake area and depth. Keller and Conlon (1994) found similar results in northern Ontario lakes, where lake depth, lake area and watershed area were positively related to the species richness of zooplankton communities. The variability among studies in terms of the key factors that influence zooplankton community structure makes it difficult to assess how communities might change in the face of a warming climate.

On a regional scale, questions of dispersal are important to consider for zooplankton community organization (Jenkins & Buikema, 1998). Zooplankton can disperse using several vectors, including vertebrates, insects, wind and rain (Jenkins & Buikema, 1998). In the Northwest Territories, vertebrate vectors include black bears (*Ursus americanus*), grizzly bears (*Ursus arctos*), beaver (*Castor canadensis*), ruddy duck (*Oxyura jamaicensis*), herring gull (*Larus argentatus),* and the common loon (*Gavia immer*). It is often assumed that zooplankton disperse readily and have a cosmopolitan distribution due to desiccation-resistant resting eggs, their ability to reproduce parthenogenetically and their small size (Jenkins & Buikema, 1998). However, dispersal can be limited by the harshness of Arctic habitats (Swadling et al., 2000), and past studies suggest variability in dispersal ability among zooplankton species (Jenkins, 1995). Common species with large populations are more likely to disperse via resting eggs due to having a larger source pool (Jenkins, 1995). Less common species with a smaller pool of resting eggs are therefore less likely to disperse (Jenkins, 1995). In addition, not all zooplankton are able to produce resting eggs. Many cladoceran and calanoid copepod species produce these structures, but cyclopoid copepods cannot (Thorp & Rogers, 2014). Since cyclopoids are only able to produce subitaneous eggs that are not resistant to desiccation, they are less likely to survive overland transport (Thorpe & Rogers, 2014).

Many studies provide evidence that dispersal is an important force structuring zooplankton communities. Studies examining the distributional patterns of zooplankton show spatial autocorrelation and a role for spatial variables in explaining differences in communities across a landscape of lakes (Gray & Arnott, 2011; Shurin et al., 2009). Studies also show limited dispersal levels (Jenkins, 1995; Jenkins & Underwood, 1998), and divergence of community structure in lakes or ponds with similar environments. For example, Jenkins and Buikema (1998) compared zooplankton communities in ponds with similar physical and chemical variables to evaluate whether or not dispersal was a regulator of community structure. They found that zooplankton communities were structurally different in terms of the presence/absence of species, taxa density and biomass (Jenkins & Buikema, 1998). As a result, they concluded that dispersal was a regulator of zooplankton communities because it did not occur uniformly among similar ponds (Jenkins & Buikema, 1998). It is possible that in northern lakes, species richness may be low with few species having the opportunity for colonization (Swadling et al., 2000). Species capable of high dispersal rates with life stages that are capable of withstanding extreme temperatures will be the most successful colonizers in these high-latitude lakes (Swadling et al., 2000).

1.5 Climate Change in the Northwest Territories

Over the past decades, the global average annual air temperature has increased 3-4^{o}C, a trend that is predicted to continue over the next century (Frey & McClelland, 2009; Houben et al., 2016). In Arctic regions, temperatures are expected to increase an additional 5-7^{o}C by the end of the 21st century, which is twice the average global rate (Houben et al., 2016). Climate change is already causing changes in precipitation patterns, the thinning of ice, and permafrost thaw (MacDonell, 2015). In addition, the snow-cover extent in the northern hemisphere has decreased 10% since the 1970s (Dore, 2005). A decrease in snow-cover coupled with the thinning of ice is impacting flow patterns, lake evaporation regimes, and water levels (Prowse et al., 2011). The continued increases in air temperature have also led to permafrost thaw (Frey & McClelland, 2009). Permafrost is defined as a layer of soil that has been frozen for at least two years and permafrost is present in 25% of the Northern Hemisphere (Frey & McClelland, 2009) and 80% of the Northwest Territories (Andrews et al., 2016). Permafrost can be characterized as either continuous or discontinuous (Figure 1.1; Kokelj et al., 2009). The thickness of continuous permafrost ranges from 100 to 800 m while discontinuous permafrost ranges from 25 to 100 m (Frey & McClelland, 2009). Increases in permafrost temperatures can lead to retrogressive thaw slumps which most often occur along ice rich shorelines (Houben et al., 2016). Thaw slumps are polycyclic in nature, and therefore have the potential to alter hydrological processes and cause long-lasting impacts over several hectares of terrain (Lantz & Kokelj, 2008). Permafrost degradation can also influence the biology and water quality of aquatic ecosystems (Chin et al., 2016; Throop et al., 2012). Arctic permafrost contains some of the highest concentrations of organic carbon globally due to cool temperatures and the anaerobic conditions of waterlogged frozen permafrost soils (Frey & McClelland, 2009). As permafrost continues to slowly thaw, carbon will become labile and may enter the carbon cycling process, further contributing to climate warming (Frey & McClelland, 2009; Wauthy et al., 2018).

1.5.1 Climate Change and Water Quality

Canada's Arctic is dominated by lakes and ponds which span a diverse range of environmental conditions (Vincent et al., 2012). Fortunately, past studies provide a wealth of baseline water chemistry data for lakes in the Northwest Territories. Permafrost thaw is one of the main drivers leading to changes in water quality in northern regions. Kokelj et al. (2005) collected water samples from 22 lakes in the Mackenzie Delta region, where 11 lakes were impacted by retrogressive thaw slumping and the others were undisturbed (Kokelj et al., 2005). In lakes that were undisturbed, the mean DOC level was 16.3 mg/L (Kokelj et al., 2005) and the dominant cations in undisturbed lakes were calcium, magnesium, sodium and potassium with means of 9.6, 3.6, 2.7 and 1.1 mg/L (Kokelj et al., 2005). The conductivity levels of undisturbed lakes ranged from 35 to 174 μS/cm, and the pH ranged from 6.6 to 7.5 (Kokelj et al., 2005). In contrast, in lakes that had experienced retrogressive thaw slumping DOC concentrations were lower (10.5 mg/L) and the water was clearer. In addition, the concentrations of calcium, magnesium, sodium and potassium were elevated in the disturbed lakes with mean concentrations of 72.6, 26.8, 14.9 and 3.7 mg/L (Kokelj et al., 2005). The range for conductivity was also elevated in this study ranging from 274 to 1680 μS/cm (Kokelj et al., 2005) and pH levels were elevated ranging from 7.6 to 8.1 (Kokelj et al., 2005). Similar results were seen in a study by Houben et al. (2016) which analyzed the impact of permafrost thaw in 39 lakes in the Tundra, north of Inuvik.

Impacts of permafrost thaw and retrogressive thaw slumps may not be permanent. Kokelj et al. (2009) showed that elevated ionic concentrations in lakes were associated with the age of disturbance, described as whether or not the slump was active, stable or ancient (Kokelj et al., 2009). Active slumps were considered to be consistently thawing, stable slumps are those that are well defined but inactive, and ancient slumps are covered in vegetation with visible foot-slopes (Kokelj et al., 2009). A decline in ionic concentrations was associated with the age of disturbance, therefore declines in hardness and alkalinity were seen with an increase in the age of the thaw slump (Kokelj et al., 2009). As a result, this study suggests that short term effects of permafrost thaw slumping will change the ionic chemistry of lakes, however, lakes may be able to recover and return to their former undisturbed state over time (Kokelj et al., 2009).

Thus, permafrost thaw results in an increase of inorganic nutrients and major ions in water systems (Frey & McClelland, 2009). Lakes affected by thaw slumping are known to have clearer water, lower levels of DOC, and higher ion concentrations (Moquin & Wrona, 2015). The contribution of large volumes of previously frozen inorganic materials by retrogressive thaw slumps will lead to a rise in ionic concentrations in water systems, including calcium, magnesium, potassium and sodium (Frey & McClelland, 2009; Lantz & Kokelj, 2008). There is the possibility that over time, lakes may be able to recover from thaw slumping activities (Kokelj et al., 2009) however, coupled with other effects of climate change there is no guarantee that lakes will ever revert back to their previous state.

1.5.2 Climate Change and Zooplankton

The Arctic region is a harsh ecosystem, as the area is subject to short ice-free periods, low temperatures, high levels of ultraviolet radiation and low nutrient levels (Samchyshyna et al., 2008). These conditions make it difficult for freshwater organisms to survive, resulting in low biodiversity (Samchyshyna et al., 2008). Many arctic organisms are cold water stenotherms adapted to living in frigid temperatures and may be negatively impacted by temperature increases (Samchyshyna et al., 2008). In addition to the direct effects of rising temperatures, climate change also has the potential to affect phytoplankton and zooplankton community structure through changes in precipitation patterns, the thinning of ice, and alterations in water quality as a result of permafrost thaw (Houben et al., 2016; MacDonell, 2015). Changes in the thickness and timing of ice break up can lead to impacts on biota in lakes (Prowse et al., 2011). For example, with warmer winters and increased precipitation as snow, the ice thickness will decrease (Prowse et al., 2011), which could increase the survival of organisms in lakes that formerly froze to the bottom in winter. Furthermore, with ice breaking earlier in the spring, there will be a longer open-water season and earlier starts to primary production (Prowse et al., 2011). This will influence the seasonal succession of plankton likely resulting in early spring phytoplankton blooms and zooplankton biomass peaks (Prowse et al., 2011). Moreover, changes in water quality due to permafrost disturbance could lead to significant reductions in periphyton and phytoplankton communities (Houben et al., 2016). Taken together, the influx of nutrients from thawed soils can impact food web dynamics in affected lakes by causing shifts in community structures (Houben et al., 2016).

1.6 Infrastructure Development in the Northwest Territories

An increase in development also raises great concern for northern ecosystems. Since 2002, $1.2 billion dollars has been invested in infrastructure within the Northwest Territories with 69% of that funding being used for highways and roads (Infrastructure Canada, 2019). With the demand for infrastructure, there is a need for the mining of sand and gravel creating new gravel pits. Through an influx of groundwater, rainfall, snowmelt and connections with nearby lakes, these gravel pits can become new aquatic ecosystems (Gammons et al., 2009; Mollema et al., 2016; Søndergaard et al., 2018). In the Northwest Territories, the demand for gravel mining is expected to increase owing to the growing population, increased development and increased tourism. For example, the Inuvik-Tuktoyaktuk highway opened in November 2017, being the first highway to access the southern coast of the Arctic ocean which is a region where increased development is anticipated (Kiggiak-EBA Consulting LTD., 2011).

Gravel extraction is also projected to increase with ongoing maintenance of roadways built over permafrost with an active layer experiencing damaging freeze thaw cycles. With the development of highways and roads in the north also comes the concern of impacts of road dust on roadside ecosystems as these areas are surrounded by thousands of lakes. As a result, the formation of gravel-pit lakes has the potential to create new aquatic systems however, the ongoing inputs of road dust from the calcareous gravel roads may negatively impact surrounding areas.

1.6.1 Infrastructure Development and Water Quality

Gravel pit lakes and natural lakes exhibit differences in physical and chemical properties (Boyes, 1999; Hindák & Hindáková, 2003). Typically, these artificial lakes are deeper with a higher depth:surface area ratio (Blanchette & Lund, 2016; Kalin et al., 2001; Mollema & Antonellini, 2016). These lakes are also clear with neutral to alkaline pH levels (Hindák & Hindáková, 2003; Søndergaard et al., 2018). Although these man-made lakes have the potential to be beneficial due to their ecological value and recreational purposes, concern arises due to the lack of vegetation surrounding the area leading to elevated conductivity levels (Søndergaard et al., 2018).

Development in the north can also have implications for water quality due to road dust from the calcareous gravel roads. The construction of roads has been associated with negative effects to both terrestrial and aquatic ecosystems (Trombulak & Frissell, 2000). These effects can be direct through impacts of road dust and indirect through changes to surface albedo (Auerbach et al., 1997). During initial construction, change is associated with the removal of vegetation and addition of culverts for stream and river crossings (Gill et al., 2014). This modifies the local hydrology, increases soil erosion, temperature, soil water content, light levels, dust, patterns of run-off, and adds metals, salts and nutrients to roadside ecosystems (Auerbach et al., 1997; Gill et al., 2014; Trombulak & Frissell, 2000). Furthermore, the development of roads creates a deeper permafrost active layer and alters snowpack (Auerbach et al., 1997). After road construction, road dust, run-off, trash and vehicle pollution continue to influence the local area (Gill et al., 2014). The Arctic has been documented to have the greatest sensitivity to road dust (Farmer, 1993). Myers-Smith et al. (2007) examined 13 years of calcareous road dust deposition in northern Alaska and found that dust loading continues to alter substrate properties and community composition. For example, the tundra soil had a pH of 5.5 in 1989 which rose to a pH of 6.0 in 2002 (Myers-Smith et al., 2007). Gunter (2017) assessed these impacts of dust and found that alkalinity, conductivity, total dissolved solids (TDS), pH, calcium, hardness, magnesium, nitrate, sulfate and strontium decreased with distance from the highway. This indicates that a highway is a potential source contributing to variation in water quality. However, it is difficult to assess whether these changes in water quality are due to road dust alone or if they are coupled with the effects of climate change (ex. permafrost thaw).

1.6.2 Infrastructure Development and Zooplankton

Little is known about differences in zooplankton communities between natural and gravel pit lakes, however, it is predicted that zooplankton communities will be less abundant and diverse in gravel pit lakes as species have had less time to colonize these young ecosystems and nutrient levels are typically lower (Gammons et al., 2009; Mollema & Antonellini, 2016). Direct effects of road dust on aquatic communities in the north have not been studied, however, it is likely the calcareous road dust from the gravel roads and lack of riparian vegetation surrounding gravel pit lakes will alter water chemistry influencing aquatic community structure. Previous studies have found strong relationships between zooplankton and conductivity (Bos et al., 1996; Soto & Rios, 2006). For example, Bos et al. (1996) examined the relationship between zooplankton, conductivity and lake-water ionic composition in British Columbia lakes and found that chydorids, calanoids, cyclopoids and nauplii had a wider tolerance to conductivity in comparison to other species. Furthermore, Soto and Rios (2006) examined how zooplankton are impacted by changes in trophic status and conductivity. This study concluded that calanoids dominated lakes with high conductivity while *Daphnia* were abundant in lakes with lower conductivity levels (Soto and Rios., 2006).

1.7 Objectives and Research Questions

The overarching goal of my research was to describe how zooplankton communities may change due to climate change and development. More specifically, the main purpose of my research was to: (i) Collect baseline data on water chemistry, lake bathymetry, and zooplankton communities for lakes along the Tuktoyaktuk-Inuvik-Fort McPherson (TIF) transportation corridor which runs through the Gwich’in Settlement Area (GSA) and Inuvialuit Settlement

Region (ISR) in the Northwest Territories (Figure 1.2); (ii) Compare water quality and biota in gravel pit lakes and natural lakes; (iii) Develop statistical models to describe how zooplankton are influenced by factors related to permafrost thaw and use these models to project future changes in zooplankton communities. This research will contribute to understanding the fundamental processes that structure zooplankton communities in northern lakes and how the structure of communities may change in response to climate change and development.

1.8 Structure of Thesis

This thesis contains four chapters. The first chapter is a literature review providing background information on topics covered in the following chapters. Chapter 2 focuses on development in the Northwest Territories discussing the differences in biology, water quality and morphometry between natural and gravel pit lakes along the Dempster Highway in the Northwest Territories. Chapter 3 examines the variables that are most important in structuring zooplankton communities in these northern lakes. This chapter also uses modelling to project future change in zooplankton abundance, evenness and diversity. Chapter 4 is a general discussion looking at the major findings in my research as well as links my research to other related projects.

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1.10 Figures

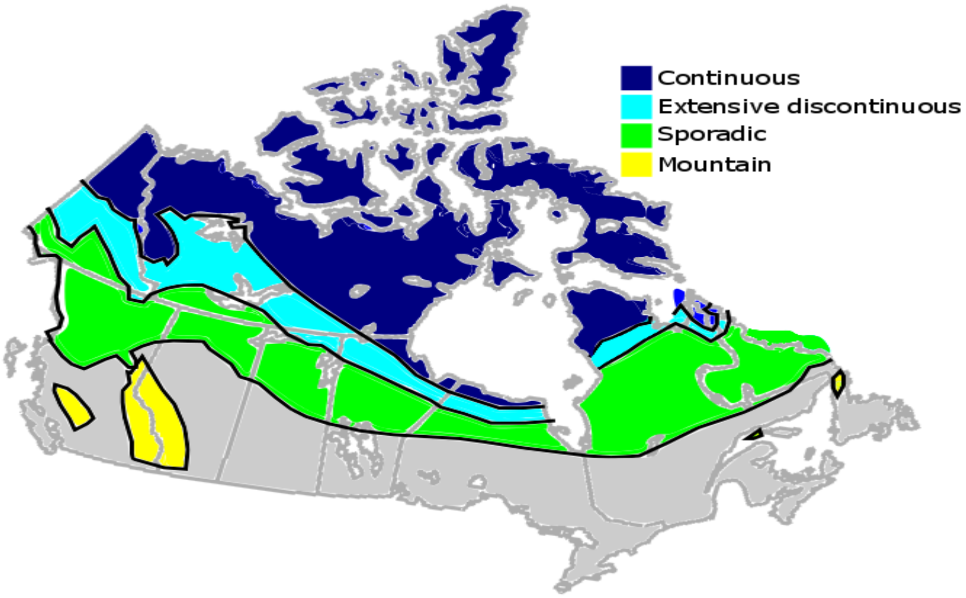

Figure 1.1 Permafrost regions of Canada divided into four permafrost zones. The Northwest Territories is underlain by continuous permafrost as well as extensive and sporadic discontinuous permafrost *(Image adapted from Heginbottom* et al.*1995).*

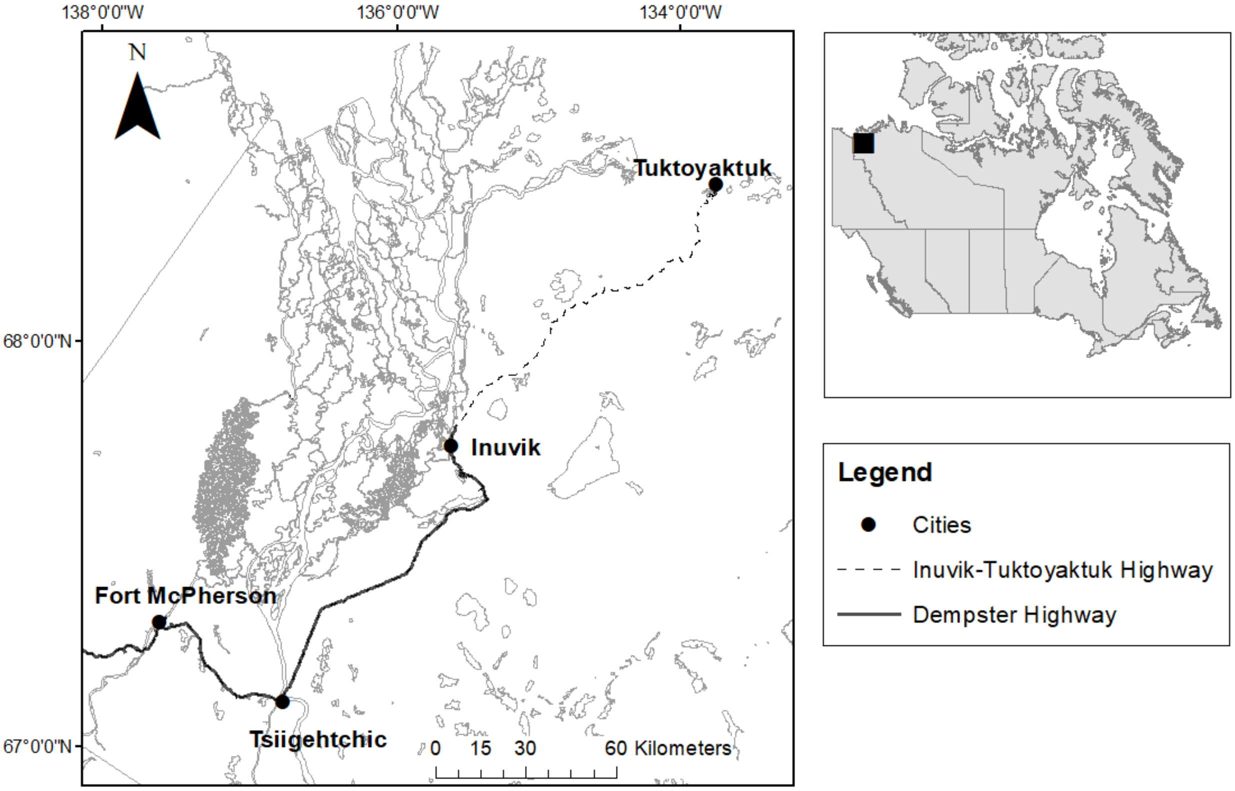

Figure 1.2. Map of study area.

CHAPTER 2

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

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Role of Co-authors: Rachel S. Cohen (contributed to macroinvertebrate 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)

2.1 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 (zooplankton, 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, pelagic zooplankton and littoral macroinvertebrate communities did not differ significantly between the two lake types. Therefore, we conclude that despite their recent formation and unnatural morphometry, gravel pit lakes along the Dempster Highway can support invertebrate communities typical of natural lakes in the region.

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

2.2 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 & Önsoy 2014; Mollema & 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 & 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 & 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 & Hindáková, 2003). Past studies suggest that most gravel pit lakes are oligotrophic, clear, and exhibit neutral to alkaline pH levels (Hindák & 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 (Blanchette & Lund, 2016; Kalin et al., 2001; Mollema & Antonelli, 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 & 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 (Alfonso et al., 2010; Ejsmont-Karabin 1995; Hindák & Hindáková, 2003; Lipsey, 1980). 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 (Allen & VanDyke, 2011; Audet et al., 2013; Beisner et al., 2006). Zooplankton and phytoplankton can disperse to gravel pit lakes using several vectors, including movement through streams, attachment to vertebrates, insects, and through heavy wind and rain events (Jenkins & Buikema, 1998). 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)*. However, the colonization of newly formed lakes may occur slowly for zooplankton, as many studies have identified low dispersal rates for this group (Gray & Arnott, 2011; Jenkins & Buikema, 1998). Macroinvertebrates are less likely to 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. 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 (Gray &Arnott, 2011; Louette et al., 2008; Shurin et al., 2009), 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 biological 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 zooplankton and 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 (Søndergaard et al., 2018); (ii) Species abundance, richness, and diversity will be lower in gravel pit lakes for both macroinvertebrates and zooplankton owing to their young age (Alfonso et al., 2010; Ejsmont-Karabin, 1995; Hindák & Hindáková, 2003; Lipsey, 1980), and low nutrient levels (Dodson et al., 2000); and iii) Macroinvertebrate and zooplankton 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 & Lund, 2016; Mollema & Antonellini, 2016).

2.3 Methods

2.3.1 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 17th and September 1st, 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 subjective 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 & Kokelj, 2009; Kokelj et al., 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). It is difficult to provide an exact age for the lakes sampled in this study, however, it is likely that the natural lakes are much older than the gravel pit lakes. 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 to ~13 000 years ago during the Last Glacial Maximum (Dredge & Thorleifson, 1987; Hill, 1996). Although the construction of the highway may have changed the hydrology for some lakes in the region (Kiggiak-EBA Consulting Ltd., 2011; Trombulak &

Frissel, 2000), 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 & Resources, 1973).

2.3.2 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 using 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 (DO), pH, total nitrogen (TN), total phosphorus (TP), total organic carbon (TOC), 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, 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, total phosphorus 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 5th, 2018 and collected shoreline water samples for measurement of TP and TN. Samples for TP 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 TP 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).

2.3.3 Zooplankton and Macroinvertebrate Communities

Zooplankton samples were collected from each lake at the point of maximum depth and preserved on site using 95% ethanol. For lakes greater than 3 m in depth, a single vertical haul using a 35-cm diameter, 50 μm mesh size zooplankton net was collected from each sample site. For shallow lakes less than 3 m in depth, where a vertical tow was not possible, a horizontal tow was collected by towing the net behind the boat for approximately 60 seconds. In both cases, a mechanical flowmeter attached to the mouth of the net was used to determine the volume of water that passed through the net. To calculate zooplankton densities, the number of individuals in each sample was divided by the volume of sampled water. In the laboratory, individuals were identified to the species level according to Haney et al. (2013) using a magnification of 40x to

400x depending on the size of the species. Zooplankton were collected from all fifteen natural lakes and from five of the six gravel pit lakes in 2017 (one sample container was damaged during shipping). A zooplankton sample from the missing gravel pit was collected in August 2018 and added to our dataset.

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^2 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). 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 & 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 & 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 & Colwell, 2001). For zooplankton species richness, we rarefied communities to 142 individuals, which was the lowest number of individuals identified from a single lake. Similarly, for macroinvertebrate taxa, 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 estimateD 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).

2.3.4 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, TOC, conductivity, chlorophyll-*a*, zooplankton abundance, 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 zooplankton and 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 & Anderson, 2001). In this case, the response variables were zooplankton or macroinvertebrate species 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, TOC, 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 & 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).

2.4 Results

2.4.1 Morphometry and Water Quality

There was a significant amount of variation in morphometry and water quality variables among our study lakes (Table 2.1). In terms of morphometry, 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). For water quality, 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 2.2A, E). TN concentrations were twice as high in natural lakes compare to gravel pit lakes and TP was 1.5 times higher in natural lakes (Figure 2.2D, G; Table 2.2). However, gravel pit lakes and natural lakes had similar values for pH, water temperature, DO, conductivity, chlorophyll-*a*, TOC, and calcium (Table 2.1; Table 2.2; Figure 2.2E, F). 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).

2.4.2 Zooplankton and Macroinvertebrate Communities

Species abundance, richness, and diversity for both zooplankton and macroinvertebrates were similar in gravel pit and natural lakes (Figure 2.4; Welch's t-tests $p>0.1$ in all cases). Fish presence/absence, mean depth, Secchi depth, turbidity, and latitude were significant predictors of zooplankton community composition with the first two RDA axes explaining 38.40 % of the variation (Figure 2.5A, $F = 2.68$, $p<0.005$, adjusted $R^2 = 0.29$). The RDA suggests that species of

Daphnia were associated with deeper lakes and cyclopoid copepods were more abundant in shallow lakes. Additionally, the calanoid copepod *Skistodiaptomus pallidus* was abundant in fishless, less turbid lakes. 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 2.5B, F=1.59, $p<0.05$, adjusted $R^2 = 0.08$). The RDA hinted that Gastropoda may be positively associated with fish absence, and Hemiptera with mean depth, but for the most part, distinct correlations between macroinvertebrate species and predictor variables were not observed.

2.5 Discussion

Gravel pit lakes were markedly different in their morphometry and in several water quality characteristics compared to natural lakes, but surprisingly, zooplankton and macroinvertebrate communities did not differ between lake types. The relatively deep basins and low nutrient, chlorophyll-*a*, and turbidity levels in gravel pits 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. Species richness, species diversity, and abundance for zooplankton and macroinvertebrates were not lower in gravel pit lakes, providing no support for our second hypothesis. Finally, community structure for zooplankton and 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.

2.5.1 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 & 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 & 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 pits 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 TN and TP concentrations than natural lakes. These differences indicate that gravel pits are relatively unproductive in comparison with natural lakes (Brylinsky & Mann, 1973; Smith, 1982). Finally, TOC 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 gravel pit lakes. Decreasing terrestrial biomass has been associated with decreases in lake TOC levels, so we suspect that lower TOC levels may be related to the clearing of vegetation in the watershed 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 (Houben et al., 2016; Kokelj et al., 2009; Swadling et al., 2000), 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 TOC 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 Swalding 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 TN 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 Swalding et al. (2000), whose TN concentrations ranged from 0.25 mg/L to 1.58 mg/L. Our TP 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 µg/L.

2.5.2 Zooplankton and Macroinvertebrate Communities

Our results did not support the hypothesis that gravel pit lakes contain lower zooplankton richness and diversity due to their younger age. These results contrast with those of Lipsey and Malcom (1981), where zooplankton were collected from seven gravel pit lakes. In that study, older pit lakes had a greater species richness and diversity than newer ponds (Lipsey & Malcom, 1981). In a separate study, a similar relationship between lake age and diversity was also found for phytoplankton (Lipsey, 1980). Other studies also show relationships between age and plankton diversity in artificial lakes (Alfonso et al., 2010; Dodson et al., 2007; Ejsmont-Karabin, 1995). In our study, we may have failed to detect a difference between natural lakes and gravel pits because of the relatively old age of the gravel pits (minimum ~25 years; AlecSandra MacDonald, Gwich'in Land and Water Board, personal communication). Both Ejsmont-Karabin (1995) and Alfonso et al. (2010) found that differences could be detected on the time scale of 1-3 decades, but past that point, dispersal and colonization processes allowed artificial lakes to achieve an equilibrium number of species. The age of the gravel pits in Lipsey and Malcom (1981) and Lipsey (1980) varied between 1-13 years, a timeframe where differences in diversity based on age would be most evident (Alfonso et al., 2010; Ejsmont-Karabin, 1995).

We also hypothesized that the structure of zooplankton communities (relative abundance of species) would differ between gravel pit lakes and natural lakes owing to differences in morphometry and water quality. However, our ordinations did not display any obvious differences between the lake types. When developing this hypothesis, we assumed that the physical parameters that differed between the two lake types would be important for structuring zooplankton communities. Significant differences between lake types were evident for lake depth, water clarity, TP, and TN. Our redundancy analysis identified mean depth and water clarity variables (Secchi depth and turbidity) as significant predictors of community structure, but not TP or TN. It is likely that the difference in community structure between lake types did not materialize as expected because other physical variables that did not differ between lake types were also controls on community structure. For example, in our redundancy analysis for zooplankton, latitude was significant, but did not consistently differ between lake types. Other northern studies have identified temperature, dissolved organic carbon, fish presence/absence, phytoplankton (chlorophyll-*a*), and total phosphorus as major controls on zooplankton community structure (Moore, 1978; Richardson, 2008; Schilling et al., 2009; Sweetman et al., 2010; Sweetman & Smol, 2006). It is possible that our study did not include a large enough gradient (range) for those variables such that they would be selected as significant in our statistical analyses.

We also 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. Similar to zooplankton, 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 (Bass, 1992; Layton & Voshell, 1991; Voshell & Simmons, 1984). 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. As with the zooplankton, 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.

2.5.3 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. Our study was also limited in that we chose to focus on pelagic zooplankton and littoral macroinvertebrates, but excluded littoral zooplankton and profundal 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).

2.5.4 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

& 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 both littoral macroinvertebrates and pelagic zooplankton. This is consistent with other studies that suggest gravel pit lakes can have ecological value by providing habitat for aquatic species, increasing biodiversity (Alfonso et al., 2010; Ejsmont-Karabin, 1995; Gammons et al., 2009). 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).

2.5.5 Conclusions

In summary, gravel pit lakes differed in key morphometric and water quality parameters in comparison with natural lakes, however, littoral macroinvertebrate and pelagic zooplankton communities were similar. Gravel pit lakes were clearer and deeper, with lower nutrient levels. Despite these differences in morphometry and water quality, zooplankton and macroinvertebrate communities did not differ in richness, diversity, abundance, or structure between the two lake types. 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.

2.6 Acknowledgements

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2.8 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 (^{o}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^3 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-*a* (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.

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

2.9 Figures

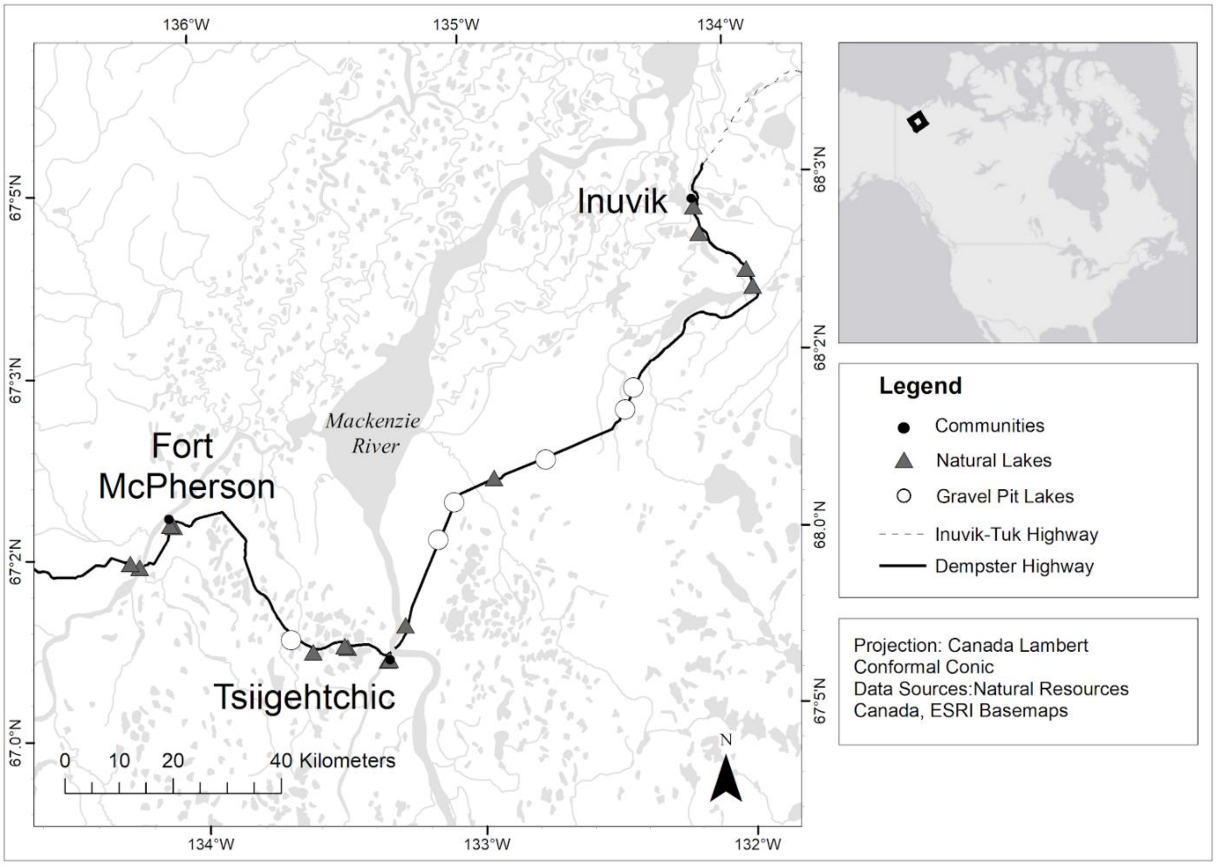

Figure 2.1. Map of lakes sampled along the Dempster Highway between Fort McPherson and Inuvik, Northwest Territories.

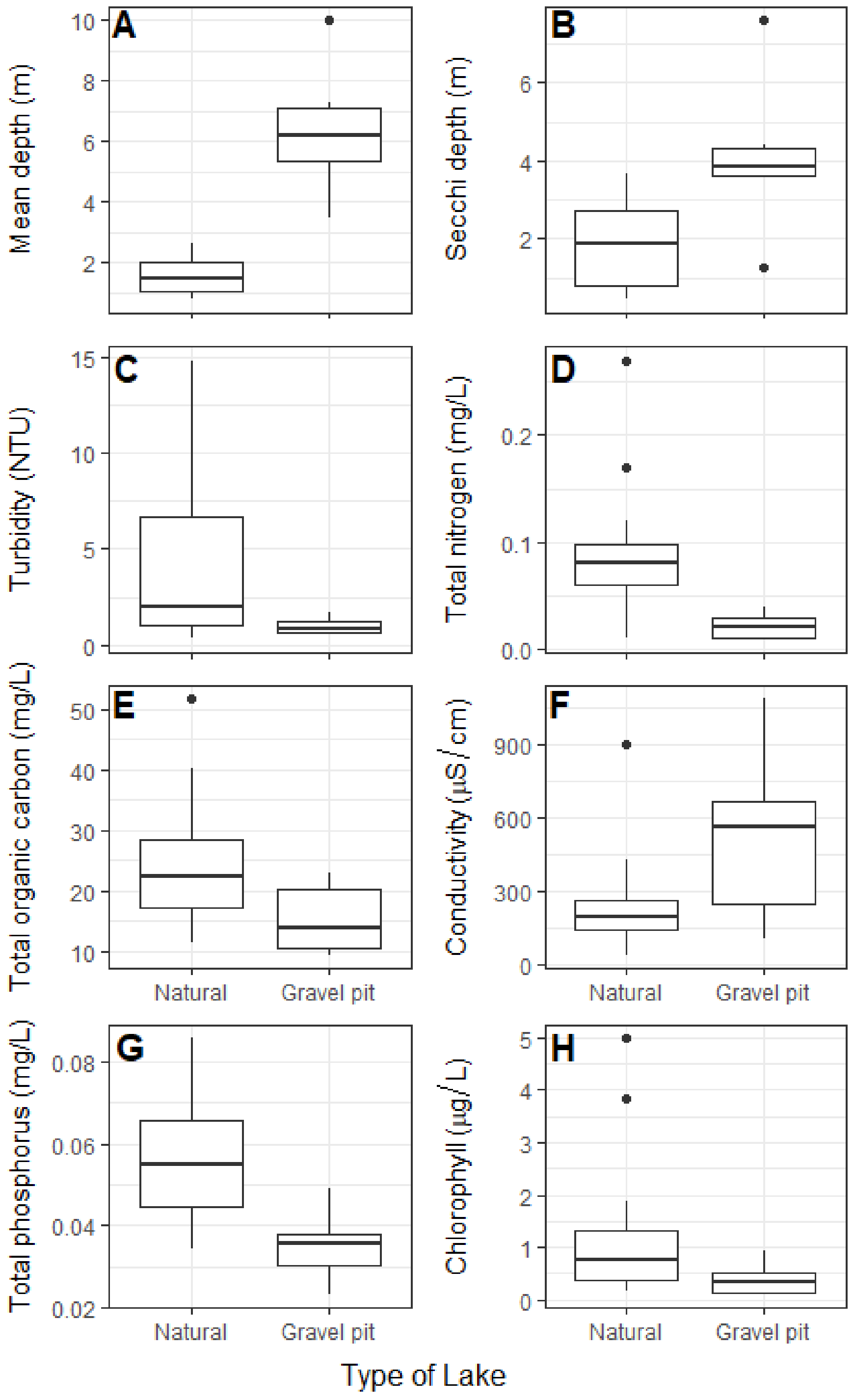

Figure 2.2. Comparison of selected morphometric and water quality variables between natural and gravel pit lakes. Bolded line=median, lower end of box=first quartile, upper end of box= third quartile, whiskers=range of data, dots=outliers.

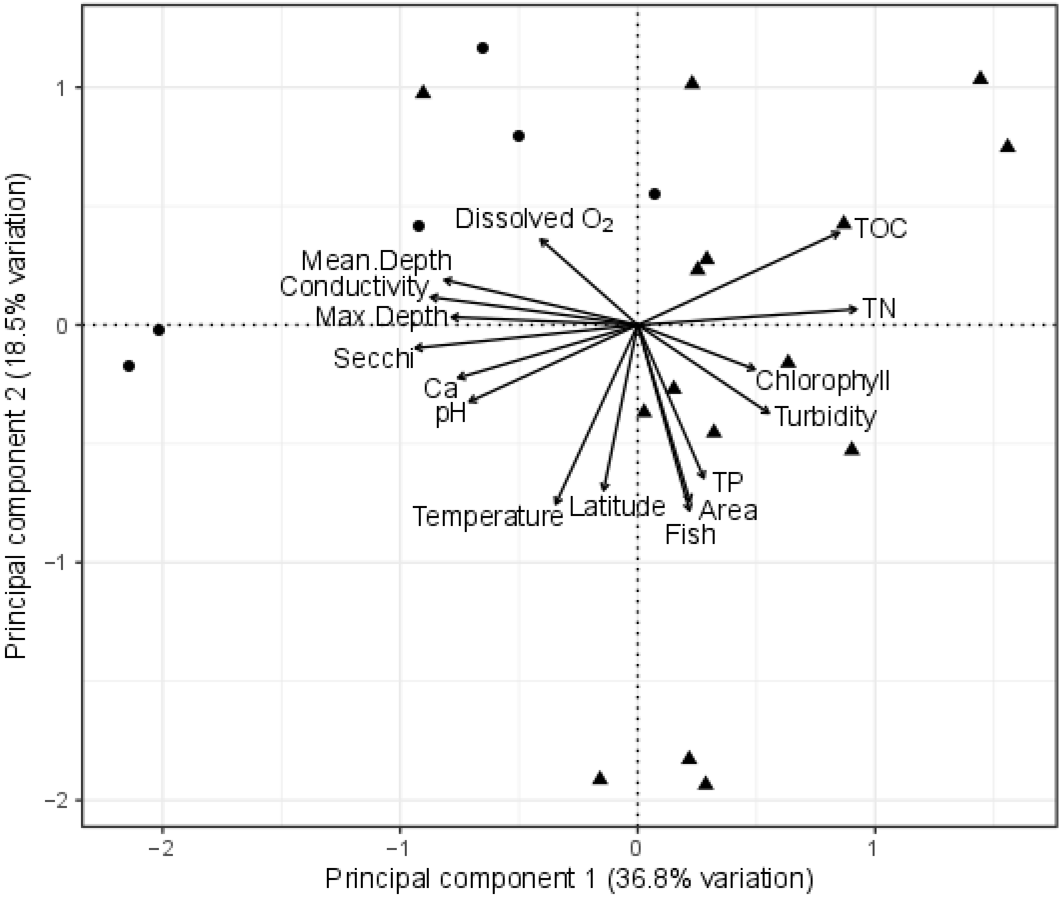

Figure 2.3. Principal component analysis (PCA) conducted with morphometry and water quality data for each of our 21 study lakes. Circles represent gravel pit lakes and triangles represent natural lakes. Sites that are closer together tend to have similar morphometry and water quality than sites that 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.

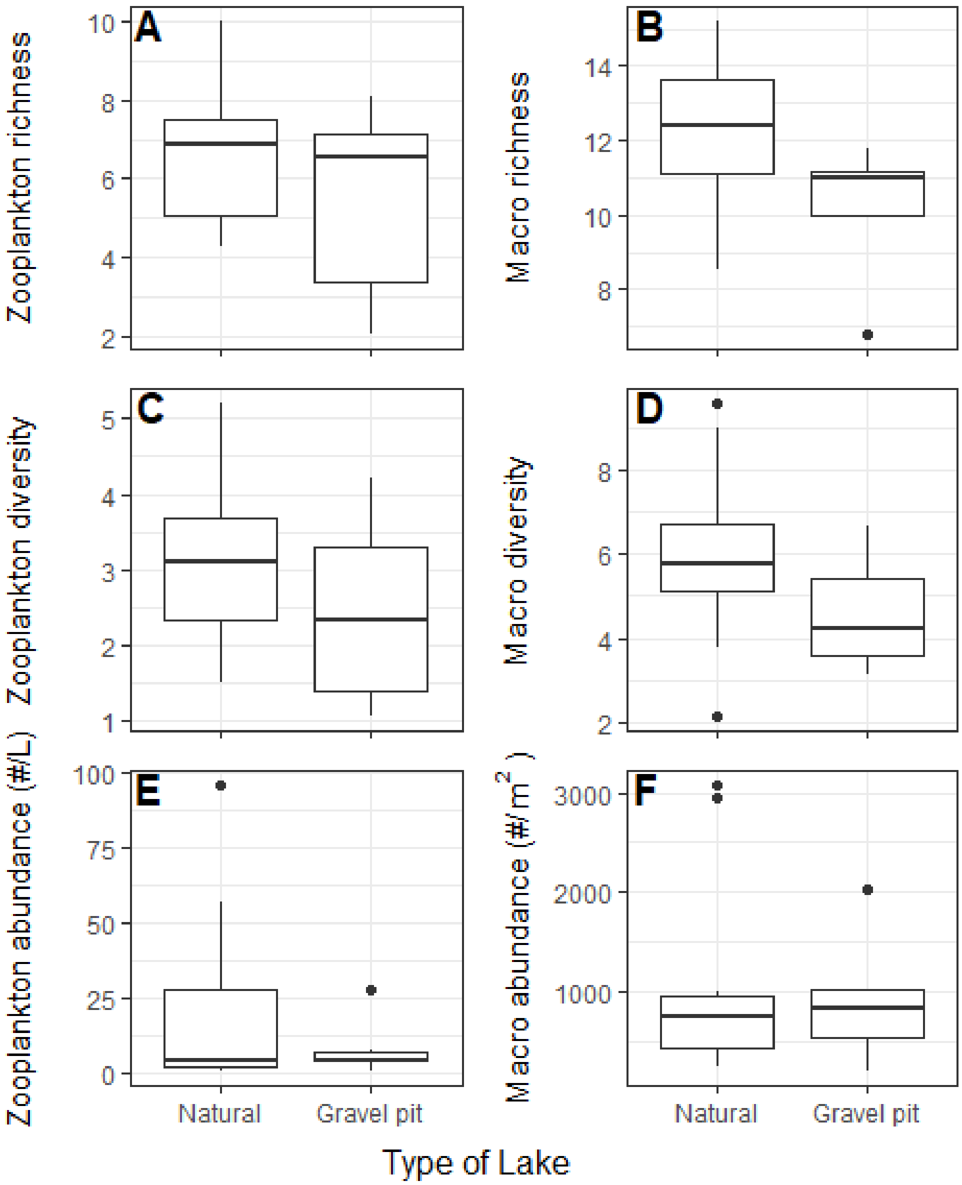

Figure 2.4. Comparison of rarefied species richness, diversity (Hill numbers), and abundance of zooplankton and macroinvertebrates in natural lakes and gravel pit lakes.

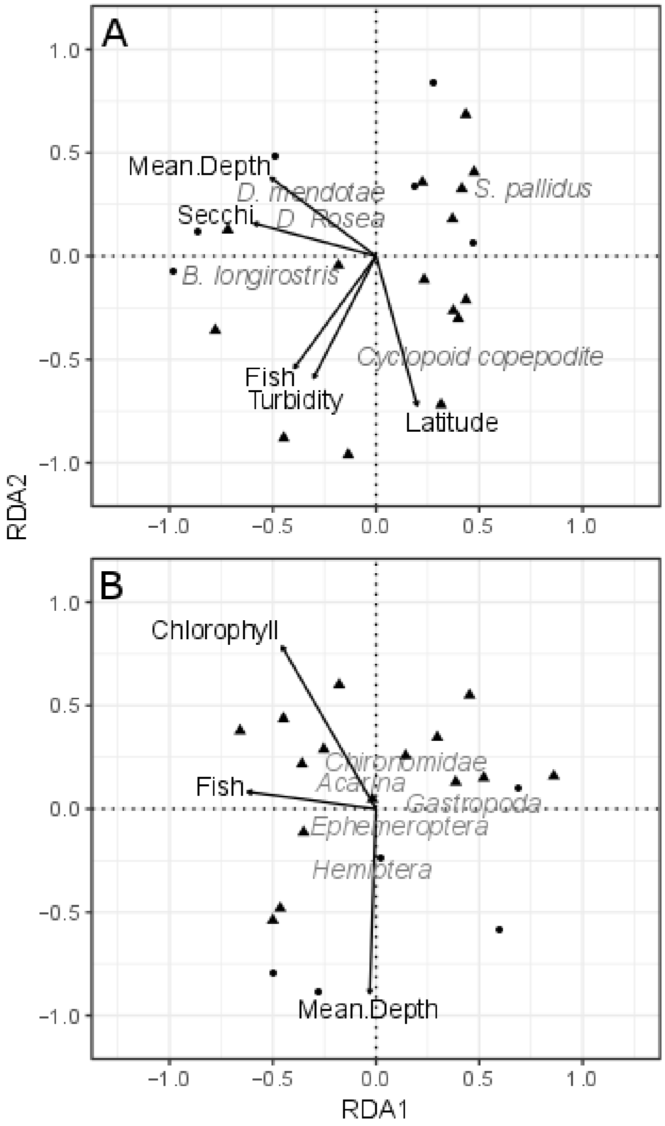

Figure 2.5. Results of redundancy analyses displaying predictor variables (morphometry and water quality) with zooplankton (A) and macroinvertebrate (B) abundances as response variables. Circles represent gravel pit lakes, triangles represent natural lakes. Species are represented by their text labels.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

CHAPTER 3

Changes in water quality related to permafrost thaw may significantly impact zooplankton communities in small Arctic lakes.

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3.1 Abstract

Rising temperatures are leading to permafrost thaw over vast areas of the northern hemisphere. In the Canadian Arctic, permafrost degradation is causing significant changes in surface water quality due to the release of solutes that can alter conductivity, water clarity, and nutrient levels. For this study, we examined how changes in water quality associated with permafrost thaw might impact zooplankton, a group of organisms that play an important role in the food web of arctic lakes. We conducted a biological and water quality survey of 37 lakes in the Mackenzie Delta region of Canada’s Northwest Territories. We then used this dataset to develop models linking variation in the abundance, diversity, and evenness of zooplankton communities to physicochemical, biological, and spatial variables. Subsequently, we used these models to predict how zooplankton communities might respond as water quality is altered by permafrost thaw. Our models explained 47%, 68%, and 69% of the variation in zooplankton abundance, diversity, and evenness, respectively. Importantly, the most parsimonious models always included variables affected by permafrost thaw, such as calcium and conductivity. Predictions based on our models suggest significant increases in zooplankton abundance (1.6-3.6-fold) and decreases in diversity (1.2-1.7-fold) and evenness (1.1-1.4-fold) in response to water quality changes associated with permafrost thaw. These changes are in line with those described for significant perturbations such as eutrophication, acidification, and the introduction of exotic species such as the spiny water flea (*Bythotrephes*). Given their important role in aquatic food webs, we expect these changes in zooplankton communities will have ramifications for organisms at higher (fish) and lower (phytoplankton) trophic positions in Arctic lakes.

3.2 Introduction

The Canadian Arctic has been warming at an unprecedented rate, affecting both terrestrial and aquatic environments (Walther et al., 2002; Frey & McClelland, 2009; Kokelj et al., 2009; Houben et al., 2016). As the climate warms, one of the most important drivers of water quality change in the north will likely be permafrost thaw (Kokelj et al., 2009; Chin et al., 2016). Permafrost is defined as a layer of soil that has been frozen for at least two years (Kokelj et al., 2009). When thawed, permafrost adversely affects terrestrial ecosystems and modifies the water chemistry of streams, lakes, and wetlands (Kokelj et al., 2009; Chin et al., 2016). In comparison with the surficial active layer which freezes and thaws annually, permafrost in this region contains elevated levels of solutes, including calcium, magnesium, sodium, and phosphorus (Keller et al., 2007; Burn & Kokelj, 2009). The deepening of the active layer can allow for weathering of these minerals and their transportation into aquatic systems (Keller et al., 2007). The quantity of minerals mobilized from the permafrost will depend on the magnitude of change in the depth of the active layer exposed to weathering (Kokelj et al., 2009). In extreme cases, the degradation of ice-rich permafrost can lead to thaw slumps which can expose the top several meters of permafrost to weathering. Thaw slumps often occur along shorelines, leading to increases in inorganic nutrients and higher ion concentrations, including calcium, magnesium, potassium, and sodium (Lantz & Kokelj, 2008; Frey & McClelland, 2009). Affected lakes are also known to have clearer water and lower levels of dissolved organic carbon (Moquin & Wrona, 2015). These physicochemical changes related to permafrost thaw have been shown to impact biota in lakes, including diatoms, macrophytes, and benthic invertebrates (Mesquita et al., 2010; Thienpont et al., 2013; Moquin et al., 2014).

Previous studies have examined how the physical and chemical changes caused by permafrost thaw might impact some taxa in Arctic lakes (Mesquita et al., 2010; Thienpont et al., 2013; Moquin et al., 2014), but zooplankton have not been considered. The lack of studies on zooplankton is surprising, as they are especially sensitive to changes in calcium and conductivity levels, both of which are influenced by permafrost thaw (Green, 1993; Bos et al., 1996; O'Brien et al., 2004; Shiel et al., 2006; Soto & Rios, 2006; Bégin & Vincent, 2017). Zooplankton are critical members of freshwater food webs, as they allow for the transfer of energy from primary producers to larger organisms such as macroinvertebrates and fish (Richardson, 2008). Both local and regional processes influence the composition of zooplankton species in local communities and the relative abundances of those species (Beisner et al., 2006). Past studies of zooplankton communities at high latitudes show that local variables such as temperature, pH, conductivity, primary productivity, calcium, and nutrient levels can be important determinants of zooplankton community composition (Moore, 1978; Bos et al., 1996; Swadling et al., 2000; Soto & Rios, 2006; Richardson, 2008; Frey & McClelland, 2009; Sweetman et al., 2010; Moquin & Wrona, 2015; Thienpont et al., 2015; Houben et al., 2016). As described above, many of these local variables are expected to change in response to a warming climate. Regional processes such as dispersal are also important determinants of local community composition. Many studies have identified spatial autocorrelation in zooplankton communities distributed across lakes within a region that is independent of spatial structure in local environmental variables (Shurin et al., 2009). This spatial autocorrelation is either the result of unmeasured spatially-structured environmental variables or is a result of dispersal limitation and colonization/extinction dynamics (Shurin & Allen, 2017). Dispersal of zooplankton among lakes can occur through several vectors, including attachment to vertebrates or insects, or through wind and rain events

(Jenkins & Buikema, 1998). As zooplankton communities are structured by both local and regional variables, statistical models that include both environmental and spatial variables can better account for the variability in zooplankton communities across lakes in a region (Austin, 2002).

Understanding the factors that influence the structure of Arctic zooplankton communities is a key prerequisite for developing predictions about their response to environmental change. To assess how zooplankton communities might respond to water quality changes related to permafrost thaw, we conducted a survey of 37 lakes in the Gwich'in and Inuvialuit Regions of the Northwest Territories that varied in their physicochemical and biological characteristics. We then used the resulting dataset to produce models that describe how zooplankton community structure was related to physicochemical, biological, and spatial variables. The models were then used in conjunction with data from the literature to forecast changes in zooplankton communities as a result of permafrost thaw (e.g. increases in conductivity levels). Our models predicted significant changes in the abundance, diversity, and evenness of zooplankton communities. Given the importance of zooplankton in lake food webs, these changes could affect organisms found at higher (fish) and lower (phytoplankton) trophic levels (Carpenter, 1987; Elser et al., 1987; Carpenter et al., 2010). Understanding potential changes in freshwater food webs related to a warming climate are especially important in Canada's north, as Indigenous communities, such as the Gwich'in and Inuvialuit, depend on these resources as a source of food and to maintain their way of life (Furgal & Seguin, 2006).

3.3 Materials and Methods

3.3.1 Study Area

Our study includes 37 lakes located along the Dempster and Inuvik-Tuktoyaktuk Highways in the Northwest Territories (Figure 3.1). Lakes along the Dempster Highway were sampled between August 17th and September 1st, 2017 while lakes along the Inuvik-Tuktoyaktuk Highway were sampled between August 6st and August 27th, 2018. Along the Dempster Highway, lakes were located in the Boreal Forest region dominated by coniferous trees, such as black spruce (*Picea mariana*), white spruce (*Picea glauca*) and jack pine (*Pinus banksiana*; Sweetman et al., 2010). This region contains a layer of discontinuous permafrost (ranging from 25-100 m thick) covering, between 50-90% of the total area (Kokelj et al., 2009). Along the Inuvik-Tuktoyaktuk Highway, lakes are located in the Tundra region dominated by sedges (*Carex spp*.), lichen-heath and various dwarf shrubs (Sweetman et al., 2010). This region is underlain by continuous permafrost (ranging from 100-800 m thick) covering 100% of the total area (Kokelj et al., 2009). The study area contains thousands of lakes and the landscape is comprised of sediments deposited by the Mackenzie and Peel Rivers, draining out into the Beaufort Sea (Burn & Kokelj, 2009). Three of the study lakes were located in the town of Inuvik (population ~3200), two near the hamlet of Fort McPherson (population ~700), and one was near the hamlet of Tuktoyaktuk (population ~898).

3.3.2 Morphometry and Water Quality

We collected data on surface area and maximum depth for each lake by constructing bathymetric maps using a Humminbird Helix 5 chartplotter (Johnson Outdoors Marine Electronics, Inc), in combination with Reefmaster bathymetry software (Reefmaster Ltd.). We also collected water quality data including Secchi depth (water clarity), turbidity, conductivity, dissolved oxygen (DO), pH, total nitrogen (TN), total phosphorus (TP), total organic carbon (TOC), calcium, chlorophyll-*a*, and water temperature (Table 3.1). To obtain water clarity measurements, we lowered a Secchi disk over the shady side of the boat at the deepest point on the lake. At the same location, we measured turbidity, conductivity, DO, pH, and temperature, using a Manta+ multiparameter probe (Eureka Water Probes) at a depth of 1 m. We also collected water for the measurement of TOC and calcium levels at the same site using a 3 m polyethylene integrated tube sampler. We used a Perkin Elmer Optima 8000 Inductively Coupled Plasma Optical Emission Spectroscopy (ICP-OES) instrument to measure calcium concentrations, and a Shimadzu TOC-LCPH Carbon and Nitrogen analyzer (Shimadzu Corp.) to measure TN and TOC. We collected surface water samples from the shoreline of each lake for chlorophyll-*a* and TP measurements. To measure TP, we digested samples in an autoclave with ammonium persulfate and sulfuric acid following EPA method 365.1. We then used SEAL method G-103-93 to measure TP colorimetrically using the SEAL Continuous Segmented Flow Analyzer (SEAL Analytical, Inc.). To measure chlorophyll-*a* levels we filtered 250 mL water samples through Fisherbrand G4 glass fiber filters, extracted chlorophyll-*a* from the filters using methanol, and analyzed the quantity of chlorophyll using a Turner TD700 fluorometer (Symons et al., 2012).

3.3.3 Biological Data

We collected zooplankton samples from each lake at the point of maximum depth and preserved them on site using 95% ethanol. For lakes greater than 3 m in depth, we collected a single vertical haul using a 35-cm diameter, 50 μm mesh size zooplankton net. For shallow lakes less than 3 m in depth, where a vertical tow was not possible, we collected zooplankton by towing the net behind the boat for approximately 60 s. In both cases, we used a mechanical flowmeter attached to the mouth of the net to determine the volume of water that passed through the net. In the laboratory, we identified crustacean zooplankton to the species level according to

Haney et al. (2013) using a magnification of 40x to 400x depending on the size of the species. We identified rotifers to the genus level using the same classification key by examining samples in a Sedgewick Rafter counting slide at 40x to 400x magnification. To calculate Shannon diversity for each lake we used the “diversity” function, found in the Vegan package (Oksanen et al., 2015). Species evenness was calculated by dividing species diversity by the log of species richness for each lake (Magurran, 2013).

To determine fish presence and absence in our study lakes, we used a combination of surveys with gillnets and the presence/absence of the phantom midge *Chaoborus americanus* (Sweetman & Smol, 2006). Fish presence or absence was confirmed using gill nets in 28 lakes. The absence of fish was inferred in an additional 9 lakes based on presence of *Chaoborus americanus* in zooplankton samples, which is a common species found in northern lakes that does not usually coexist with fish (Sweetman & Smol, 2006).When 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. We distributed gillnets over varying lake strata according to the BSM protocol, for a duration of 16-22 h (left overnight) per lake in 2017. In 2018 our protocol was modified due to community concerns and nets were set during daytime hours and checked every 45-60 minutes. Sampling effort in 2018 varied depending on lake size, with nets deployed for an average of 11 net-hours in small-medium lakes (<500 ha), versus 37 net-hours in large lakes (>500ha). We included the presence or absence of common fish species in our analyses rather than catch per unit effort due to differences in sampling protocol between field seasons. The fish species identified and used in statistical analyses were least cisco (*Coregonus* *sardinella*), lake whitefish (*Coregonus clupeaformis*), and inconnu (*Stenodus nelma*). Least cisco was identified in 14 lakes, lake whitefish in 11 lakes, and inconnu in 3 lakes.

3.3.4 Statistical Analyses

We ran multiple linear regressions to identify which variables were important for predicting zooplankton evenness, diversity and abundance. We selected regression models using the glmulti function in R (Calcagno, 2019). This function performs exhaustive screening of potential models and ranks the best models according to a specified information criterion (Calcagno, 2019). For our models, we used a modified version of the Akaike Information Criterion called AIC-c. The use of AIC-c is recommended to avoid overfitting where the number of parameters assessed is large in comparison with the sample size (Burnham & Anderson, 2004). We tested that our models met the assumptions of multiple linear regression analysis by using the gvlma function in R (Peña & Slate, 2019) which is based on the tests described in Peña & Slate (2006). In order to meet all assumptions, we $\log_{10}$ transformed diversity and $\log_e$ transformed abundance to improve their linear relationship with predictors. We calculated Variance Inflation Factors (VIFs) of the final models to ensure that collinearity among predictors was not an issue (VIF <3 in all cases).

We used the adespatial package in R to construct spatial variables for use in models (Dray et al., 2019). Briefly, candidate spatial weighting matrices were constructed with the listw.candidates function using a variety of connectivity matrices and weighting matrices. The connectivity matrices considered were based on Delaunay triangulation, minimum spanning tree, or nearest neighbour connection schemes, while the weighting matrices were based on linear, concave up, or concave down functions, or had no weights added (Borcard et al., 2011). The listw.select function was then used to test candidate spatial weighting matrices against the residuals of the fitted models for zooplankton abundance, diversity, and evenness. The listw.select function selects the best spatial weighting matrix and best subset of eigenvectors for use as spatial variables in models (Bauman et al., 2018). These spatial variables were then used in our regression models along with local physicochemical variables.

We used hierarchical partitioning to quantify the importance of individual physicochemical, biological, and spatial variables in explaining zooplankton community structure (Chevan & Sutherland, 1991; Mac Nally, 2000). This method ranks all significant variables in a regression model and determines the independent contribution of each variable (Chevan & Sutherland, 1991). The R^2 values produced through typical multiple regression analyses are often not an adequate measure of the importance of individual variables owing to multicollinearity between the predictor variables (Mac Nally, 2000, 2002). Hierarchical partitioning minimizes this problem by performing an exhaustive model search and then averaging the influence of each predictor variable in each model it appears, thereby determining the independent contribution of each predictor (Mac Nally, 2000). Here, we used hierarchical partitioning to identify the most important variables for explaining variation in zooplankton evenness, diversity and total abundance. The analyses were carried out using the hier.part package in R (Walsh & Mac Nally, 2013).

To project future change in zooplankton communities due to permafrost thaw, we used the significant models generated from our multiple linear regressions. As input for our models, we used values for predictor variables that were based on three scenarios of change (low, medium, and high; Table 3.2). In Table 3.2, the base values represent the mean water quality values from our 37 study lakes. The high values are averages we selected from studies of lakes impacted by major permafrost degradation in the form of retrogressive thaw slumps (Kokelj et al., 2005; Thienpont et al., 2013; Moquin et al., 2014; Houben et al., 2016). We calculated values for the low and medium scenarios that were intermediate between the baseline and high values. Using the three scenarios as a guide, we added or subtracted values from our baseline data such that the average value for each variable matched with those in Table 3.2. For example, we added ~138 to our baseline conductivity values for each lake to move the average for all 37 lakes from ~188 to ~326. These modified predictor variables were then fed into our models for evenness, abundance, and diversity to calculate how these measures of community structure might change for each lake in response to permafrost thaw. Variables such as latitude and maximum depth, that are not expected to change as a result of permafrost thaw, remained unchanged from current conditions. For example, maximum depth was included in our model of zooplankton abundance, so the current maximum depth values for each lake were used along with modified values for pH, chlorophyll-*a*, and calcium that corresponded with our three scenarios for change (Table 3.2).

To examine differences in the relative abundance of zooplankton species among lakes, we used a principal component analysis (PCA). PCA was selected based on a detrended correspondence analysis that indicated gradient lengths were less than three (Borcard et al., 2011). Separate PCA plots were created for rotifers and crustaceans using Hellinger-transformed species abundance data using the “prcomp” function in R (R Development Core Team, 2018). We also used k-means cluster analysis to identify lakes containing similar rotifer and crustacean zooplankton communities. The cluster analysis was carried out using the “kmeans” function in R. To examine how differences in communities were associated with predictor variables, we examined Pearson correlations between axis scores and predictors using the rcorr function in the Hmisc package for R (Harrell & Dupont, 2019).

3.4 Results

3.4.1 Morphometry and Water Quality

The 37 lakes included in this study exhibited a large range in the measured morphometric and water quality variables (Table 3.1). In terms of morphometry, the lakes spanned a fairly large range of surface areas (0.01-82.9 km^2), and maximum depths (1.5-13.1 m). The lakes also varied significantly in terms of the water quality variables expected to be influenced by permafrost thaw, including Secchi depth (0.46-3.72 m), turbidity (0.14-38.25 NTU), conductivity (52-631.10 μS/cm), and calcium (10.37-51.03 mg/L; Table 3.1).

3.4.2 Zooplankton Abundance

The final zooplankton data set consisted of 19 crustacean species across the 37 study lakes and 21 rotifer genera (Table S1). The total abundance of zooplankton ranged from ~8 to 2316 individuals L^{-1}, with a mean of 217 individuals L^{-1}. The best regression model for total zooplankton abundance included pH, chlorophyll-*a*, maximum depth, and calcium (Table 3.3). The model explained 47% of variation in abundances ($p=0.0002$; Figure S1A). Based on the hierarchical regression analysis, pH and maximum depth were the most important predictors of total zooplankton abundance (Figure 3.2A). Given the environmental changes described in our three scenarios (Table 3.2), the median zooplankton abundance in our 37 study lakes is predicted to increase by approximately 1.6, 2.4, and 3.6 times under the low, medium, and high impact scenarios, respectively (Figure 3.3A).

3.4.3 Zooplankton Diversity

Shannon diversity of zooplankton communities in our study lakes ranged from 0.38 to 2.56, with a mean diversity of 1.69. The best regression model for diversity included the occurrence of cisco, latitude, conductivity, chlorophyll-*a*, turbidity, and Ca (Table 3.3). The model explained 68% of variation in zooplankton abundances ($p<0.0001$; Figure S1B). The hierarchical regression analysis revealed that conductivity, occurrence of cisco, and turbidity were the most important predictors of zooplankton diversity (Figure 3.2B). Based on the environmental changes described in our three scenarios (Table 3.2), the median diversity of zooplankton is predicted to decrease by 1.2, 1.4, and 1.7 times under the low, medium, and high impact scenarios, respectively (Figure 3.3B).

3.4.4 Zooplankton Evenness

Zooplankton evenness ranged from 0.16 to 0.86 among our 37 study lakes. The best regression model explained 69% of variation in evenness ($p<0.0001$; Figure S1C) and selected eight significant physicochemical variables including cisco occurrence, pH, conductivity, dissolved oxygen, turbidity, maximum depth, and two spatial variables (Table 3.3). According to the hierarchical regression analysis, conductivity, cisco occurrence, and turbidity were the most important predictors of zooplankton evenness (Figure 3.2C). Based on the environmental changes described in our three scenarios (Table 3.2), the median zooplankton evenness in our 37 study lakes is predicted to decrease by 1.1, 1.2, and 1.4 times under the low, medium, and high impact scenarios, respectively (Figure 3.3C).

3.4.5 Species Composition

Our cluster analysis with rotifer data showed that the communities in our 37 study lakes could be classified into three distinct groupings according to the dominant rotifer genera present in the lake: 1) *Keratella*; 2) *Kellicottia*; 3) *Asplanchna* and *Ascomorpha* (Figure 3.4A). The principal component analysis (PCA) showed a gradient in rotifer community structure along the first axis from *Keratella*-dominated communities to those with high abundances of *Asplanchna* and *Ascomorpha,* while low axis two scores were associated with *Kellicottia*-dominated communities (Figure 3.4A). Axis 1 scores from the rotifer PCA were correlated with total phosphorus levels ($r = 0.28$; $p=0.06$), and the occurrence of lake whitefish ($r= -0.37$; $p=0.02$) and inconnu ($r = -0.35$, $p=0.03$), while the second axis scores were correlated with conductivity ($r = 0.30$, $p<0.04$). Crustacean zooplankton communities in our 37 lakes clustered into one of two groups: 1) Communities dominated by the cladoceran *Bosmina longirostris;* or 2) communities with high abundances of the copepods *Skistodiaptomus oregonensis* and *Skistodiaptomus pallidus* (Figure 3.4B). Much of the variation in crustacean zooplankton communities (>56%) was oriented along the first axis, where the scores were correlated with latitude ($r = -0.37$), maximum depth ($r = -0.34$), and fish occurrence ($r = -0.58$) (all p-values <0.05). The second axis was correlated with pH ($r = 0.32$), chlorophyll-*a* ($r = 0.39$), dissolved oxygen ($r = 0.30$), and turbidity ($r=0.31$) (all p-values <0.05).

3.5 Discussion

Using data from our 37 study lakes, we were able to develop models based on physicochemical and spatial variables that provided reasonable fits to our zooplankton data for diversity, evenness, and abundance. Using these models in combination with scenarios for future changes in lake water quality, we examined how zooplankton communities might respond. Based on our models, we may see a 1.6-3.6-fold increase in abundance, 1.2-1.7-fold decrease in diversity, and 1.1-1.4-fold decrease in evenness. These predicted changes in evenness and diversity are not trivial, as they are in the range recorded for significant stressors such as acidification (Gray & Arnott, 2009) and the introduction of invasive species such as the spiny water flea (Yan & Pawson, 1997). In addition, the increase in abundance is within the range one might expect when comparing lakes of different trophic status (Canfield & Jones, 1996; Pinto-Coelho et al., 2005). The main drivers of change in our models were increased calcium resulting in higher zooplankton abundances, and increased conductivity levels driving reductions in diversity and evenness. Although other water quality variables related to permafrost thaw were included in our models (pH, chlorophyll-*a*, turbidity), the magnitude of the expected increases in calcium and conductivity were higher than these other variables (Table 3.2; Kokelj et al., 2005; Thienpont et al., 2013; Moquin et al., 2014; Houben et al., 2016).

The results of our principal component analyses and cluster analyses showed clear differences in the structure of zooplankton communities among lakes. However, the results did not allow us to reach clear-cut conclusions on how permafrost thaw may influence the species composition of zooplankton. For rotifers, there was a gradient in community types along PCA axis 1 from *Keratella*-dominated communities to those with high abundances of *Asplanchna* and *Ascomorpha*. Correlations of the axis scores with total phosphorus and fish occurrence suggested that *Keratella*-dominated communities tended to have lower total phosphorus levels and resident fish populations, while those with *Asplanchna* and *Ascomorpha* were more likely to have higher phosphorus levels and be fishless. These results are consistent with past studies that have demonstrated a significant role played by fish in depressing the abundance of larger rotifers such as *Asplanchna* in favour of smaller species such as *Keratella* (Stenson, 1982). In addition, studies have suggested that some *Keratella* spp. tend to thrive in less nutrient-rich lakes than *Asplanchna* (Sládeček, 1983; Bērziņš & Pejler, 1989). Lakes with low values along the second axis of the rotifer PCA were dominated by *Kellicottia*. Correlation of the second axis scores with conductivity indicated that lakes with lower conductivities tended to have more *Kellicottia*. We were unable to find any genus-specific information on conductivity optima for *Kellicottia*, but previous studies have shown that conductivity can significantly affect the structure of rotifer communities (Radwan, 1984; Morales-Baquero et al., 1989; Duggan et al., 2002). Based on the associations between predictors and PCA scores, rising conductivity levels may shift rotifer communities along PCA axis 2, resulting in more lakes dominated by *Keratella, Asplanchna*, and *Ascomorpha,* rather than *Kellicottia*. However, more variation in communities existed along the first PCA axis which was instead correlated with total phosphorus and fish occurrence. Crustacean zooplankton communities were separated primarily along the first PCA axis, with lower scores indicating cladoceran-dominated communities and higher scores representing communities dominated by copepods. Scores along the first axis were correlated with latitude, maximum depth, and fish occurrence, all of which have been identified in past studies as important predictors of community structure for crustacean zooplankton (Table 3.4). The variables correlated with PCA axis 1 scores are not expected to directly change in response to permafrost thaw, but the importance of latitude could indicate a relationship between community structure and climate that may be influenced by warming temperatures.

Our models predicted significant changes in plankton diversity for northern lakes exposed to permafrost thaw, raising two important questions: 1) Over what geographic range are our models valid? and 2) What will be the extent of permafrost degradation in Canada’s north? The first question is difficult to answer without collecting additional data, but a conservative approach might be to assume that our models are representative of small lakes (0.01-82 km^2) within the latitude range of our study spanning ~300 km that have similar water chemistry and morphometry (Table 3.1). In other words, we are hesitant to recommend extrapolating beyond the range of variation that exists in the dataset we used to build our models. With that caveat in mind, we have no reason to believe that our models should not adequately explain variation in zooplankton diversity, abundance and evenness in the thousands of small lakes found in the Mackenzie Delta region of the Northwest Territories. The strength of our dataset is that we were able to include lakes with a range of physical and chemical parameters that spanned the boreal-tundra transition as well as the transition from the discontinuous to the continuous permafrost zone. In addition, the variation in the physical and chemical variables for our lakes matches those found in published studies for other lakes in the region (Gunter, 2017; Swadling et al., 2000; Kokelj et al., 2009; Houben et al., 2016). The second question regarding the extent of permafrost degradation in Canada's north is also difficult to answer, but several studies have attempted to provide forecasts. Anisimov & Nelson (1996) predicted a decrease of Northern Hemisphere permafrost by 25-44% over the next century. As part of this degradation, the thickness of the active layer is projected to deepen by 30-100% (Stendel & Christensen, 2002; Woo et al., 2007; Frey & McClelland, 2009). This level of degradation could potentially expose a large portion of lakes in Canada's north to increased levels of solutes found in permafrost, including calcium, magnesium, sodium, and phosphorus (Keller et al., 2007; Burn & Kokelj, 2009). We speculate that most lakes in the Mackenzie Delta region would experience changes associated with our "low" scenario due to the thaw associated with active layer deepening (1.6-fold increase in abundance, 1.2-fold decrease in diversity, and 1.1-fold decrease in evenness). Lakes impacted to the degree suggested under our "medium" and "high" scenarios would likely be those impacted by large localized disturbances (thaw slumps). Lantz & Kokelj (2008) showed that 8% of the 2880 Mackenzie

Delta lakes they investigated were already affected by thaw slumps and that the total area impacted by slumping increased by 36% between 1950 and 2004. In addition, they predicted that thaw slumping would continue to increase in the region as the temperature warms (Lantz & Kokelj, 2008). This indicates that a significant number of lakes may be at risk of the more extreme changes we describe for the “high” scenario (up to 3.6-fold increase in abundance, 1.7-fold decrease in diversity, and 1.4-fold decrease in evenness).

If our predictions of changes in zooplankton communities are correct, what will it mean for small lakes in the Canadian Arctic? Zooplankton are an important component of the freshwater food web, providing a link between primary producers (phytoplankton), macroinvertebrates, and fish. Therefore, we suggest that the increases in abundance predicted by our models could result in changes at other trophic levels. Many studies provide evidence that changes at the top or bottom of the food web can initiate a trophic cascade, leading to changes throughout the food web (Carpenter, 1987; Elser et al., 1987; Carpenter et al., 2010). Increases in abundance of zooplankton may result in decreases in phytoplankton concentrations, especially if increases in calcium levels favour efficient filter feeders such as daphniids (Brett & Goldman, 1996). At higher trophic levels, planktivorous fish species, such as cisco, may benefit from the more abundant food resource (Ibrahim & Huntingford, 1989). This speculation aside, we are hesitant to make any firm predictions on the impacts of increased abundance of zooplankton given the complexities of freshwater food webs, and the inconsistent results of experimental food web manipulations (Brett & Goldman, 1996). In addition to predicting an increase in abundance, our models also predicted a decrease in diversity and evenness. The ultimate impact of these decreases is difficult to predict, but studies have shown that diversity in biological communities is associated with resilience in the face of environmental change (Mori, 2016). Diversity may be especially important for maintaining ecosystem services (e.g. nutrient cycling) as the environment changes (Schwartz et al., 2000; Oliver et al., 2015). Therefore, a decrease in diversity may leave zooplankton communities more susceptible to environmental perturbations, affecting important ecosystem services provided by this group (Hébert et al., 2017).

While we believe that our study design allowed us to make reasonable predictions about how zooplankton communities may respond to water quality changes associated with permafrost thaw, we also considered other approaches. First, analysis of a time series could have been used to examine trends in zooplankton communities in response to environmental changes (Magurran et al., 2010). Unfortunately, the lack of historical data made this option impossible for small lakes in our region of interest. Second, a comparative approach could have been used to examine differences in zooplankton communities between lakes affected by a disturbance (e.g. thaw slumps) in comparison with unaffected control lakes. This approach would have likely provided excellent data but has two shortcomings: 1) It is easy to do with conspicuous disturbances such as thaw slumps, but more difficult to identify candidate lakes that might be affected by active layer deepening without obvious signs of permafrost degradation; and 2) there is always a possibility that differences in zooplankton communities between impacted and control sites are caused by unmeasured differences in local environmental variables unrelated to climate change. Our approach to assessing how zooplankton communities might change was to conduct a broad survey of lakes with varying physical and chemical characteristics and use the resulting dataset to produce models that describe how zooplankton community structure is related to local chemical and physical variables. The models were then used to forecast changes given the expected impacts of climate change. This approach also has shortcomings in that values chosen to represent changes in environmental variables can be somewhat arbitrary, and there is always a chance that an important variable related to the disturbance of interest is left out of the statistical models developed from the survey data. Since each approach described above has benefits and shortcomings, we believe it would be fruitful to compare and contrast the results from all three when evaluating potential changes in arctic zooplankton communities.

To have confidence in our predictions about future changes in zooplankton communities related to permafrost thaw we needed to develop appropriate models for our metrics of community structure (abundance, diversity, and evenness). One aspect of this process was to ensure that important variables were not excluded from the final models, and that superfluous variables were not included. Important variables may sometimes be excluded during step-wise variable selection routines due to interactions among predictors (Mac Nally, 2000). Using hierarchical partitioning, we were able to identify the most important variables for explaining variation in our datasets (Figure 3.2). Fortunately, the important variables identified with this analysis were always included in the final model, giving us confidence that our models were not missing crucial predictors. To minimize the chance of including superfluous variables, we used AIC-c during model building, which can help to ameliorate some of the problems with overfitting that occur when using traditional AIC values (Burnham & Anderson, 2004). In addition, we didn’t include potential predictor variables during model fitting unless previous studies showed a relationship with zooplankton communities (Table 3.4). For example, the occurrence of various sucker species were not included in the list of potential predictors because these bottom-feeding fish are unlikely to directly interact with pelagic zooplankton communities. If we would have had access to data for a larger number of lakes in this region, we likely would have used cross validation rather than step-wise selection during the development of the models and we would have split the dataset into training and testing datasets to explore the accuracy of model predictions. However, based on our strategies to select the best variables and avoid overfitting, we are confident that our models are an acceptable outcome given the sample size available for their development.

Another consideration when building our models was whether the direction of the association (+ or -) between the predictor and response variables could be supported by the results of previous studies. Fortunately, this was the case for the variables included in our abundance, evenness and diversity models (Table 3.4). This does not mean that all published studies have found relationships with the same directionality as we did in our study, but it indicates that the relationships we describe for abundance, evenness, and diversity are not unique to our dataset, lessening the possibility that they are artefacts of data dredging (Smith & Ebrahim, 2002). Unfortunately, we could find only three studies that have looked at the variables influencing zooplankton evenness (Yan et al., 1996; Wen et al., 2011; Gray et al., 2012) , so it was difficult to provide support for some of the variables included in our evenness model (Table 3.3). In particular, cisco occurrence, dissolved oxygen, turbidity, and maximum depth required some justification. The calculation for evenness has species diversity in the numerator and species richness in the denominator, so it is likely that cisco occurrence, turbidity, and maximum depth influenced evenness due to their effects on abundance and diversity (Table 3.3). In addition, the fish species included in our models (least cisco) are known to be strong planktivores (Engel, 1976; Rudstam et al., 1993), and the positive effects of fish communities on zooplankton diversity is clearly established in the literature (e.g. Hessen et al., 2006). In our dataset, the presence of fish was also associated with the absence of the phantom midge *Chaoborus americanus*, an important invertebrate predator of zooplankton (absent in 97% of our study lakes containing fish). High densities of *Chaoborus* following their release from fish predation have been shown to have significant impacts on zooplankton community structure (Neill, 1981; Elser et al., 1987). Therefore, the relationship between cisco occurrence and zooplankton evenness in our study could also be an indirect effect caused by a decrease in invertebrate predation (Riessen et al., 2009). Finally, although dissolved oxygen did not come out as a significant predictor of diversity or abundance in our study, many studies have found a relationship between zooplankton community structure and oxygen levels (Patoine et al., 2002; Beisner et al., 2006; Strecker et al., 2008; Wen et al., 2011), so we concluded that a relationship could exist between evenness and dissolved oxygen levels.

In summary, we collected data from 37 lakes in the Mackenzie Delta region of Canada's Northwest Territories and developed simple linear models to describe variation in abundance, diversity, and evenness of zooplankton communities in these lakes. We then used these models in combination with data from the literature to predict changes in zooplankton communities associated with permafrost thaw. Our models predicted significant increases in zooplankton abundance and decreases in diversity and evenness. Given the variables incorporated in our models, we expect changes in zooplankton communities will be most severe in areas with shoreline thaw slumping; however, minerals mobilized from active layer deepening may also influence thousands of lakes in the region. The changes in zooplankton abundance and diversity we predict could impact other components of aquatic food webs, including phytoplankton and fish. Future research examining links between zooplankton and fish in these small arctic lakes would be helpful for understanding the potential impacts on subsistence and sport fish valued by northern communities.

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3.8 Tables

Table 3.1. Summary of water quality and morphometry data for the 37 lakes included in our dataset.

	Mean	Minimum	Maximum	Standard Deviation
Latitude	68.45	67.34	69.37	0.70
Longitude	-133.56	-134.91	-132.89	0.51
Surface temperature (°C)	13.14	7.47	19.54	2.84
Secchi depth (m)	1.88	0.46	3.72	0.84
pH	8.01	6.62	10.65	0.92
Conductivity (µs/cm)	188.85	52.00	631.10	114.32
Chlorophyll-*a* (µg/L)	5.16	0.09	24.19	5.72
Dissolved oxygen (mg/L)	10.34	8.61	12.58	1.10
Turbidity (NTU)	5.00	0.14	38.25	6.72
Maximum depth (m)	4.97	1.50	13.10	2.90
Surface area (km^2)	3.19	0.01	82.90	13.70
Total phosphorus (mg/L)	0.09	0.02	0.90	0.14
Total organic carbon (mg/L)	16.52	6.05	40.39	6.76
Total nitrogen (mg/L)	0.49	0.10	0.99	0.19
Calcium (mg/L)	21.29	10.37	51.03	8.77
Distance from highway (m)	78.19	10.77	351.49	70.50

Table 3.2. Scenario table used to project future change in zooplankton communities. High values are averages taken from the cited studies while base values are averages from the 37 study lakes included in our dataset. Low and medium values are equally spaced values between the baseline and high values.

	Base	**Low**	**Medium**	**High**	**Direction**	**Reference**
Calcium (mg/L)	21.29	28.93	36.97	45.00	Positive	Houben et al., 2016 Kokelj et al., 2005 Moquin et al., 2014 Thienpoint et al., 2013
Chlorophyll-*a* (µs/L)	5.16	3.54	2.02	0.50	Negative	Houben et al., 2016
Conductivity (µs/cm)	188.85	325.18	462.59	600.00	Positive	Houben et al., 2016 Kokelj et al., 2005 Moquin et al., 2014 Thienpoint et al., 2013
Secchi depth (m)	1.88	1.92	1.96	2.00	Positive	Houben et al., 2016
Turbidity (NTU)	5.00	3.92	2.96	2.00	Negative	Kokelj et al., 2005 Moquin et al., 2014 Thienpoint et al., 2013

Table 3.3. Results of multiple regression analyses for total abundance, diversity, and evenness of zooplankton communities from our 37 study lakes.

Response	Variable	Estimate	SE	t-value	p-value
Total abundance	(Intercept)	3.27	0.67	4.86	3.00E-5
	pH	-0.31	0.08	-3.89	4.70E-4
Model R^2=0.47,	Chlorophyll-*a*	0.04	0.01	2.61	0.01
Adjusted R^2=0.42,	Maximum depth	0.09	0.03	3.46	1.56E-3
p=0.0002	Calcium	0.02	0.01	2.46	0.02
	(Intercept)	5.19	1.94	2.67	0.01
Diversity	Cisco occurrence	0.13	0.03	3.63	1.03E-3
	Latitude	-0.07	0.03	-2.59	0.01
Model R^2=0.68,	Conductivity	-1.00E-3	0.00	-5.78	2.59E-6
Adjusted R^2=0.62,	Chlorophyll-*a*	8.00E-3	4.00E-3	2.21	0.03
p<0.0001	Turbidity	-0.01	3.00E-3	-3.94	4.50E-4
	Calcium	8.00E-3	2.00E-3	3.55	1.28E-3
	(Intercept)	0.91	0.19	4.93	3.38E-5
Evenness	Cisco occurrence	0.07	0.04	1.80	0.08
	pH	0.06	0.03	1.97	0.06
Model R^2=0.69,	Conductivity	-1.00E-3	0.00	-3.76	7.91E-4
Adjusted R^2=0.59,	Dissolved oxygen	-0.07	0.03	-2.65	0.01
p<0.0001	Turbidity	-5.00E-3	3.00E-3	-1.92	0.06
	Maximum depth	-0.01	6.00E-3	-1.73	0.09

	Spatial variable 1	-0.04	0.02	-2.58	0.01
	Spatial variable 2	-0.04	0.02	-2.13	0.04

Table 3.4. Directions of associations between predictors and community metrics in our multiple linear regression models along with references identifying similar relationships.

Variable	Abundance	Diversity	Evenness	Supporting references
Ca	+	+		(Cairns & Yan, 2010; Gray *et al.*, 2012)
Chlorophyll-*a*	+	+		(Hall *et al.*, 2003; Hessen *et al.*, 2006; Gray *et al.*, 2012; Dallas & Drake, 2014)
Fish occurrence		+	+	(Hobaek, Manca & Andersen, 2002; Hessen *et al.*, 2006; Gray *et al.*, 2012).
Conductivity		-	-	(Green, 1993; O'Brien *et al.*, 2004; Shiel *et al.*, 2006; Bégin & Vincent, 2017)
Latitude		-		(Hessen *et al.*, 2006; Shurin *et al.*, 2007)
Maximum depth	+		-	(Duggan, Green & Shiel, 2002; Sousa *et al.*, 2008; Anas, Scott & Wissel, 2015; MacLeod, Keller & Paterson, 2018)

pH	-		-	(Roff & Kwiatkowski, 1977; Locke *et al.*, 1994; Ivanova & Kazantseva, 2006)
Turbidity		-	-	(Hart, 1986; Lougheed & Chow-Fraser, 2011)
Dissolved oxygen			-	Impacts on community structure: (Patoine, Pinel-Alloul & Prepas, 2002; Strecker, Milne & Arnott, 2008; Holmes *et al.*, 2016)

3.9 Figures

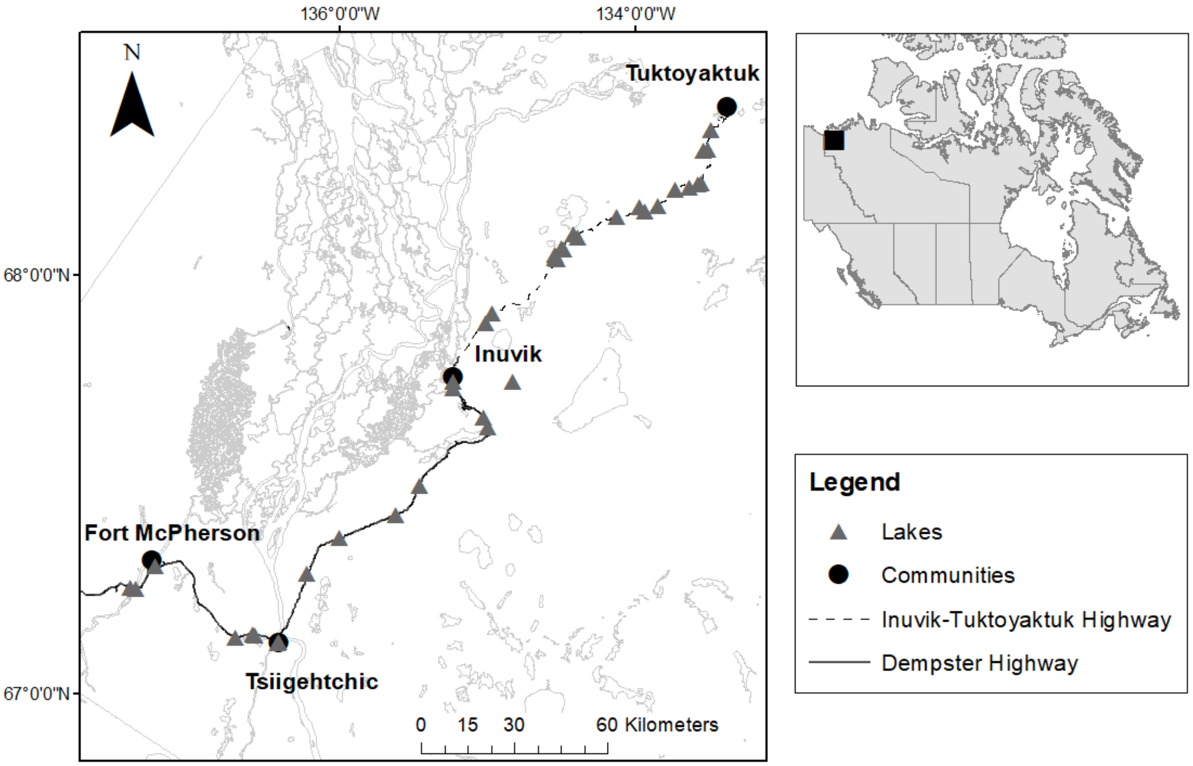

Figure 3.1. Map of the study area including 37 lakes located along the Dempster and Inuvik-Tuktoyaktuk Highways in the Northwest Territories.

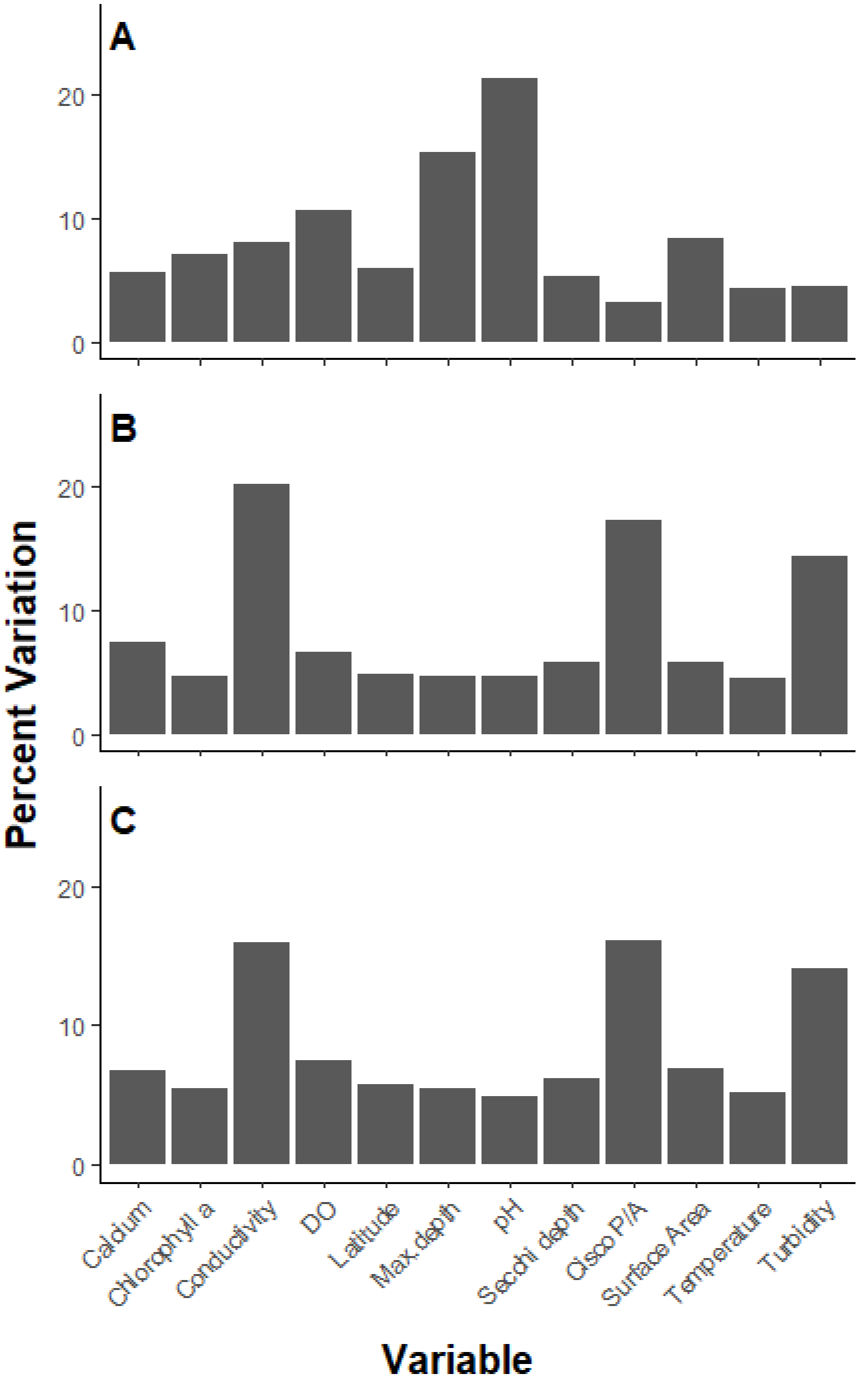

Figure 3.2. Results of hierarchical partitioning analysis to identify the most important variables associated with zooplankton total abundance (A), Shannon diversity (B), and species evenness (C).

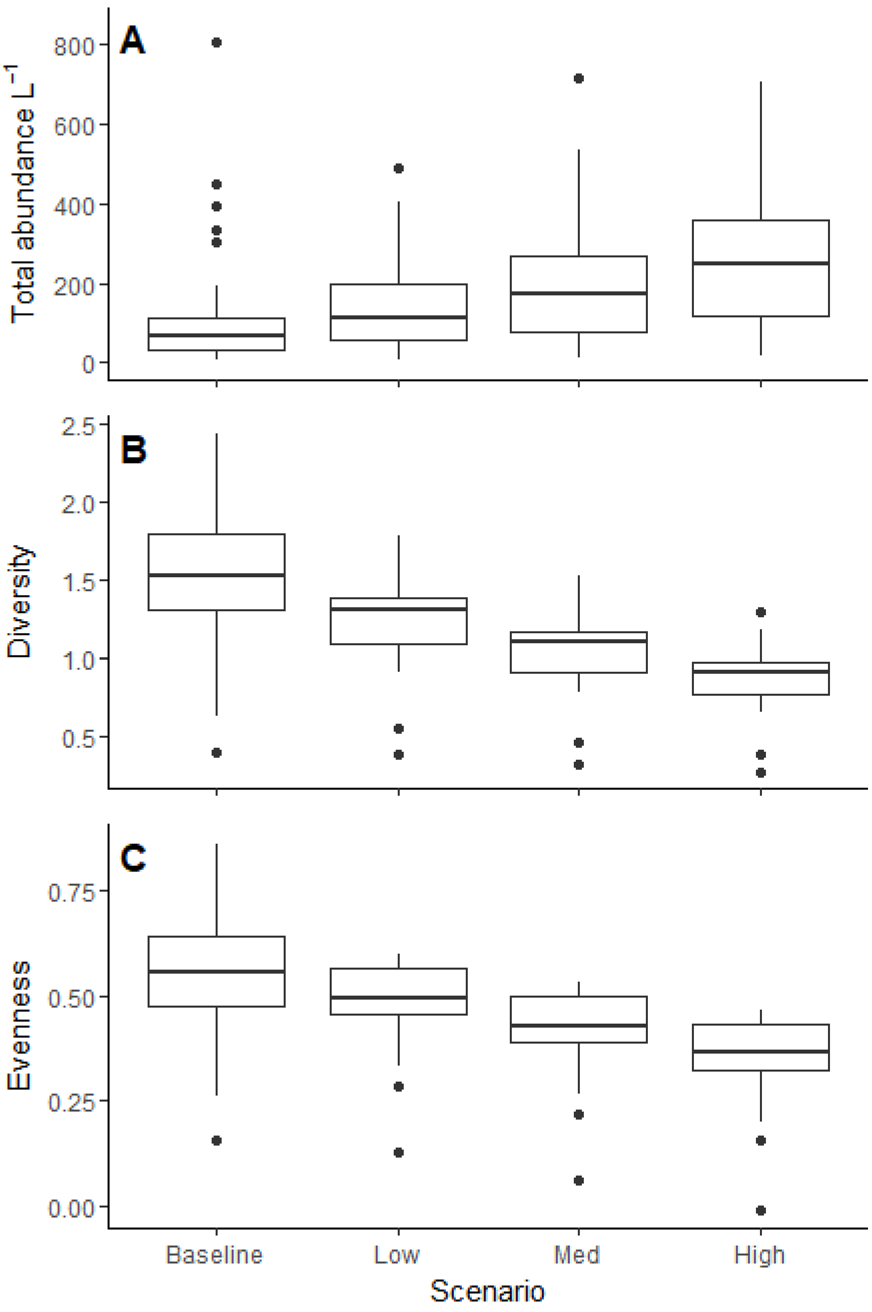

Figure 3.3. Boxplots displaying predicted values for total abundance (A), Shannon diversity (B), and species evenness (C) based on linear models developed for each of those community metrics. Baseline represents the current values in our 37 study lakes, while details on the three other scenarios can be found in Table 3.2.

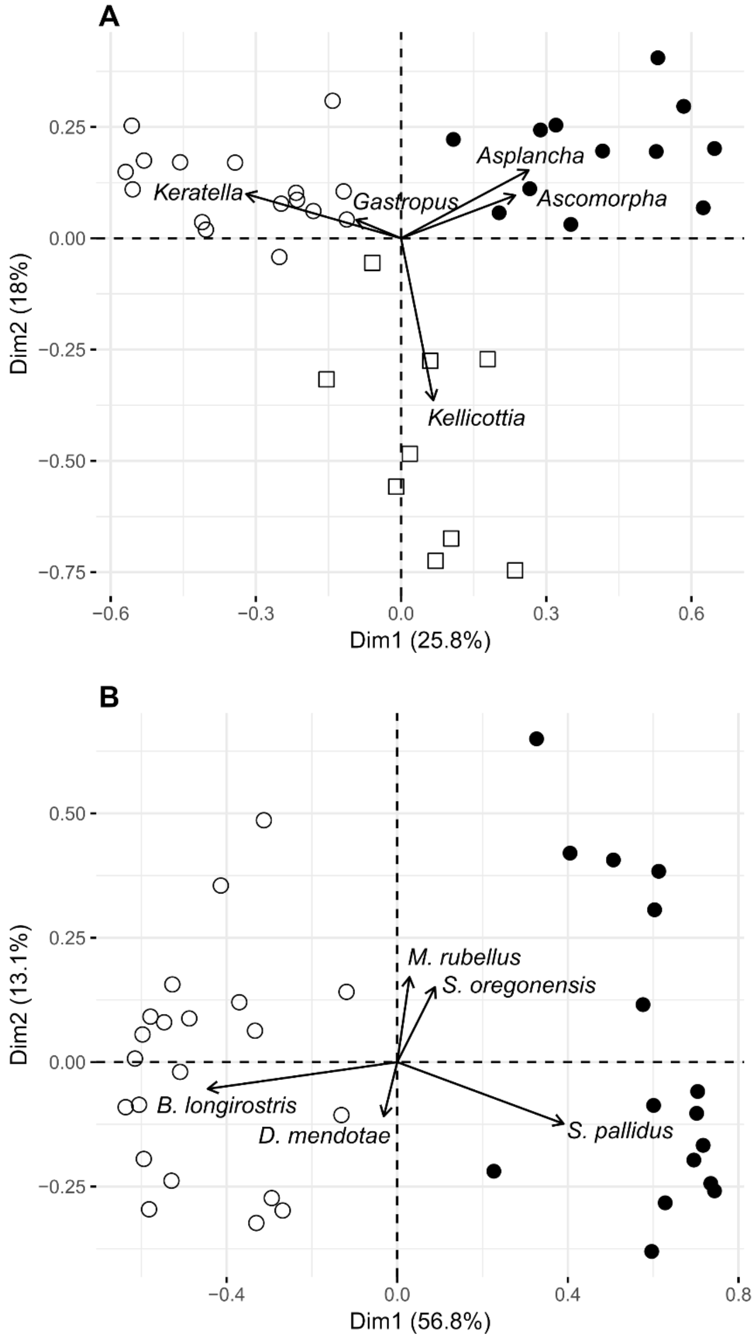

Figure 3.4. Principal component analysis showing differences in rotifer (A) and crustacean zooplankton (B) communities among lakes. Each symbol represents a zooplankton community from one lake, and the differing symbols within each panel show the clusters assigned by a k-means cluster analysis.

3.10 Supplementary material

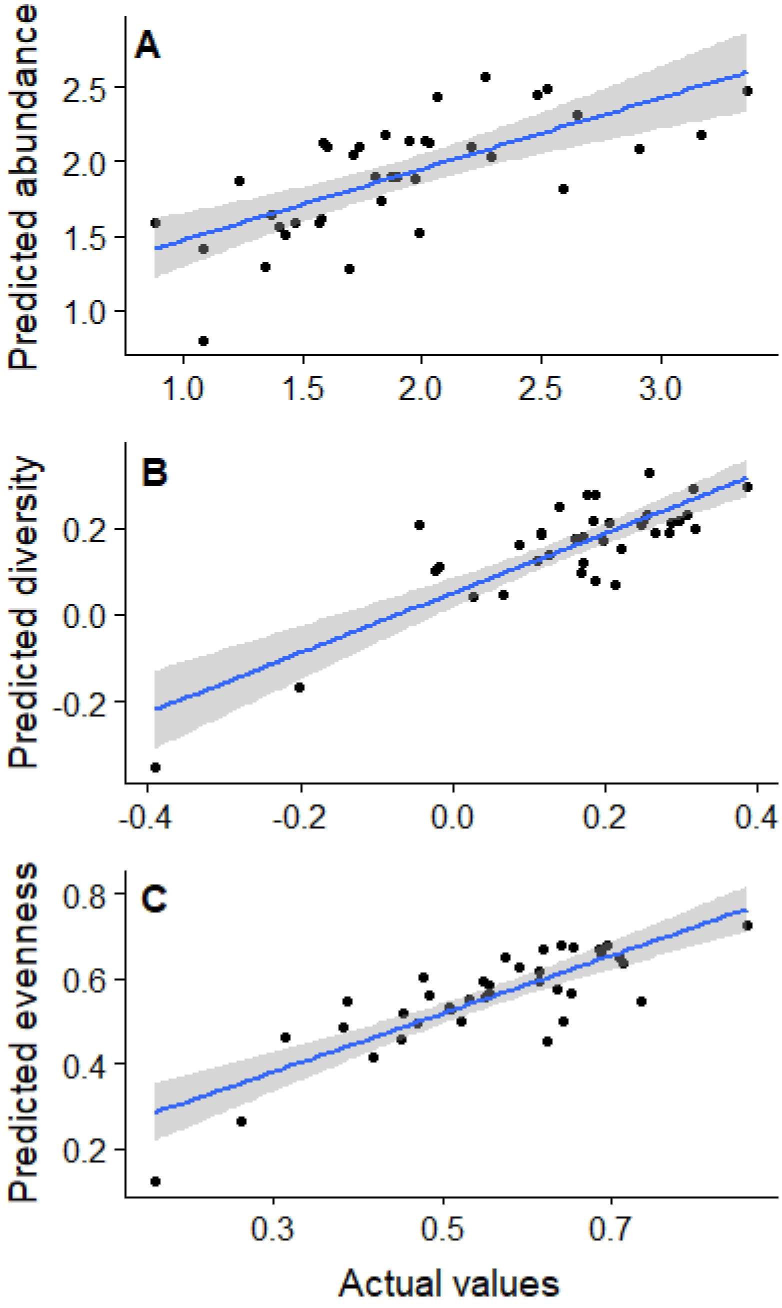

Figure S1. Actual values for abundance (A), diversity (B), and evenness (C) versus the model fit. Note that actual and fitted values for diversity and abundance are log transformed.

Table S1: List of average species abundances (#/L) in the 37 study lakes.

	Average Density (Number of Individuals/L)	**Standard Deviation**
Anuraeopsis spp.	0.407	2.138
Ascomorpha spp.	4.830	12.191
Asplancha spp.	6.588	10.383
Bosmina longirostris	11.419	45.279
Bipalpus spp.	3.107	8.927
Brachionus spp.	1.008	3.823
Chydorus sphaericus	0.007	0.034
Collotheca spp.	32.259	125.924
Conochilus spp.	14.727	77.514
Cyclops scutifer	0.110	0.424
Daphnia ambigua	0.020	0.066
Diaphanosoma brachyurum	0.288	1.237
Daphnia mendotae	8.204	42.963
Daphnia rosea	4.026	22.853
Daphnia schodleri	0.056	0.147
Epischura lacustris	0.006	0.038
Ergasilus spp.	0.014	0.034
spp.	0.564	3.296
Eurycerus spp.	0.003	0.009
Filinia spp.	3.539	10.770
Gastropus spp.	10.338	30.105
Heterocope septentrionalis	0.026	0.065
Harpacticoida spp.	0.007	0.044
Hexarthra spp.	0.164	0.436
Holopedium gibberum	0.005	0.016
Kellicottia spp.	26.211	79.708
Keratella spp.	35.074	77.498
Lecan spp.	0.015	0.049
Microcyclops rubellus	0.613	1.099
Monostyla spp.	21.165	88.110
Notholca spp.	1.108	2.927
Ploesoma spp.	1.175	3.291
Polyarthra spp.	17.793	48.817
Pompholyx spp.	0.105	0.636
Skistodiaptomus oregonensis	1.490	3.257
Skistodiaptomus pallidus	2.426	4.080

Synchaeta spp.	6.246	15.375
Trichocera spp.	2.321	4.700
Tropocyclops prasinus mexicanus	0.002	0.011

CHAPTER 4: General Discussion

4.1 General Findings

The overarching goal of my thesis was to investigate factors related to climate change and development that might influence zooplankton communities in small arctic lakes. The rapid warming of the Canadian Arctic is causing significant changes to the natural environment (Frey & McClelland, 2009; Houben et al., 2016; Kokelj et al., 2009; Walther et al., 2002). At the same time, there have been increases in development in many parts of the north (Bennett, 2017). Both these factors are leading to changes in aquatic environments including changes in water quality and biology as discussed throughout the preceding chapters (Houben et al., 2016; Kokelj et al., 2005; Myers-Smith et al., 2011; Thienpont et al., 2013). Previous studies have examined how the physical and chemical changes caused by permafrost thaw and development might impact some taxa in Arctic lakes (Mesquita et al., 2010; Moquin et al., 2014; Thienpont et al., 2013), but zooplankton have not been considered. Chapters 2 and 3 addressed this research gap through collecting baseline data on water chemistry, lake bathymetry, and zooplankton communities for Northwest Territories' lakes.

Chapter 2 focused on exploring the role of gravel pit lakes as habitat for aquatic invertebrates. The changing climate will produce challenges for northern infrastructure, but also opportunities for resource development. Warmer temperatures may limit the use of traditional ice roads, requiring the construction of other alternatives (Prowse et al., 2009). In addition, the loss of sea ice may open opportunities for marine shipping, making oil and gas extraction more attractive in some regions (Prowse et al. 2009). As development is projected to increase in the north, understanding whether gravel pit lakes can provide novel habitat of similar quality to natural lakes filled a research gap in northern Canada. The main findings suggest that gravel pit lakes differed significantly in mean depth, turbidity and nutrient concentrations (total nitrogen, total phosphorous) in comparison to natural lakes in the area. The difference in morphometry was due to the structure of gravel pits which are deep allowing for a large extraction value while minimizing cost and land disturbance (Blanchette & Lund, 2016). The low turbidity levels were likely due to the lack of bottom sediment resuspension in the significantly deeper gravel pit lakes. Differences in nutrient concentrations between lake types revealed that gravel pit lakes were relatively unproductive in comparison to natural lakes. Despite these differences, zooplankton abundance, richness and diversity did not significantly differ between lake types. These results suggested that gravel pit lakes have the potential to provide habitat of similar quality of natural lakes in northern communities. Often, the process of gravel extraction is looked at negatively due to disturbance to the surrounding land but these results suggest there may be unexpected positive effects as a result of development.

Chapter 3 shifted focus to climatic factors influencing zooplankton communities, specifically those related to permafrost thaw. As the climate warms, one of the most important drivers of water quality change in the north will likely be permafrost thaw. In comparison with the active layer which freezes and thaws annually, permafrost in this region contains elevated levels of solutes, including calcium, magnesium, sodium, and phosphorus (Burn & Kokelj, 2009; Keller et al., 2007). Here, models were developed based on physical, chemical and biological data to project how future changes in water quality will influence zooplankton communities. Results from multiple linear regressions included conductivity, chlorophyll-*a*, turbidity, Secchi depth, calcium or pH suggesting that factors associated with permafrost thaw can be expected to influence zooplankton communities. Projections from my models predicted significant increases in abundance and decreases in diversity and evenness due to water quality changes associated with permafrost thaw. Changes in zooplankton communities will be most severe in areas with shoreline thaw slumping; however, minerals mobilized from active layer deepening may influence thousands of lakes in the region. The changes to zooplankton community structure have the potential to impact other components of aquatic food webs including phytoplankton and fish. Future research investigating food web interactions would be beneficial for further understanding the effects of thaw on aquatic communities.

This thesis addressed different stressors that influence zooplankton communities in small arctic lakes. The lakes sampled in these studies provide baseline physical, chemical and biological data which can be included in long-term monitoring data sets to understand how current stressors may be leading to ecosystem change. This research has contributed to understanding the fundamental processes that structure zooplankton communities in northern lakes and how communities may change in response to climate change and development. Future studies would benefit from sampling more lakes in the study area to validate the models produced in chapters 2 and 3. Also, sampling littoral zooplankton in gravel-pit lakes in addition to the pelagic zooplankton collected may provide further insight when comparing natural and gravel pit lakes. Lastly, sampling transects further from the highway to examine the potential impacts of dust on zooplankton would be beneficial to understanding the impacts of climate change coupled with development.

4.2 Research Integration

In biology, integration suggests the unity of different disciplines. This project focuses on aquatic ecology but also takes into account chemistry, physiology and geography. Aquatic ecology addresses how organisms respond to their surroundings which is most applicable as the common theme throughout the chapters presented is understanding factors influencing zooplankton. Aspects of chemistry are integrated through water sampling and understanding the constituents present within the study lakes. Zooplankton physiology also plays a role in this thesis as changes in water properties have the potential to influence zooplankton populations due to their species-specific physiological tolerances. Geography is integrated within this study as determining whether lakes are underlain by morainal, glaciofluvial, lacustrine, or alluvial deposits can help to understand potential influences on lake water chemistry (Kokelj et al., 2009).

4.3 Contribution to Ecology

Chapters 2 and 3 both provide novel results that will contribute to the field of freshwater ecology. As discussed in Chapter 2, few studies have investigated the differences between natural and gravel pit lakes (Blanchette & Lund, 2016; Gammons et al., 2009; Hindák & Hindáková, 2003; Søndergaard et al., 2018). My manuscript was the first to address and compare natural and gravel pit lakes in the Northwest Territories while also addressing invertebrate community composition. Chapter 3 focuses on climate change, specifically permafrost thaw, which will directly influence zooplankton communities. Although permafrost thaw has been studied in northern regions (Bégin & Vincent, 2017; Houben et al., 2016; Kokelj et al., 2005, 2009; Mesquita et al., 2010; Moquin et al., 2014; Thienpont et al., 2013), no published studies have examined how thaw might effect zooplankton communities. My thesis research also contributed to increasing baseline data in Canada’s Arctic through the addition of bathymetric data, measured water quality parameters, as well as zooplankton community composition.

4.4 Relevance to other Research

This research is tightly linked with another Master’s student (Rachel Cohen) in Dr. Gray’s laboratory studying macroinvertebrates in the same set of lakes. The scope of my research and Ms. Cohen’s are similar in that both have contributed to a baseline data set for invertebrates and water quality for lakes along the Inuvik-Tuktoyaktuk and Dempster Highways’, Northwest Territories. Both studies aim to understand the factors most important for structuring invertebrate communities. My thesis is also closely related to work being led by a PhD student (Alyssa Murdoch) from Dr. Sapna Sharma’s lab at York University that is focused on fish in the same set of lakes. Once completed, these studies will assess potential food web interactions in lakes and how a changing climate may alter those interactions. Furthermore, the baseline water quality data I have collected could be used to develop habitat suitability models for dominant species, allowing for the examination of future distributional changes for the organisms living in this region.

4.5 References

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