Effects of Shoreline Retrogressive Thermokarst Slumping on the Productivity and Food Web Structure of Upland Arctic Lakes – An Experimental Approach

by

Paul Moquin
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Supervisory Committee

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Abstract

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To assess the affects of permafrost degradation on key components of the aquatic food web, an *in situ* manipulative mesocosm experiment was performed in an upland, unslumped Arctic lake located near Inuvik, Northwest Territories. In total, twelve replicate mesocosms were established, 3 control and 3 replicates of 3 treatment levels each dosed with differing amounts of sediments sourced from a nearby thermokarst slumped lake. Findings from the experiment showed that pelagic autotrophic processes had the greatest potential to contribute to higher trophic levels regardless of treatment. Even in the high sediment treatment level, which showed the least pelagic autotrophic production, pelagic autotrophic production was two orders of magnitude greater than pelagic heterotrophic production and 5 times greater than benthic autotrophic or heterotrophic production. Sediment treatment had no significant effect on benthic primary productivity; however, a 500% increase in benthic heterotrophic production was observed. This raises the possibility that increased activity in benthic heterotrophic production is the first step in thermokarst-affected lake ecosystem succession leading to the proliferation of benthic primary production observed in many slumped lakes in the western Canadian Arctic. Water column phosphorus concentrations increased with increasing sediment treatment while pelagic primary production decreased and zooplankton biomass increased. These results suggest that the initial effect of thermokarst disturbance is an enrichment of the system and that top-down predation from zooplankton regulate the abundance of phytoplankton in these systems. If incidences of thermokarst disturbance continue to increase as predicted by current climate models/scenarios, results from this study suggest that the structure and function of Arctic aquatic ecosystems will be significantly impacted. This study highlights the need for further research to obtain a better mechanistic and predictive understanding of the potential effects of thermokarst disturbance on the geochemistry and ecology of Arctic lakes at relevant spatial and temporal scales.

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CHAPTER 1: GENERAL INTRODUCTION

1.1 Current State of Knowledge on Arctic Tundra Lakes

Climate warming in northern latitudes has been occurring at nearly twice the global average (ACIA 2004; IPCC 2007; Post *et al.* 2009; AMAP 2011). Climate models predict significant increases in mean annual temperature with ramifications to snow cover and sea-ice extent as well as enhanced retreat of permafrost, glaciers and ice-caps (Prowse *et al.* 2006; Wrona *et al.* 2006). Precipitation patterns in the Arctic are also predicted to change, with increases projected for summer and winter seasons as well as increases in the occurrence of extreme precipitation events (Prowse *et al.* 2006; IPCC 2007). As a result of increased warming and precipitation, permafrost temperatures have been rising causing a deepening of the active layer and an increase in thermokarst activity (Hobbie *et al.* 1999; Lantz & Kokelj 2008; Burn & Kokelj 2009). Permafrost degradation has implications to the hydrology and ecology of permafrost regions because the thawing of ice-rich ground affects terrain stability as well as the chemical composition of soil and surface waters (Hobbie *et al.* 1999; Kokelj *et al.* 2009b). Landscape subsidies resulting from thermokarst activity have been associated with large-scale changes in chemical and biological parameters in permafrost-embedded lakes throughout the northern regions of the globe (Czudek & Demek 1970; Burn 2002; Luoto & Seppälä 2003; Wrona *et al.* 2006; Lantz & Kokelj 2008). The incidence of thermokarst activity have increased significantly over the past 35 years (Lantz & Kokelj 2008; Burn & Kokelj 2009) and rates of occurrence are expected to increase with further climate warming (Hobbie *et al.* 1999; Wrona *et al.* 2006; Laybourn-Parry & Vincent 2008). Given the large extent of lakes in the northern landscape, knowledge of how permafrost degradation affects aquatic ecosystems will be integral in predicting and mitigating the impacts of future climate change.

The study of the effect of permafrost degradation on aquatic ecosystems would benefit from an area where multiple thermokarst disturbances are readily identifiable and occur in relatively homogenous catchments within a reasonable distance from each other. This list of criteria is met in the region of the Mackenzie Delta in the western Canadian Arctic (Thompson 2009) (Figure 1.1). This area is comprised of thousands of small lakes underlain by permafrost (Burn 2002). A survey of four areas 49 km^2 between Inuvik and

Richards Island comprised of 298 lakes showed that 5 to 15% of all lakes are affected by thermokarst degradation (Kokelj *et al.* 2005).

Figure 1.1. Map of the Mackenzie Delta area, Northwest Territories.

A number of synoptic geochemical and ecological studies in this area have revealed two lake types associated with the presence and absence of shoreline thermokarst disturbances in this region (Kokelj *et al.* 2005; Mesquita 2008; Kokelj *et al.* 2009b; Thompson 2009). Contrasts between lakes affected by thermokarst disturbance and those unaffected span chemical, physical and biological parameters. Undisturbed lakes are typically unproductive systems with high concentrations of dissolved organic carbon (DOC sometimes referred to as CDOC for coloured DOC when the optical properties of DOC are important) and low concentration of nutrients. These conditions are prevalent in undisturbed catchments because surficial water flow is confined to the active layer, which is rich in humic organic matter but leached of ions and nutrients (Kokelj & Burn 2003). In contrast, ion-rich Quaternary sediments are exposed in thermokarst-affected catchments, and thus interact with surficial flow and as a result, minerals, ions and organic matter are transported to the lake (Kokelj *et al.* 2005, 2009b; Burn & Kokelj 2009). Aboveground catchment processes can be influential in permafrost-dominated catchments as ground-water flow is negligible (Quinton & Marsh 1999). Permafrost thawing in areas rich in ground ice, may lead to the development of retrogressive thaw slumps (Burn & Lechowicz 1990). These disturbance features can perpetuate into the landscape as newly thawed material falls as a mud slurry to the base of the thaw scar thus exposing fresh permafrost for the process to repeat (Figure 1.2). In this fashion, the thaw horizon can retreat several meters in a single season. These conspicuous features often occur directly adjacent to lakes and are referred to as shoreline retrogressive thaw slumps (SRTS).

Figure 1.2. Shoreline retrogressive thaw slumps in the uplands of the Mackenzie Delta, Northwest Territories.

Interestingly, slumping in the lakes of this region is associated with overall decreases in turbidity and water colour (Kokelj *et al.* 2005) as well as water-column nutrient availability (Thompson 2009). This counter-intuitive observation is opposite to what is predicted by alternate stable state theory (ASST) developed in temperate lakes (See Scheffer *et al.* 2001a for an overview of ASST).

Preliminary experimental work by Thompson *et al*. (2008) suggests that the "clear" pelagic water observed in slumped lakes may be a result of interactions between coloured humic matter and permafrost-related sediments released from thermokarst disturbance. An incubation experiment was conducted by Thompson *et al*. (2008) in which humic lake water from a non-disturbed Arctic lake was exposed to sediments collected from a permafrost thaw scar in small microcosms. After 52 days of incubation, the water became significantly clearer with increasing sediment concentrations. Given that permafrost–related sediments contain large amounts of charged particles such as clays and cations/anions (Kokelj & Burn 2003; Keller *et al*. 2007), and humic matter is known to aggregate with charged particles (Stumm & Morgan 1981; Rasmussen *et al.* 1989), Thompson *et al.* (2008) proposed that these particles must be interacting to form heavier compounds which settle to the lake bottom. Since large portions of the compounds in humic matter are coloured (Jones 1992), this leads to a "clearing" of the water column. A complimentary study by Mesquita (2008) found lakes affected by SRTS had significantly greater abundance of macrophytic growth than unaffected lakes (Mesquita 2008). It was proposed that higher water transparency and increases in the availability of key nutrients bound to the sediment make disturbed lakes more favourable for the growth and maintenance of the macrophyte community (Mesquita 2008).

1.1.1 An Expanded Conceptual Model of Energy Mobilization in Aquatic Systems

Recent literature has expanded the conceptual model of energy mobilization in aquatic ecosystems (Jansson *et al.* 2000). Aquatic researchers formulating energy budgets for lakes found discrepancies in the photosynthetic primary productivity and total metabolic activity (Kling *et al*. 1992; Polis *et al.* 2004). Subsequent studies determined that this discrepancy is explained by microbial respiration; most often respiration of allochthonous DOC (Jones 1992; del Giorgio *et al.* 1997; Polis *et al.* 2004). The realization that heterotrophic processes mobilize important amounts of energy in certain lake systems has expanded the traditional conceptual paradigm where the bottom of all lacustrine food webs are based on autotrophic processes. The mineralization of DOC by bacteria can be an important basal link in aquatic food webs as bacteria are in turn grazed by micro and macro-zooplankton (Salonen *et al.* 1992; Jansson *et al.* 1996; Vadeboncoeur *et al.* 2002; Polis *et al.* 2004). Heterotrophic processes represent a particularly important entry point of carbon into aquatic food webs in humic lakes and can be several times that of autotrophic production (Jansson *et al.* 1996; Crump *et al.* 2003).

A new conceptual model inclusive of autotrophic and heterotrophic processes may also include subdivision by habitat type (benthic or pelagic). Abundant literature points to the importance of benthic processes both autotrophic and heterotrophic (Reviewed in Vadeboncoeur *et al.* 2002 but also see Rautio & Vincent 2006 and 2007 for high latitude-specific examples). Vadeboncoeur *et al.* (2002) report on a study where whole-lake sediment bacterial production was estimated to be one to three orders of magnitude higher than whole-lake measurements of bacterioplankton production. Benthic production can be important to higher trophic levels (Hecky & Hesslein 1995). Rautio & Vincent (2006) demonstrated that zooplankton use benthic microbial mats as a food source in shallow arctic lakes. Benthic primary production was also shown to be important in a whole-lake fertilization experiment where increases in pelagic primary productivity shaded benthic primary productivity thus resulting in little net gain in whole-lake primary productivity (Vadeboncoeur *et al.* 2002).

Four process-environment combinations result when heterotrophic and autotrophic processes are considered in both pelagic and benthic environments. Table 1.1 represents this conceptual model and includes an example of a functional group of organisms that belongs in each category.

Table 1.1. Conceptual model of the basal components of the aquatic food web including an example of a functional group of organisms that belongs in each category.

	Autotrophic	**Heterotrophic**
Pelagic	Phytoplankton	Bacterioplankton
Benthic	Periphyton	Decomposers

When the source of carbon is external to the system each of these process-environment combinations or "energy pathways" represents a potential entry point for new carbon into the aquatic food web providing carbon to higher trophic levels. Changes to which energy pathway dominates in a food web is likely to have implications on the structure and function of the lake ecosystem and may have profound effects on the productivity of higher trophic levels (Polis *et al.* 2004). For example, a heterotrophic-based ecosystem will contain more trophic levels than an autotrophic one. Longer food chains result in greater energy loss from the base to the top of the food chain and lead to lower overall productivity (Jansson *et al.* 2000). This is often the case in humic lakes and is proposed as one of the reasons humic lakes have low fish abundance (Jones 1992).

A thermokarst disturbance may cause shifts in which energy pathway dominates in a lake by affecting the physical and chemical environment. For example, thermokarst disturbance has been shown to reduce concentrations of CDOC (Kokelj *et al.* 2005). CDOC has implications to energy pathways as it attenuates the light entering the water column, reducing the depth of penetration of photosynthetically active radiation (PAR) thus reducing pelagic and benthic autotrophic productivity (Rasmussen *et al.* 1989; Jones 1992; Salonen *et al.* 1992). While reducing light available for primary production, CDOC also serves as a substrate for bacterial production. Therefore reductions in CDOC may simultaneously improve conditions for autotrophic processes in the benthic and pelagic environments while reducing heterotrophic processes in the pelagic environment.

Furthermore, SRTS have been associated with changes in turbidity, nutrient abundance and ratios, ion concentration and depth (Kokelj *et al.* 2005; Thompson 2009) all of which have biological implications which may affect energy pathways (Moss 1972; Krantzberg 1985; O'Brien *et al.* 1992; Pace & Cole 1994). Thus, investigations into the basal components of the food web may provide insight into the mechanisms that cause the differences observed between slumped and unslumped lakes.

1.2 Hypotheses/Questions/Theoretical Rational

Given the potential of thermokarst disturbance to affect the basal components of the food web and upon reviewing the evidence from the studies highlighting the contrasts between affected and unaffected lakes, I hypothesize that permafrost-related sediments mediate a shift from heterotrophic/pelagic-dominated pathways in undisturbed lakes to autotrophic/benthic-dominated pathways in disturbed lakes. To address this hypothesis, a mesocosm experimental approach will be used to address four questions listed below. To provide a theoretical framework to the study, the rationales for the questions are based on alternate stable state theory (ASST).

The theory of alternate stable states proposes the possibility that ecosystems exist in more than one stable configuration (Holling 1973; May 1977). First proposed as a theoretical possibility, ASST has gained acceptance as a central ecological theory as empirical evidence from disparate ecosystems has supported it (Scheffer *et al.* 2001a). Of the various ecosystems displaying alternate states, theory surrounding shallow lakes is particularly well developed (Scheffer *et al.* 2001a, 2001b; Jackson 2003; Bayley *et al.* 2007). The theory proposes two main states for shallow lakes: a turbid, phytoplankton dominated state and a clear-water state dominated by macrophytes. According to ASST, shifts from the clear to turbid state are caused by allochthonous additions arising from the landscape. Shifts are caused as these inputs supplement phytoplankton growth, which eventually shades out the macrophytes. When macrophytes are lost, sediment and nutrients are easily resuspended thus maintaining the turbid state (Jackson 2003).

Preliminary work by Thompson (2009) and Mesquita (2008) suggests that current ASST does not account for the phenomena observed on the lakes of the Mackenzie Delta uplands, thus presenting a unique opportunity for my research to contribute to a deeper understanding of ASST.

Four general questions / predictions arise from ASST that apply to Arctic upland lake systems:

Question 1 - Does the relative importance of benthic- and pelagic-based processes change as a result of shoreline slumping events?

The likely reason that alternate stable state theory does not apply to these lakes is that ASST does not account for allochthonous inputs, which lead to reductions in pelagic nutrient concentrations and improved water-column light conditions. Traditional theory assumes instead that all allochthonous inputs cause increases in pelagic nutrients and reduced light penetration into the water column.

***Question 2* - Does the relative importance of heterotrophic and autotrophic processes as entry points of new carbon/energy into the food web change as a result of shoreline slumping events?**

ASST is based on the out-dated conceptual lake models where autotrophic processes are considered the only significant mechanism of energy mobilization. Recent work has expanded our understanding of the potential of heterotrophic processes as important energy mobilizers in lacustrine environments, often exceeding that of autotrophic processes (Salonen *et al.* 1992; del Giorgio *et al.* 1997; Biddanda *et al.* 2001; Ask *et al.* 2009). Given that the addition of allochthonous material is likely to affect the heterotrophic/autotrophic balance and have repercussions to the food web, provisions for impacts to autotrophic and heterotrophic processes may be worthy addition to ASST.

***Question 3* -How does the relative importance of heterotrophic and autotrophic processes in the benthic and pelagic environments change over time starting from the initial slumping event?**

ASST highlights the potential of time lags and hysteresis to delay shifts to alternate states (Scheffer *et al.* 1993). As such, significant changes to the system may occur latter in time than the factors that precipitated them (Scheffer *et al.* 2001a). As such, monitoring key ecological parameters over time will be an important component of the proposed experiment. Identification of time lags, should they exist, may be important for future management considerations.

***Question 4* - Does the magnitude of a slumping event affect the differences observed between slumped and undisturbed lakes?**

ASST has forwarded the notion of ecological thresholds (Holling 1973; May 1977). The theory predicts that for certain systems, ecological state does not change along a gradient of some ecologically relevant parameters (for example nutrient concentration) until a threshold is attained and a shift occurs (Scheffer *et al.* 2001a). Applied to lakes affected by thermokarst slumping, the theory raises the question of the existence of thresholds in these systems as well as the severity of a slumping event required to affect such change. Thompson *et al.* (2009) has demonstrated experimentally that reductions in water colour is proportional to the volume of thermokarst sediments, indicating there may be a relationship between slump magnitude and observed changes in geochemistry.

ASST does not specifically address distinctions between the frequency, magnitude or duration of allochthonous inputs. However, it is reasonable to assume that significant impacts or thresholds in the system may be attained by modification of any one or all of these parameters. As will become clear in the methods, this experiment specifically addresses the question of magnitude. Manipulation of this parameter keeps the experimental design as simple as possible while offering the potential of identifying the existence of thresholds and gaining insight into the potency of permafrost-related sediments to affect change. Questions pertaining to the frequency and duration of slumping events could be the pursuit of future studies.

1.3 Study Objectives

The objectives of the research are to address the questions outlined above using an experimental mesocosm approach. Using a series of dose-response systems, the effects of thermokarst slumping on water column geochemistry (Chapter 3), energy pathways/basal components of the food web (Chapter 4) and, zooplankton community and biomass (Chapter 5) are assessed. Chapter 6 provides a synthesis of the results and forwards outstanding research gaps and next steps.

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CHAPTER 2: STUDY DESIGN

Our current understanding of thermokarst affected systems is derived primarily from studies using a phenomenological approach (Kokelj *et al.* 2005; Mesquita 2008; Kokelj *et al.* 2009b; Thompson 2009). While these studies have been successful in describing the broad effects of shoreline disturbances, a mechanistic understanding of the key geochemical and ecological processes leading to the contrasts between disturbed and undisturbed lakes has not been reached. A valuable approach that has provided insight into complicated systems in aquatic research is the use of experimental enclosures and mesocosms (O'Brien *et al.* 1992; Beisner *et al.* 1997; Drenner & Mazumder 1999). Drenner & Mazumder (1999) argue that a combination of enclosure, whole-lake and observational studies yield the most research progress in complex aquatic ecosystems. In the case of thermokarst disturbances, enclosure experiments offer numerous benefits that are not possible using the phenomenological approach. These benefits include replication, assurance of identical initial conditions and, the elimination of confounding variables.

2.1 Study Lake and Area Description

The experimental lake is located on the uplands east of the Mackenzie Delta. The area is comprised of thousands of pothole-depression lakes embedded within the permafrost (Burn 2002) (Figure 2.1). The area has been the focus of numerous studies dealing with the geochemistry and hydrology of the Canadian Arctic (Lantz & Kokelj 2008; Kokelj *et al.* 2009a; Thompson 2009). Surficial materials consist of glacial till, ice contact deposits and outwash derived predominantly from carbonate and shale bedrock of the Mackenzie Basin (Kokelj *et al.* 2005). The experimental lake (named 5A), is a typical fishless tundra lake unaffected by retrogressive permafrost slumping. Its close proximity to our labs in Inuvik as well as its physical parameters similar to many other lakes in the area were the main factors leading to its selection for this study (Figure 2.2). Lake 5A, like the majority of the lakes on the Mackenzie uplands, is isolated and snowmelt within the lake catchment represents the most significant annual influx of water while evaporation during the open water season is the primary drain (Kokelj *et al.* 2005). The open-water season for lakes in the area typically lasts from mid-June to mid-October with a mean maximum ice thickness of 170 cm (Pienitz *et al.* 1997). Lakes in the area are classified as oligotrophic and receive DOC and minimal nutrients from runoff that is confined to a thin active layer, which is nutrient-poor but rich in organics (Burn & Kokelj 2009). As such, lakes in the area tend to be high in humic matter and highly coloured.

Figure 2.1. In the uplands of the Mackenzie delta, there are thousands of permafrost-embedded lakes.

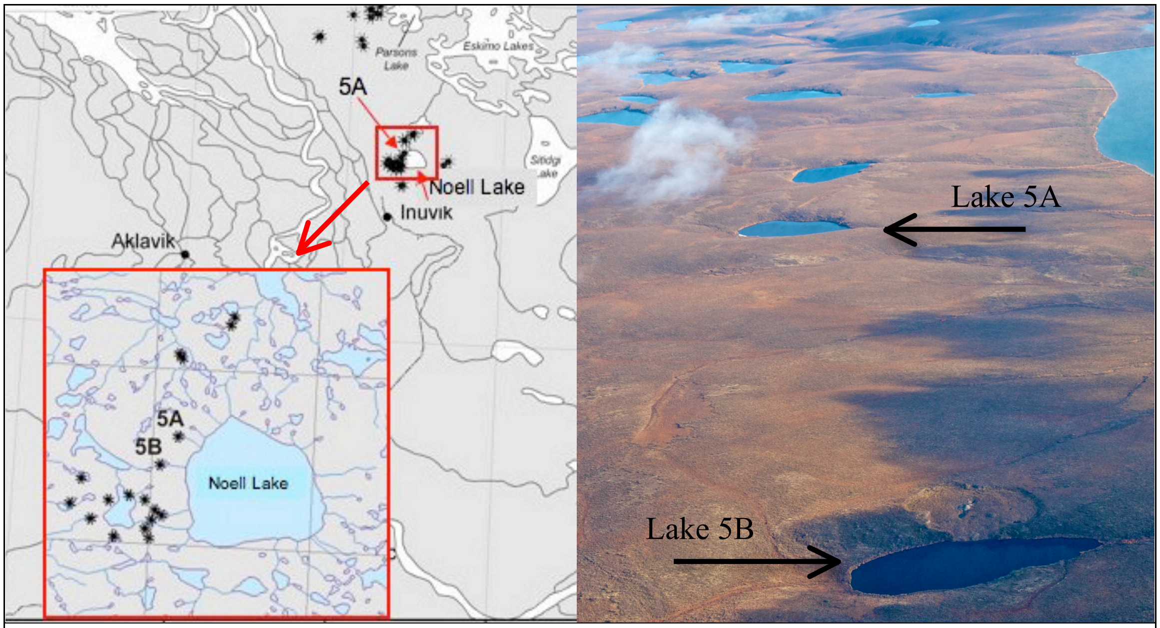

Figure 2.2. Lake 5A is an undisturbed lake which was the installation site for the mesocosms while lake 5B is a disturbed lake which was the source of the sediments. Sediments were transported1 km trip between lake 5A and 5B by helicopter in 5-gallon pails. Asterisks indicate lakes involved in past studies by Kokelj *et al.* (2005) and Thompson (2009).

2.2 Mesocosm Study - Experimental Design

The experiment consisted of twelve mesocosms (MCs) installed in a typical tundra lake (described above) (Figure 2.3, left). MCs were 121 cm square and placed at a depth of one meter thus giving a total volume of 1464 litres per MC. MCs were installed along the northern shore where the gradient was the shallowest and access was easiest. MCs were constructed of 2x2 spruce wood framing with walls of nylon-reinforced clear plastic sheeting and galvanized steel at the bottom to form a seal with the sediment (Figure 2.3, right). Once fixed onto the lake floor with rebar, MCs were watertight but open to the bottom sediments and open-air. The MCs were dosed with permafrost-related sediments taken from the thaw scar of a thermokarst-affected lake 1 km away (Lake 5B, Figure 2.2). The sediments were transported by helicopter in 5-gallon pails. Three sediment treatment levels were applied: added quantities of sediment were based on a hypothetical layer of uniform thickness of 1.5, 3 and 9 cm in the MC resulting in additions of 22, 44 and 132 litres of sediment for the low, medium and high treatment levels respectively. A control with no sediment addition was also included. Each treatment level and control had 3 replicates for a total of 12 MCs.

Figure 2.3. **Left:** Mesocosms set up at 1 meter depth of Lake 5A, a typical tundra lake on the uplands of the Mackenzie Delta. **Right:** Mesocosm assembly prior to installation.

The MCs were set-up in a randomized block design (Figure 2.4). This classic experimental design implies that all levels of an experimental treatment are equally represented and randomly distributed within each block. In this study the blocking factor is lake area (physical location within the lake). This design was chosen because there is potential variation in factors that may affect results depending on the physical location of the MCs in the lake. For example, quality and nutrient level of the sediments or macrophyte density may differ between locations in the lake. The assumption is that MCs that are closer to each other will be more similar than MCs that are far apart.

Furthermore, assessment of primary production (light and dark bottle procedures: Chapter 4) may have varied depending on time of day but could not be done simultaneously in all MCs. However, all MCs within a block were performed simultaneously therefore the block variable also incorporates potential differences due to time-of-day. The experiment lasted 11 weeks not including a 13-day transient period between sediment additions and initial sampling. The experiment thus represented the majority of one open-water growing season, from mid-June to mid-September 2010.

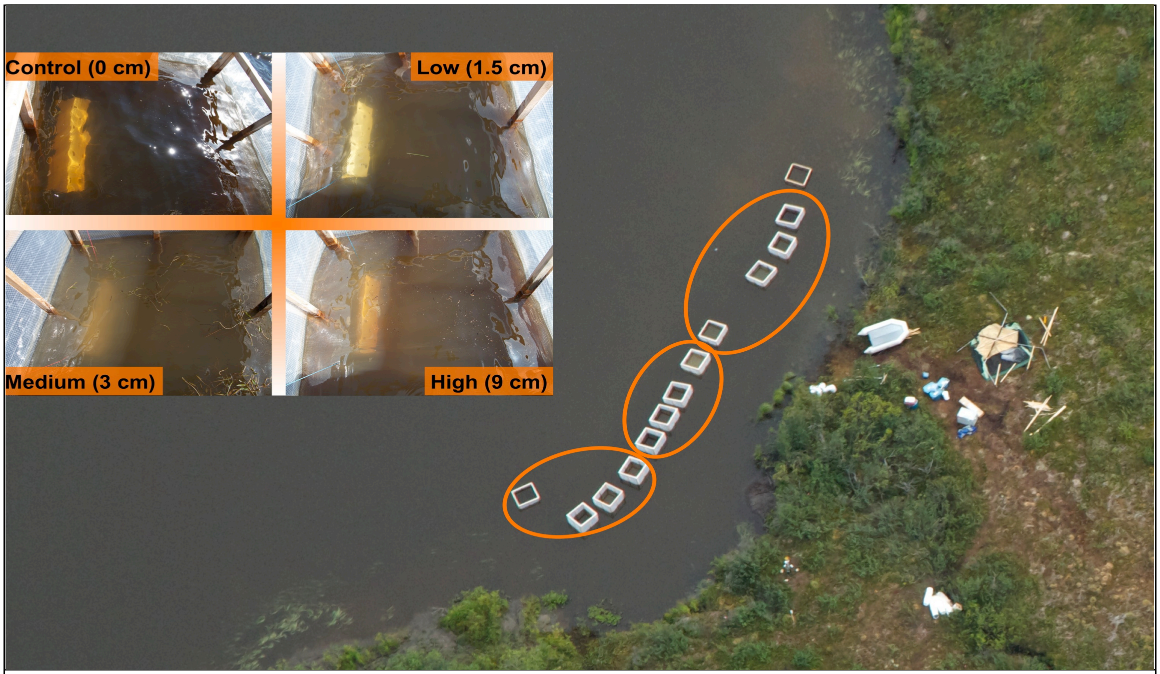

Figure 2.4. Mesocosms set up in a randomized block design. All treatment levels and one control are represented in each block.

2.3 Statistical Design and Analyses

Data were tested using mixed effects analysis of variance (Pinheiro & Bates 2009). Mixed effect models are comprised of fixed and random effects. Often, random effects are variables that potentially differ between experimental subjects but are not of particular interest to the study (Crawley 2007). Accounting for the error variance in the random effects increases the power to detect differences in the fixed effects, which are of interest. The mixed effects statistical procedure compliments the randomized block design with the block variable set as the random effect. Applied to this experiment, this design and analysis combination accounts for variation between MCs due to lake location and time of day while maximizing statistical power on testing sediment treatment effects.

The mixed-effects models tested throughout this study were comprised of three fixed-effect parameters and a single random-effects parameter. The three fixed-effects parameters were: a) sediment treatment level, b) time in weeks, c) an interaction term of sediment treatment and time. The random-effect was block which, as discussed, encompasses lake location and time-of-day. Backward stepwise selection procedure was used to reduce the model until all remaining terms were significant (Crawley 2007). Differences between the control and each treatment level were tested with a series of post-hoc, non-orthogonal contrasts within the model, values are adjusted for multiple comparisons (Crawley 2007). While this method most effectively utilizes the full potential of the experimental design and ensures the most statistical power, the contrasts are limited to each treatment level with the control and do not include inter-level comparisons. Further contrasts were carried out as needed. Statistical analysis was carried out using R, version 2.10.1 (R Development Core Team 2010). The identical three-parameter model is used to test all dependent variables throughout the study.

In addition, a two-sample t-test between results from the control MCs and lake were used to assess if the MCs affected any of the response variables.

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CHAPTER 3: EFFECTS OF THERMOKARST SLUMPING ON WATER COLUMN GEOCHEMISTRY

3.1 Introduction

Much of the preliminary work on the impacts of thermokarst activity has focused on the geochemical contrasts between slumped and unslumped lakes. A number of multi-lake comparative studies have found that mean concentrations of major cations and anions such as Ca, Mg and SO_4 are over an order of magnitude higher in slumped lakes compared to unslumped lakes while mean levels of water colour and dissolved organic carbon (DOC) are lower in affected lakes (Kokelj *et al.* 2005, 2009a; Thompson 2009; Kokelj *et al.* 2009b). Furthermore, increases in ion concentration and decreases in DOC and colour were proportional to the percentage of total basin area influenced by thermokarst disturbance (Kokelj *et al.* 2005).

Experimental work by Thompson *et al.* (2008) suggests that the “clear” pelagic water observed in slumped lakes may be a result of interactions between coloured humic matter and permafrost-related sediments released from thermokarst disturbance. They conducted an incubation experiment in sealed 2 litre clear acrylic tubes where coloured humic lake water from a typical non-disturbed Arctic lake was exposed to sediments collected from a permafrost thaw scar in small microcosms. After 52 days incubation, the water became significantly clearer. Furthermore, the degree to which the water cleared was related to the volume of sediment added to the tube. They proposed that charged particles such as ions and clays associated with thermokarst disturbance interact with the organic particles in the water column to form heavier compounds, which settle to the lake bottom. The theory is based on evidence that has shown that such interactions readily occur in the pelagic (Stumm & Morgan 1981; Rasmussen *et al.* 1989) and benthic (Hobbie *et al.* 1999) environments. Since large portions of the compounds in humic matter are coloured (Jones 1992), this leads to a clearing of the water column.

This study seeks to revisit Thompson *et al.* (2008) experiment on a larger scale and include biological parameters that may have been excluded in Thompson’s sealed experimental tubes. This chapter summarizes the physical and chemical results of a mesocosm (MC) experiment where MCs were dosed with permafrost-related sediments mimicking differing levels of a shoreline disturbance.

3.2 Methods

3.2.1 Sampling

Initial samples to test for uniform initial conditions were taken from every second MC just before the addition of the sediments on 22 June 2010. The first full run of samples, which included all 12 MCs, plus a lake sample was July 5th (week 1) and taken every two weeks thereafter until September 19th (week 11) for a total of 6 time steps.

Water samples were taken with a 1 litre Nalgene bottle attached to a graduated steel rod plunged down to 0.5 m below the surface. The water was transferred into clean, pre-labeled bottles stored in a chilled cooler and air transported with ice packs within 24 hours of collection for analysis at Environment Canada Laboratories (Saskatoon and Burlington). All analyses were performed in Environment Canada/CALA accredited laboratories (the Canadian Association for Laboratory Accreditation) using standard methods as described by the American Public Health Association (2005) and Environment Canada's Standard Operating Procedures manual (SOP)(2009). All measured water quality parameters are listed in Table 3.1.

Light profiles were taken weekly with a Li-Cor spherical quantum sensor (LI-193) on a LI-1400 data logger at the surface, 50cm and bottom. Presented light attenuation coefficients *(k)* were calculated with the equation:

$$\ln(I_{bot}/I_0)=-k_{bot}/\text{meter}$$

where I_{bot} is the irradiance at the bottom (1 meter depth) and I_0 is that irradiance at the surface (Kalff 2001).

Lake samples were taken at random locations adjacent to the MCs using identical methods as described above.

3.2.2 Statistical Analyses

As described in section 2.3, a three-parameter mixed-effects analysis of variance was used to analyze all dependant variables for treatment effects. The procedure allows for the assessment of whether dependent variables measured in the MCs:

1) had a significant treatment effect,
2) varied significantly over time,
3) differed significantly in temporal trend depending on treatment level

In this chapter, dependent variables consist of physical and chemical parameters including the major cation and anions, nutrients, light attenuation coefficients and colour. Two-sample t-tests between results from the control MCs and lake were used to assess if the MCs affected any of the response variables. All analyses were conducted using R version 2.10.1 (R Development Core Team 2010).

3.3 Results

The water chemistry and physical parameters measured for this experiment were categorized into four functional groups. Detailed probability values for the mixed effects models and associated contrasts as described in section 2.3 (Statistical design and analysis) are presented in table 3.2.

3.3.1 Nutrients

Increasing sediment treatment effects were associated with increases in all phosphorus parameters including total phosphorus (TP), dissolved phosphorus (DP) and orthophosphate (OP). Potassium (K) and ammonia (NH_3) also increased with sediment treatment; however, no significant trends were found for total nitrogen (TN) or total dissolved nitrogen (TDN). Although for TN, low treatment was significantly different than the control. TP, DP and NH_3 were the only nutrients that changed significantly over time; they did so in a downward trend.

3.3.2 Cations/Anions

All cations and anions measured increased with increasing sediment treatment as indicated by increasing conductivity, a general indicator of ion concentrations. Over time, calcium (Ca), magnesium (Mg) and sodium (Na) increased while chloride (Cl) and silicon dioxide (SiO_2) decreased. Sulfate (SO_4) did not change significantly over time. Sodium was the only variable which had a significant treatment by time interaction. The high treatment level increased over time while the concentration of other treatments did not vary significantly with time. In natural systems, sodium tends to correlate with distance from the sea (Pienitz *et al.* 1997; Kokelj *et al.* 2005). Sodium is likely released from the added sediments over time in all treatments but only in the high treatment level are additions large enough to be detected over the background variation between MCs.

3.3.3 pH and Inorganic Carbon Complex

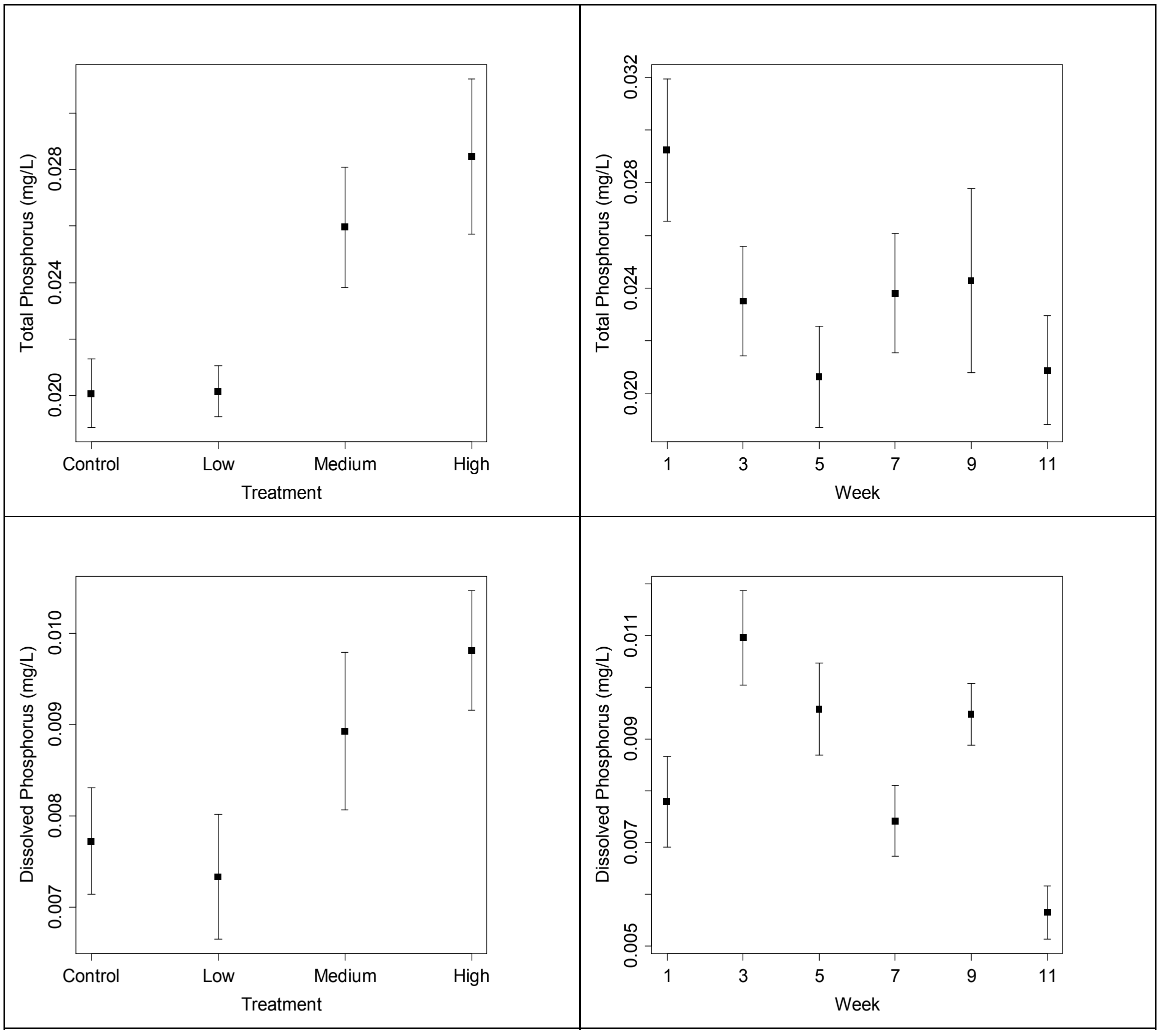
Alkalinity and dissolved inorganic carbon (DIC) increased with treatment and increased over time. pH decreased with sediment treatment but increased over time.

3.3.4 Physical/Water Quality Parameters

Treatment effects were associated with significant increases in colour, turbidity, and light attenuation coefficient. No sediment treatment effects were found for DOC. None of these physical parameters changed significantly over time.

Table 3.1. Summary table of probability values of physical/water quality and chemical variables tested with a three-parameter mixed-effects model, which included: a) treatment level, b) time in weeks, c) an interaction term of treatment and time. Significant p values ($p<0.05$) are shaded with grey. The final column refers to the trend of the response to increasing treatment. Other than standard chemical abbreviations, the following abbreviations are used: total phosphorus (TP), dissolved phosphorus (DP), orthophosphate (OP), total nitrogen (TN), total dissolved nitrogen (TDN), conductivity (Cond.), alkalinity (Alk.), dissolved inorganic carbon (DIC), dissolved organic carbon (DOC), turbidity (Turb.), and light attenuation coefficient *(k)*.

Parameter	**Fig #**	**Significance of Time**	**Contrasts Relative to Control**			**Trend**
			Low	**Medium**	**High**	
Nutrients						
TP	3.1	0.034 (-)	0.79	0.027	0.0024	+
DP	3.1	0.012 (-)	0.72	0.20	0.032	+
OP	3.1	0.52	0.58	0.024	0.0014	+
NH_3	3.2	0.049 (-)	0.15	0.10	0.025	+
TN	3.2	0.58	0.011	0.25	0.33	Mixed
TDN	NA	0.66	0.15	0.36	0.59	NA
K	3.3	0.87	<0.0001	<0.0001	<0.0001	+
Cations/Anions						
Cond.	3.8	0.17	<0.0001	<0.0001	<0.0001	+
Ca	3.4	0.0017 (+)	<0.0001	<0.0001	<0.0001	+
Mg	3.4	<0.0001(+)	<0.0001	<0.0001	<0.0001	+
Na	3.5	0.011 (+)	0.038	0.022	<0.0001	+
Cl	3.5	0.028 (-)	0.048	0.63	0.0028	+
SiO_2	3.6	0.047 (-)	0.47	0.035	<0.0001	+
SO_4	3.6	0.067	<0.0001	<0.0001	<0.0001	+
Carbonate Complex						
pH	3.7	<0.0001 (+)	0.29	0.78	0.0002	-
Alk.	3.7	<0.0001 (+)	0.0071	0.010	0.048	+
DIC	3.7	<0.0001 (+)	0.0067	0.0045	0.075	+
Physical/Water Quality Parameters						
DOC	NA	0.87	0.21	0.10	0.60	NA
Colour	3.8	0.44	0.36	0.15	<0.0001	+
Turb.	3.8	0.26	<0.0001	<0.0001	<0.0001	+
k	3.8	0.31	0.91	0.0005	0.0001	+



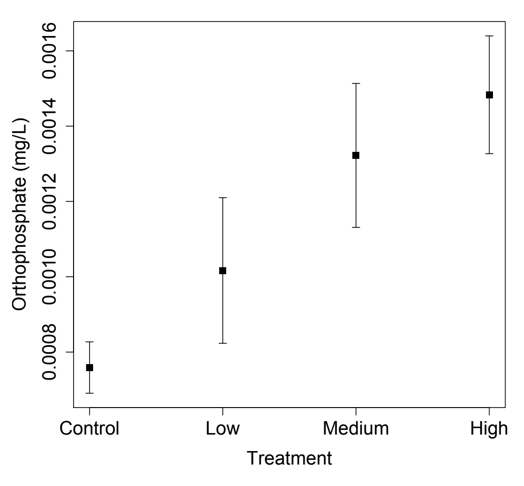
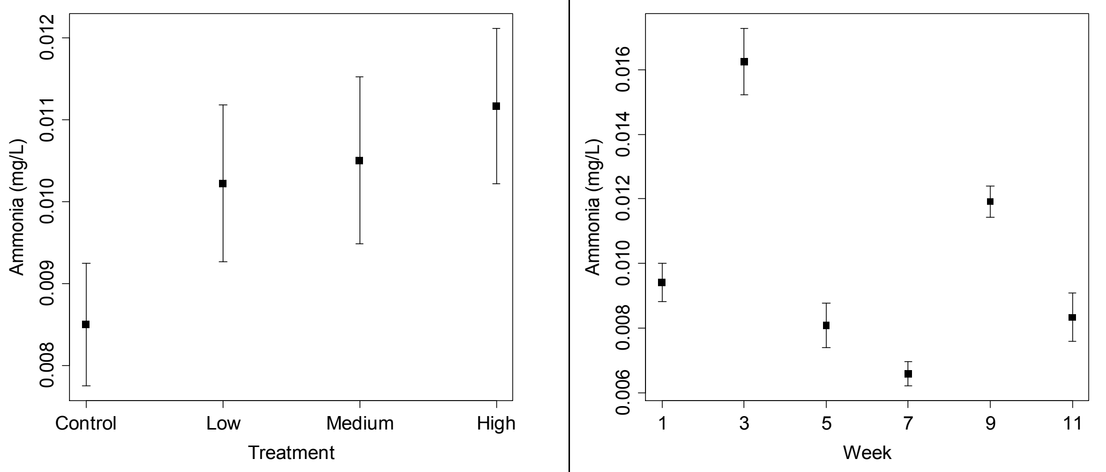


Figure 3.1. *Phosphorus parameters.* **Top**: Mean concentration of total phosphorus by treatment level (left) and over time (right). The medium (p=0.027) and high (P=0.0024) treatment levels were significantly greater than the control. The decrease over time was significant (p=0.012). **Middle**: Mean concentration of dissolved phosphorus by treatment level (left) and over time (right). Only the high treatment level was significantly greater than the control (P=0.032). The decrease over time was significant (p=0.034). **Bottom**: Mean concentration of orthophosphate (OP) by treatment level. The medium (p=0.024) and high (P=0.0014) treatment levels were significantly greater than the control. OP did not change significantly over time. *Error bars represent the standard error of the mean.



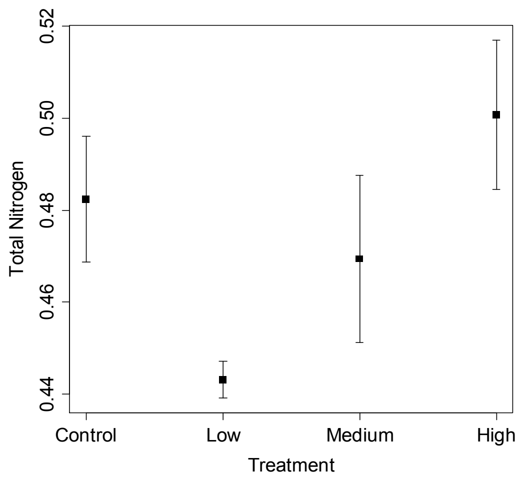


Figure 3.2. *Nitrogen parameters.* **Top**: Mean concentration of ammonia (NH_3) by treatment level (left) and over time (right). Only the high treatment level was significantly different than the control ($p=0.025$). The decrease over time was significant ($p=0.049$).
Bottom: Mean concentration of total nitrogen (TN) by treatment level. Only the low ($P=0.011$) treatment level was significantly different than the control. TN did not change significantly over time.
*Error bars represent the standard error of the mean.

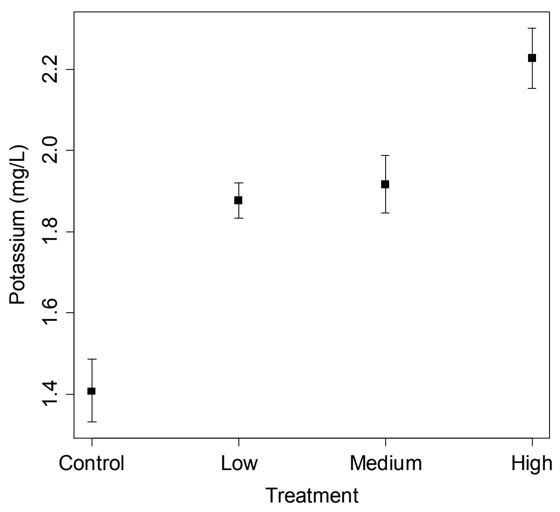


Figure 3.3. Mean concentration of total potassium (K) by treatment level. All treatment levels were significantly greater than the control ($p<0.0001$). K did not change significantly over time.
*Error bars represent the standard error of the mean.

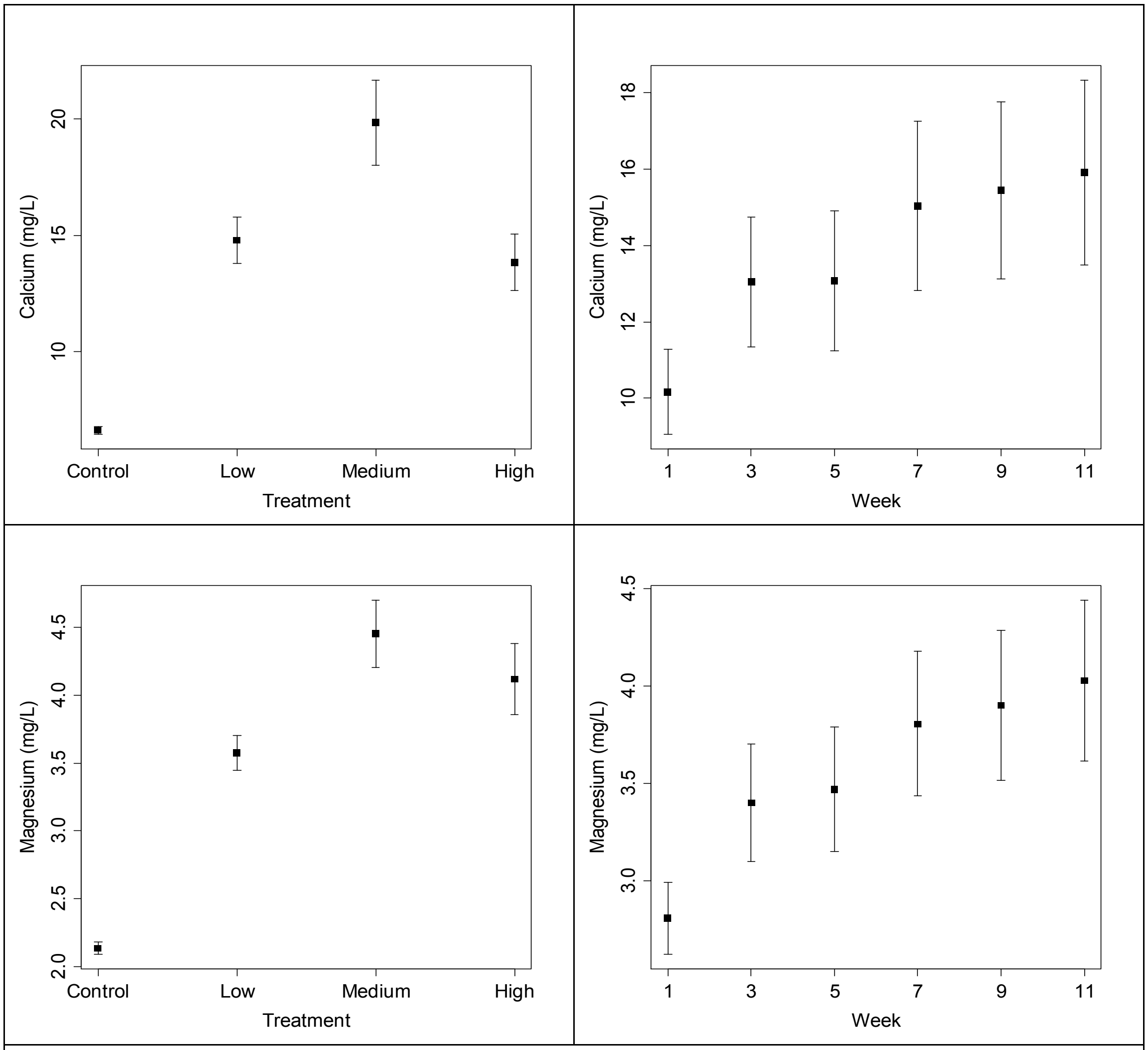


Figure 3.4. *Major Cations.* **Top:** Mean concentration of calcium (Ca) by treatment level (left) and over time (right). All treatment levels were significantly greater than the mean ($p<0.001$). Ca increased significantly over time ($p=0.0017$).
Bottom: Mean concentration of magnesium (Mg) by treatment level (left) and over time (right). All treatment levels were significantly greater than the control ($P<0.001$). Mg increased significantly over time ($p=0.0017$).
*Error bars represent the standard error of the mean.

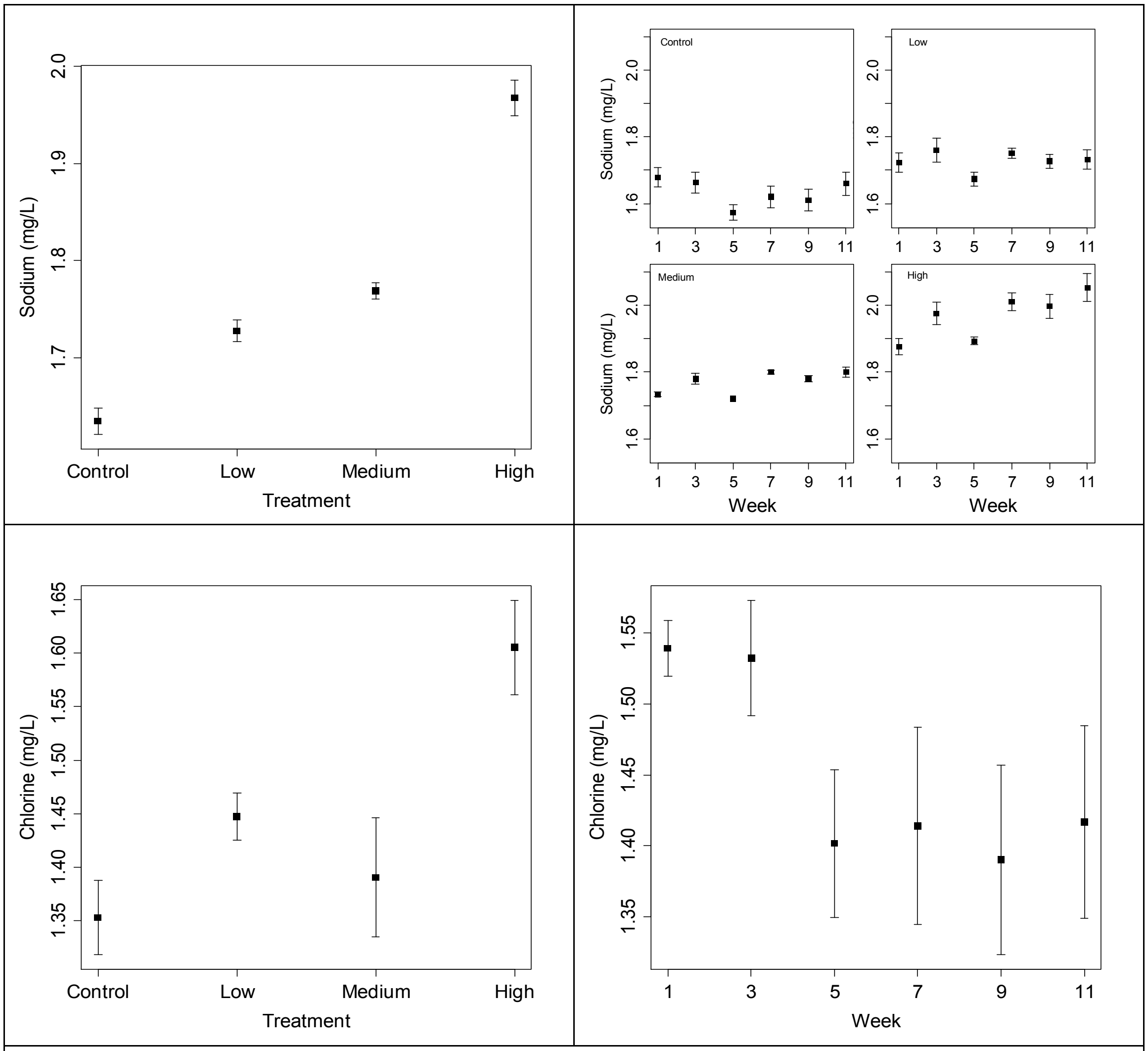
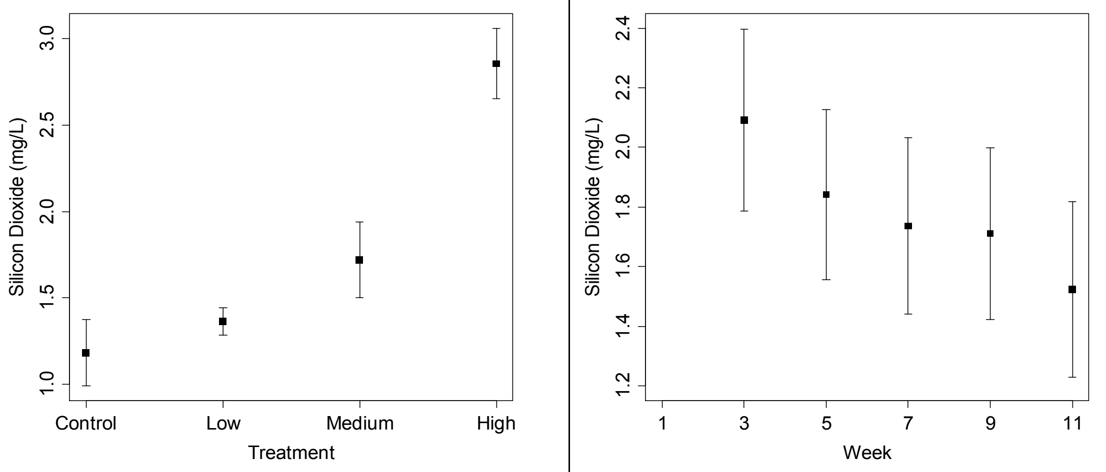


Figure 3.5. *Sodium and chloride ions.* **Top:** Mean concentration of sodium by treatment level (left) and over time (right). All treatment levels were significantly greater than the control ($p<0.05$). There was a significant interaction ($p=0.003$) between treatment level and time derived from the high treatment increasing over time while the other treatments did not. **Bottom:** Mean concentration of chloride (Cl) by treatment level (left) and over time (right). Both the low ($p=0.048$) and high ($p<0.0001$) treatment levels were significantly greater than the control while the medium treatment level was not ($p=0.63$). Cl decreased over time ($p=0.028$). *Error bars represent the standard error of the mean.



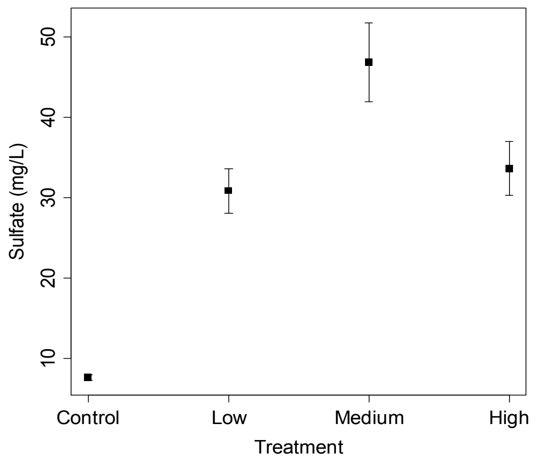


Figure 3.6. *Silicon dioxide and sulfate.* **Top**: Mean concentration of silicon dioxide (SiO_2) by treatment level (left) and over time (right). The medium ($P=0.035$) and high ($P<0.0001$) treatment levels are significantly greater than the control. SiO_2 decreased significantly over time ($p=0.047$). **Bottom:** Mean concentration of sulfate (SO_4) by treatment level. All treatment levels were significantly greater than the control ($P<0.001$). SO_4 did not change significantly over time. *Error bars represent the standard error of the mean.

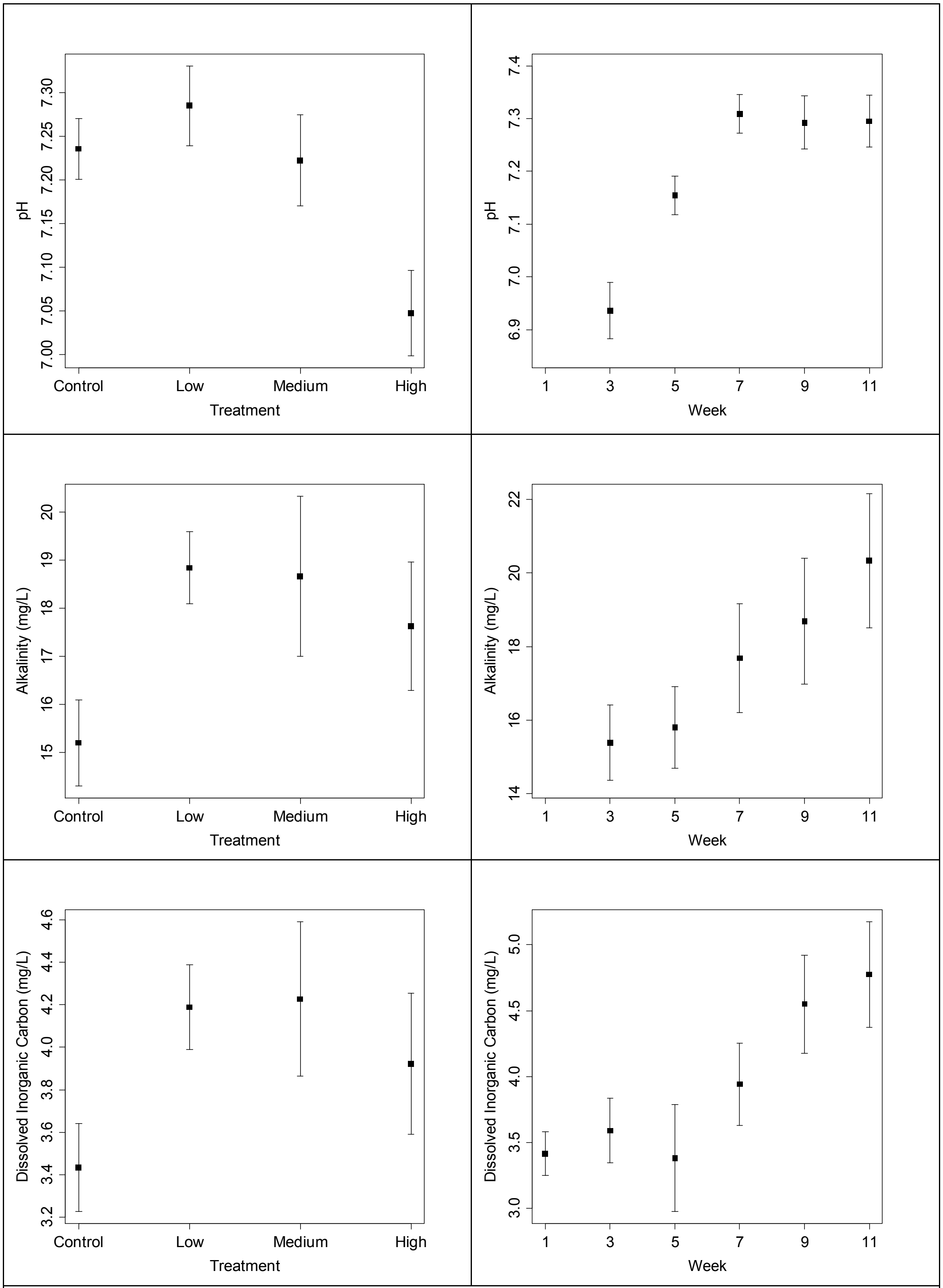


Figure 3.7. *Carbonate Complex.* **Top:** Mean pH by treatment level (left) and over time (right). Only the high treatment was significantly lower than the control (p<0.0001). pH increased significantly over time (p<0.0001).

Middle: Mean alkalinity (Alk.) by treatment level (left) and over time (right). All treatment levels were significantly greater than the control ($p<0.05$). Alkalinity increased significantly over time ($p<0.0001$). **Bottom**: Mean concentration of dissolved inorganic carbon (DIC) by treatment level (left) and over time (right). Both the low ($P=0.0067$) and medium ($P=0.0045$) treatment levels had DIC concentrations significantly greater than the control however the difference between the control and high treatment was marginally non-significant ($p=0.075$). DIC increased significantly over time ($p<0.0001$). *Error bars represent the standard error of the mean.

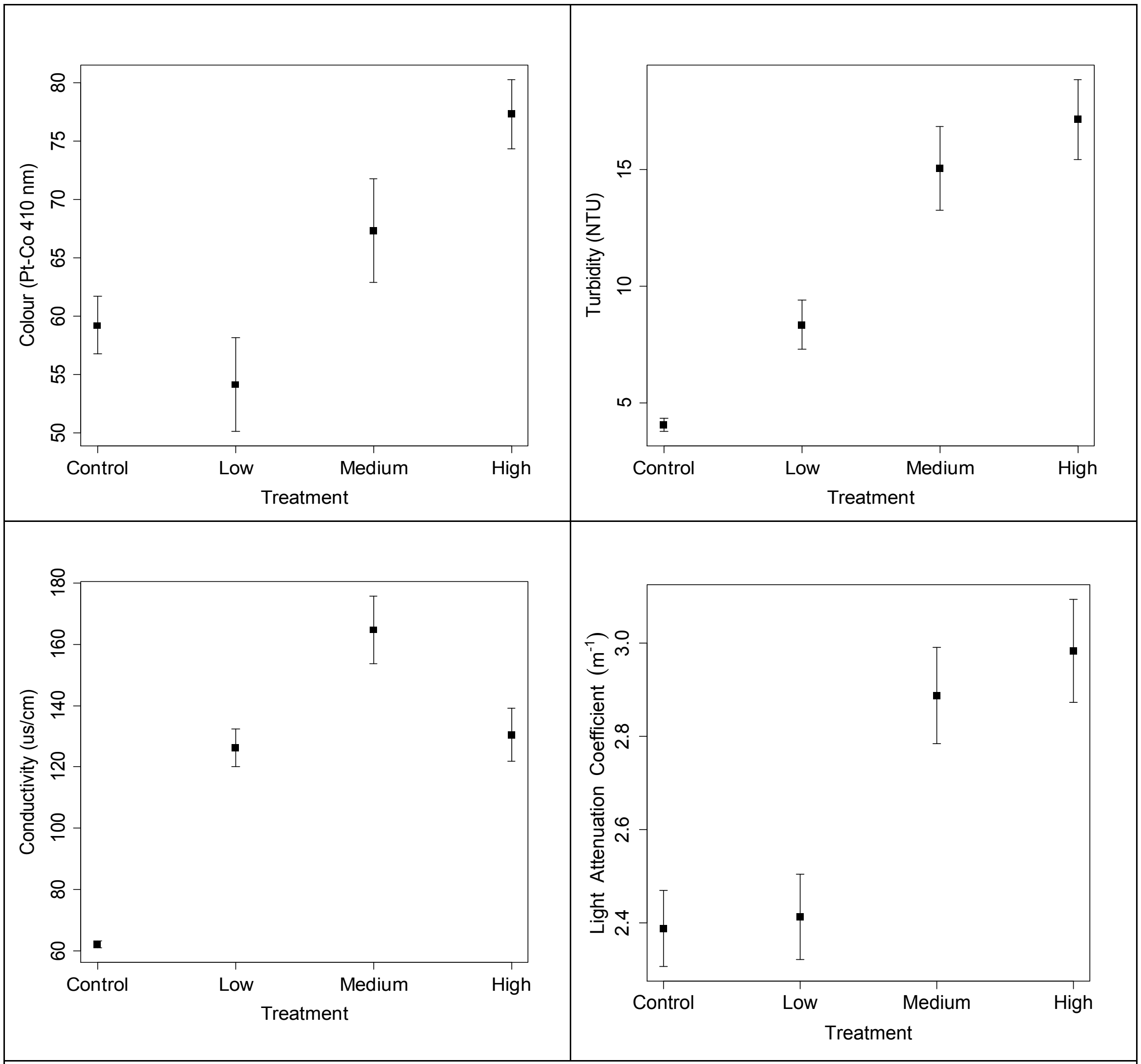


Figure 3.8. *Physical/Water Quality Parameters.* **Top left:** Mean concentration of colour by treatment level. Only the high treatment level was significantly different than the control ($p<0.0001$). **Top right:** Mean turbidity by treatment level. All treatment levels were significantly greater than the control ($P<0.001$). **Bottom left:** Mean conductivity by treatment level All treatment levels were significantly greater than the control ($P<0.001$). **Bottom right:** Mean light attenuation coefficient by treatment level. The medium ($p=0.0005$) and high ($P=0.0001$) treatment levels were significantly greater than the control.
*None of the physical parameters measured changed significantly over time.
*Error bars represent the standard error of the mean.

3.3.5 Mesocosm Effects- Comparison of Lake and Control Measurements

Table 3.2 lists the dependant variables for which a significant difference was found between lake and control means, potentially indicating a MC effect. Parameters were tested using a two-sample t-test. With the exception of silicon dioxide, the mesocosm effect is positive, causing increases in mean concentrations relative to the lake. Relative to the treatment effect, the mesocosm effect was particularly large in DOC, DIC, alkalinity and chlorine but relatively small in conductivity, calcium and magnesium.

Table 3.2. List of parameters with significant differences ($p<0.05$) between control mesocosms and lake, potentially indicating a MC effect. The final column refers to the direction of the response to the MC. Other than standard chemical abbreviations, key for abbreviated row headings: total phosphorus (TP), total nitrogen (TN), total dissolved nitrogen (TDN), alkalinity (Alk.), dissolved inorganic carbon (DIC), dissolved organic carbon (DOC), and conductivity (Cond.).

Parameter	**Lake** (μ ± s.e.) **(mg/L)**	**Control** (μ ± s.e.) **(mg/L)**	**P value**	**Effect**
TP	0.014 ± 0.0008	0.020 ± 0.0012	<0.001	+
TN	0.42 ± 0.0096	0.48 ± 0.014	0.002	+
TDN	0.38 ± 0.0058	0.41 ± 0.0093	0.011	+
Alk.	11.28 ± 0.36	15.19 ± 0.90	<0.001	+
DIC	2.82 ± 0.075	3.43 ± 0.21	0.001	+
DOC	14.45 ± 0.31	16.78 ± 0.41	<0.001	+
Cond.	55.54 ± 0.6 (us/cm)	62.004 ± 1.12 (us/cm)	<0.001	+
K	0.86 ± 0.023	1.41 ± 0.077	<0.001	+
Ca	6.12 ± 0.10	6.64 ± 0.18	0.017	+
Mg	2.14 ± 0.047	1.94 ± 0.014	<0.001	+
Na	1.57 ± 0.017	1.63 ± 0.014	0.009	+
SiO_2	2.33 ± 0.085	1.18 ± 0.19	<0.001	-

3.4 Discussion

3.4.1 Nutrient Effects

Additions of permafrost-related sediments were associated with significant increases in nutrient concentrations within treated mesocosms. All phosphorus parameters, potassium and ammonia increased with sediment treatment. These results are contrary to expectations. In a synoptic study of 60 tundra lakes, Thompson (2009) found no increases in nutrient concentration related to thermokarst activity. This may be a result of the relative fresh nature of the simulated slumping event in the MCs. While Thompson's (2009) study included active slumps, it also included lakes with stable but recently active slumps and ancient slumps making a comparison to these MCs tenuous. Temporal data from this experiment indicate that most nutrient concentrations decreased throughout the length of the experiment. There are a number of processes that may sequester nutrients from the water column over time. They include biological uptake (Levine & Schindler 1989), binding directly with sediments (Hobbie *et al.* 1999) as well as various settling processes (Forsberg 1989). In particular, the binding and settling of nutrients to inorganic particles in suspension such as fine silts and clays (Stumm & Morgan 1981) which are also part of the slump material, may be an important mechanism sequestering nutrients from the water column. These processes may have continued to function reducing nutrient concentrations to background levels given a longer experimental length. The system may require ice cover to still the water sufficiently to allow the particles to settle and therefore still registered in the water chemistry tests.

3.4.2 Cations/Anions

Concentrations of major cations and anions (Ca, Mg, Na and SO_4) were greater in the treated MCs compared to the control MCs. This was expected as the sediments from this area are from ancient marine deposits (Mesquita 2008; Burn & Kokelj 2009). However, compared to the slumped lakes in Thompson's (2009) study, the ionic concentrations in the MCs were low. Ion concentrations trended upwards over the course of the season. Temporal trends towards concentrations found in natural systems in nutrients and cations/anions suggest that ion exchange with new slump material may be a multi-year process. As such, the potential of this experiment to address long-term questions regarding the potency of permafrost-related sediments to affect geochemical change is limited.

3.4.3 Inorganic Carbon/pH Complex

Alkalinity and dissolved inorganic carbon (DIC) increased with treatment and increased over time. As alkalinity depends on the abundance of DIC (in its various species: $CO_{2(aq)}$, HCO_3- and CO_3^{2-}), alkalinity moves in lockstep with DIC (Small & Sutton 1986). The pattern of increased alkalinity in treated MCs reflects the empirical data from the multi-lake study by Kokelj *et al.* (2009b) where slumped lakes had higher alkalinity. Given that alkalinity is a measure of buffering capacity (Kalff 2001), slumped lakes will be more resistant to changes in pH than unslumped lakes. pH tended to decrease with treatment and increase over time. And though there were some statistically significant differences, it is unlikely that the range in pH (~0.3) across treatments has any ecological relevance (Fryer 1993).

3.4.4 Physical/Water Quality Parameters

Increasing sediment treatment was associated with significant increases in colour, turbidity, conductivity and light attenuation coefficient. No treatment effects were found for DOC. None of these parameters changed significantly over time.

Patterns of conductivity in the experiment are reflected in natural systems in that slumped lakes have greater conductivity than unslumped likely reflecting the greater concentration of ions in slumped lakes and treated MCs. However, experimental turbidity and light attenuation coefficients greater than found in natural systems and not changing over the course of the experiment suggests that a portion of slump material is composed of fine light-attenuating particles that remained in suspension and may require a season of ice cover to sufficiently still the water to allow the particles to settle.

DOC and colour were expected to decrease with treatment as patterns of lower DOC and colour have been found in slumped lakes relative to unslumped lakes (Kokelj *et al.* 2005; Thompson 2009). Furthermore Thompson *et al.* (2008) found that humic water exposed to permafrost-related sediment in two litre microcosms became clearer over time. Instead, colour was found to increase and DOC did not change significantly with increasing sediment treatment. The differing results obtained in these mesocosm experiments may be related to the sediment treatment level not being large enough or the experimental time being of too short a duration. In this experiment, nutrient concentrations, which were greater than found in natural systems decreased over time while ion concentrations, which were less than found in natural systems, increased. This suggests that time was lacking in this experiment. However, the decrease in colour observed in Thompson *et al*'s (2008) microcosms was achieved in 52 days, an experimental period shorter than this study. There are likely numerous factors including time, slump size and other physical parameters that determine the extent of impact of a slump on the receiving body. Note that the MCs received much smaller doses of sediment relative to the total volume of the container compared to Thompson's experimental tubes. In their experiment, Thompson et al. (2008) based treatment levels on a percentage of the total volume of the container. Treatment levels were: 10, 25 and 50% of the total volume of a 2 litre clear acrylic tube. In contrast, treatment levels in the MC experiment were based on the thickness of a uniform layer of sediment at the bottom of the MC and represented only 1.5, 3 and 9% of the total MC volume. Furthermore, the ratio of sediment surface area to water volume was much greater in the tubes than in the MCs. For example, the high treatment for the tube had a ratio of 0.25 verses only 0.01 in the MCs. In addition, because the tubes were lying on their side, each sediment treatment increase (up to 50% total volume) also represents an increase to the benthic surface area (and ratio to volume). In contrast, increases in treatment level within the MCs would not have affected the surface area. The mean benthic surface area to volume ratio of several typical lakes in the area of the experimental lake was 0.20±0.06. In that respect, the tube experiment was a closer approximation of those lakes than the MCs. Benthic-based processes that may affect water chemistry and colour may be chemical and biological. Benthic surface area is important in ion exchange (Boström *et al.* 1988) and coloured humic matter is known to bind to mineral particles, oxides and clays (Tipping 2002). Biological degradation of coloured DOC occurs when humic substances are used as a carbon source by bacteria and so are reduced to less coloured by-products (Moran & Hodson 1990; Curtis & Schindler 1997). This process is not restricted to the benthos and would also occur in the water column however numerous studies have supported the ideal that bacterial activity in the benthos is greater than in the pelagic zone, particularly in shallow lakes (Vadeboncoeur *et al.* 2002). Vadeboncoeur *et al.* (2002) report on a study where whole-lake sediment bacterial production was estimated to be one to three orders of magnitude higher than whole-lake measurements of bacterioplankton production. Given its potential to affect water colour, the ratio of benthic surface area to water volume may influence the effectiveness of benthic-based processes to impact a volume of water.

Not all processes that can impact water colour are benthic-based. Biological and chemical processes are also likely occurring in the pelagic zone. Humic matter is also known to bind with polyvalent cations, flocculate and precipitate out of the water column (Engstrom 1987; Römkens & Dolfing 1998). For example calcium additions were found to reduce the DOC concentration of humic water by up to 50% through flocculation in small container experiments (Römkens & Dolfing 1998). Whether by virtue of greater surface area or greater sediment to water ratios, conductivity results (a proxy to evaluate the concentration of ions) confirm that not as many ions were delivered to the MC water column compared to the tubes or natural systems. The range of conductivity reported from Kokelj et al.'s study of 11 slumped lakes was 274 to 1680 µS/cm and a mean of 600 μS/cm. In comparison, the tube experiment yielded means of 893, 1382 and 1966 μS/cm for the low, medium and high treatments while 165μS/cm was the highest mean conductivity attained in the MCs. Here again, tubes approximate the levels found in natural systems better than the MCs. Not surprisingly, the greater the cation concentration, the greater the potential for this mechanism to contribute to a significant clearing of the water column (Curtis & Schindler 1997).

It is also reasonable to assume that stirring regimes would influence a number of the processes described here. The positive effects of biotubation and abiotic processes such as wind-induced currents on the diffusion of phosphorus and other elements between the benthic and pelagic environments are well documented (Krantzberg 1985; Boström *et al.* 1988). With the exception of bi-weekly experimental procedures, the benthic-pelagic interface at the bottom of each MC is likely to be quite still compared to natural systems. Sediment treatments were administered without any further stirring in the MCs. In contrast, solutes in naturally disturbed systems may enter the water column via runoff passing over freshly exposed, ion-rich thermokarst scars (Kokelj *et al.* 2005, 2009b) or enter a water body directly, often as a mud slurry (Lantz & Kokelj 2008). Both of these methods involve dynamic processes and are likely more efficient at exchanging ions with the environment than simply dropping sediments into a still environment such as a MC (Rees *et al.* 1996; Kim *et al.*2003). Thompson *et al.* (2008) stirred their experimental tubes prior to incubation (Fred Wrona, personal communication).

Another mechanism that may influence lake colour is photolysis. The potential of this mechanism was removed in the tube experiment because the containers they used restricted the passage of UV light to the inside environment of the tubes. Photolysis was unlikely to be an important factor in the MC experiment as the turbidity across all treatments would have limited this process. Turbidity ranged from 1.2 to 3.9 NTU in Kokelj's (2005) study of 11 slumped lakes in contrast, treatment means were 8.4, 15 and 17 NTU for low, medium and high treatment levels respectively. The elevated turbidity is likely to have prevented the deep penetration of UV rays into the water column decreasing photolysis.

To some degree, contrasts drawn between MC results and thermokarst affected lakes as reported by Kokelj *et al.* (2005, 2009a) and Thompson (2009) are somewhat trivial. The most relevant comparison to the conditions recreated in the treated MCs would be a fresh shoreline thermokarst disturbance into a previously undisturbed lake (from which we have a pre-existing baseline of key parameters); a set of conditions unlikely to occur without direct manipulation. However, drawing on the empirical evidence from synoptic studies and the results from Thompson *et al.*'s (2009) experimental work, this chapter has narrowed the scope on the complex issue of the impacts of thermokarst disturbance to a few key processes. In particular, evidence points to the importance of the scaling of physical parameters such as water volume to benthic surface area ratios and disturbance volume to water volume ratios as well as slump magnitude and time. Results from this experiment suggest that lakes with smaller benthic surface area to volume ratio (typically meaning deeper lakes) may be more resilient to the effects of thermokarst degradation and that larger lakes will require proportionally larger sediment inputs to affect significant changes.

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CHAPTER 4: EFFECTS OF THERMOKARST SLUMPING ON THE BASAL COMPONENTS OF THE FOOD WEB

4.1 Introduction

A key knowledge gap in our understanding of the impacts of enhanced thermokarst activity on Arctic lake ecosystems is to obtain an improved mechanistic understanding of how chemical, physical and biological processes interact to produce the regime changes observed in thermokarst-affected (slumped) lakes (Mesquita 2008; Thompson 2009). In a study involving a series of oligotrophic lakes spanning a range of coloured dissolved organic carbon (CDOC) concentrations, Ask *et al*. (2009a) found significant differences in the magnitude and type of energy mobilization along a CDOC concentration gradient. Benthic primary production dominated energy mobilization in lakes having a “clear” pelagic zone but decreased in importance with increasing CDOC, while the importance of heterotrophic bacterioplankton increased with CDOC concentration and were the dominant energy mobilizers in the lakes with the highest CDOC concentrations. This suggests that CDOC mediates the relative importance of autotrophic and heterotrophic processes and may have cascading effects across the food web. This interaction may be relevant because of observed contrasts in CDOC concentrations between disturbed and undisturbed lakes (Kokelj *et al.* 2005; Thompson 2009). In addition, relatively small changes in CDOC concentrations have been found to affect the autotrophic-heterotrophic balance (Jansson *et al.* 2000; Ask *et al.* 2009a). This is because CDOC serves simultaneously as a food substrate for heterotrophic processes and as an inhibitor of primary production through its optical properties (Jones 1992; Jansson *et al.* 2000). A shift in dominant energy pathways within a food web can have large impacts on the system (Jansson *et al.* 2000). If the entry point for the majority of new energy to a lake is allochthonous CDOC metabolized by bacteria, as it is likely to be in undisturbed lakes, the dominant food chain is projected to be: CDOC→bacteria→bacterivore→zooplankton. In contrast, if allochthonous inputs from a thermokarst disturbance reduce CDOC, light conditions for primary productivity could improve and the pathway using: atmospheric CO_2→phytoplankton→zooplankton, could become more important (Jones 1992; Salonen *et al.* 1992). There is therefore the potential that the assemblage of species diverges along a disturbance gradient and, because there is an extra trophic level in the CDOC chain, energy losses from the base to the top of the food chain will be lesser in the autotrophic systems potentially leading to overall productivity increases (Jansson *et al.* 2000; Ask *et al.* 2009a). Figure 4.1 provides a simplified illustration of two potential food chains differing in basal carbon source.

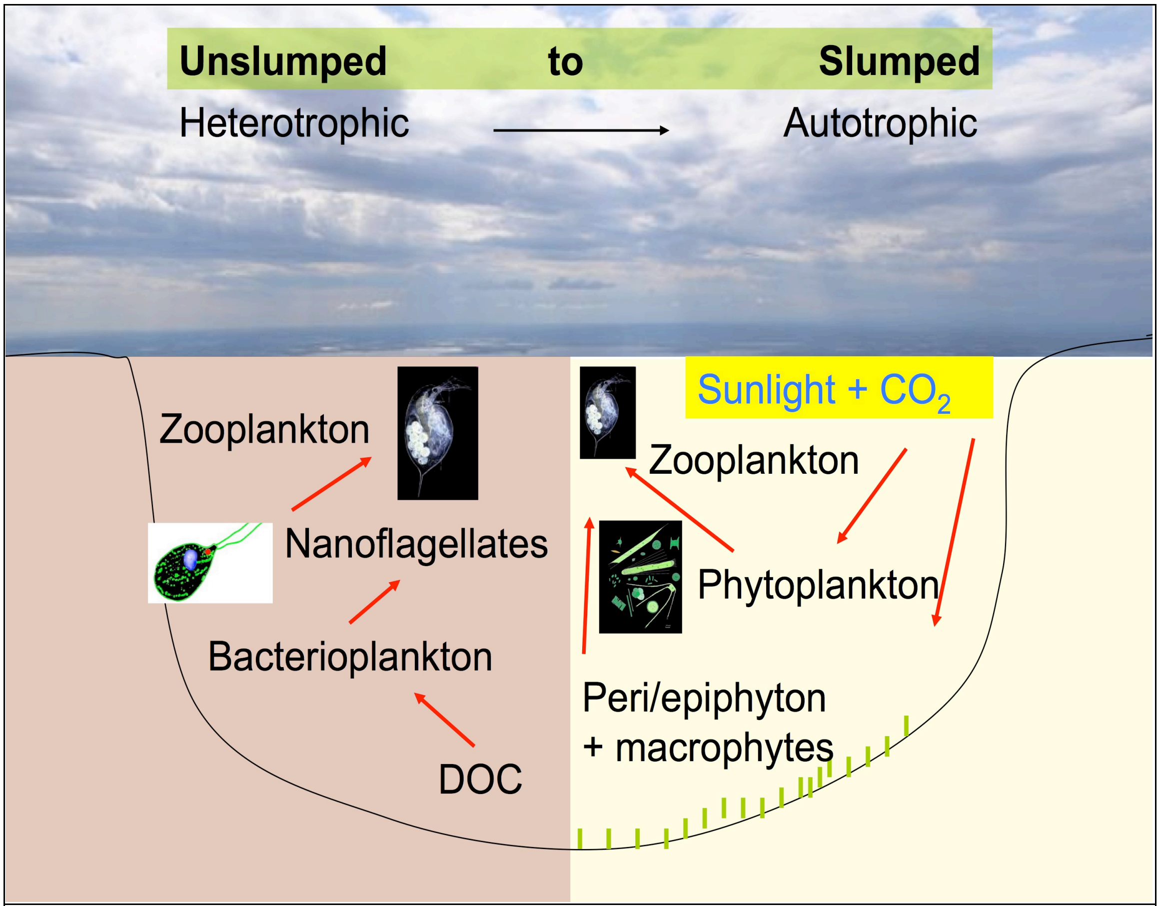


Figure 4.1. Two potential food webs differing in carbon source. The food web based on DOC (left) has 4 levels while the food web based on CO_2 and sunlight has 3.

Prior synoptic work suggests that thermokarst disturbance may cause CDOC-mediated shifts in energy pathways. Kokelj *et al.* (2005) found that lake colour was lighter in slumped lakes. Thompson (2009) corroborated these findings and also found that concentrations of chlorophyll *a* were greater in stabilized slumped lakes relative to actively slumping and unaffected lakes. Furthermore, Mesquita (2008) found that slumped lakes had greater macrophyte biomass than unslumped lakes. Together these findings imply that dominant energy pathways may be different in slumped and unslumped lakes (i.e., shifting from a heterotrophic-dominated system in unslumped lakes to an autotrophic-dominated system in unslumped lakes). Though Thompson (2009) found no correlation between the status of slump activity and bacterioplankton in lakes of the same region, the measurements were density point estimates and would not have captured differences in productivity between lake types.

Very few studies have compared the relative importance of autotrophic and heterotrophic processes in the context of food webs in Arctic lakes. Rautio & Vincent (2007) found that microbial mats on the lake bottom provided the bulk of the carbon sustaining higher trophic levels in shallow Arctic lakes. However, this study was specific to shallow lakes with maximum depth of one meter and may not be applicable to deeper lakes.

Autotrophic processes consume CO_2 and produce O_2 while heterotrophic processes consume O_2 and produce CO_2. Given that the by-products of metabolism of each pathway are opposing allows for a relatively simple methodology of testing for changes in dominant pathways associated with thermokarst activity. Light and dark bottle experiments measure bulk production and consumption of oxygen and are the classic methodology for estimating primary production and respiration (Wetzel & Likens 2000). This method was therefore used to estimate the relative importance of heterotrophic and autotrophic processes in the mesocosm (MC) treatments in this study.

A further consideration as water bodies are affected by permafrost degradation is whether they remain sources or sinks of CO_2. Clear-water oligotrophic lakes are known to be net autotrophic and a sink for CO_2 (Schindler *et al.* 1972), while humic oligotrophic lakes are known to be net heterotrophic and a source of CO_2 (del Giorgio *et al.* 1997). As thermokarst activity increases, it will be important for those considering CO_2 budgets to have a better mechanistic understanding of how thermokarst activity alters the CO_2 balance of affected lakes.

Using an experimental mesocosm approach, the objective of this study is a first ever attempt to assess how varying levels of thermokarst slumping affect pelagic and benthic autotrophic and heterotrophic production. An innovative light and dark bottle measurement system was developed and implemented and used simultaneously with radiolabeled leucine uptake incubations to assess the relative importance of autotrophic and bacterioplankton production.

4.2 Methods

4.2.1 Light and Dark Bottle Theory

Light and dark bottle experiments measure bulk oxygen production and consumption and are used to quantify photosynthesis and respiration at the community level (Warkentin *et al.* 2007). The technique involves measuring the oxygen concentration in light and dark bottles of a known volume before and after an incubation period of a known duration. Autotrophic processes generate oxygen while heterotrophic processes consume it. Since both autotrophic and heterotrophic processes happen simultaneously in the light bottle, net productivity may be measured. If the concentration of oxygen increases over the course of the incubation in the light bottle, autotrophic process dominated, if oxygen concentration decreases, heterotrophic processes dominated. The dark bottle provides an estimate of community respiration as no photosynthesis will occur. Results from the dark bottle are used to account for respiration in the light bottle making it possible to calculate the contribution of primary production to the net oxygen differential. In summary, light and dark bottle experiments provide 3 pieces of information:

1. Net production
2. Respiration
3. Gross primary production.

Unless fractional filtration or pure cultures are used, results from unfiltered light and dark bottle experiments integrate biological community-level responses and are not capable of parsing out which functional groups are most influential to the overall result. Furthermore the procedure makes the assumption that the impact of light to respiration rates is low too negligible, an assumption that some have argued is false (Brooks & Farquhar 1985; Wetzel & Likens 2000). Another criticism associated with this methodology is the potential for fluctuations in primary production over the course of a day (Wetzel & Likens 2000). Given that we are more interested in relative differences between treatments rather than absolute values, no provisions were taken to correct for the potential effect of light on respiration. The issue of fluctuations in primary productivity due to differences in time of day is expected to be minimal since incubations were performed at a consistent time and furthermore, due to the high northern latitudes, the day's apex is long especially through the months of June and July. Additionally, the random variable “block” used in the mixed effects model (see section 2.3, “Statistical Design and Analysis”) incorporates time of day and thus removes error associated with that possible source of variation.

4.2.2 Light and Dark Bottle Design and Measurement System

While the basis of light and dark bottle experiments has remained unchanged over the years, the techniques and equipment used to measure oxygen have changed. Techniques like the Winkler titration, are fairly time intensive and particularly impractical for field applications. Early oxygen sensors, based on coated platinum cathodes, suffered from a number of problems; they were expensive and required a large amount of training to prepare and maintain (Warkentin *et al.* 2007). They also consumed O_2 potentially interfering with the experiment and impacting precession over time. Many methods suffer from a lack of sensitivity. At low temperatures where oxygen saturation is high, or at low productivity levels, small changes in oxygen concentration may be below the detection limit of the method. To compensate, incubation times must be increased at which point changes in community composition over the period of incubation become a concern (Wetzel & Likens 2000).

More recently, the use of “optrodes” (the optical analogue to electrodes) has been developed for a number of applications. With optrodes, the analyte interacts with an indicator whose optical properties are modified in a quantifiable way by the analyte and can thus be related back to its concentration (Wolfbeis 1991). Optrodes have been developed for various ionic species, pH, CO_2 as well as O_2 (Klimant *et al.* 1995). Oxygen optrodes operate by the ability of oxygen to act as a dynamic fluorescence quencher and so reduce the quantum yield of a fluorophore indicator. The oxygen sensor used in this experiment (Fibox Trace by Presense) is capable of determining the concentration of oxygen inside a closed system by reading an inert sensor spot glued to the inside of any transparent container. The sensor spot is made primarily of a matrix impregnated with a fluorophore indicator and held in place with an oxygen-penetrable film. A fibre-optic cable affixed to the outside of the container reads the sensor spot through the glass and relates the information to a hand held device in real-time. The system offers a number of advantages over traditional oxygen methods.

- does not consume O_2

- does not require or depend on flow or have any stirring sensitivity (Wolfbeis 1991)
- no interference from other species such as CO_2 and H_2S or pH which affected electrode-type sensors
- no interference from electromagnetic fields
- no chemicals used
- high sensitivity: detection limit of 15 parts per billion
- allows for a short incubation time thus reducing the concern of community shifts in the bottle during the incubation period

The ease of use *in situ* in combination with independence from chemical use is particularly relevant to studies in pristine environments such as those encountered in the Arctic. The use of chemicals in this environment would likely have precluded our research licensing applications.

4.2.3 Radiolabeled Leucine Uptake Theory and Background

The use of radiolabeled markers to quantify bacterial production evolved throughout the 1980s (Kirchman *et al.* 1985; Simon & Azam 1989). At the onset, the method was labour intensive and generated a lot of radioactive waste in addition to other dangerous chemicals. The method was refined and described by Smith & Azam (1992) whose work has been the basis for most bacterial production studies to date (Karlsson *et al.* 2008; Ask *et al.* 2009b). The technique is inexpensive and accurate while generating minimal amounts of radioactive waste (Smith & Azam 1992). The method is based on microbial uptake of a radiolabelled amino acid from the environment for incorporation into their proteins. Leucine is a good amino acid for this purpose as it is a consistent constituent of all proteins and its addition to the environment does not stimulate or inhibit bacterial production rates (Simon & Azam 1989). This is important as enough radiolabelled leucine must be added to completely dilute the ambient leucine pool. The quantity of labelled leucine taken up during the incubation can be calculated by measuring the radioactivity in the bacteria after the incubation period. The bacteria are isolated from the rest of the sample by centrifugation. The final calculation of bacterial production relies on two constants: the ratio of leucine to total protein and the ratio of protein to carbon. Interestingly, these constants don't change with cell size and so bacterial carbon production can be calculated without knowing cell abundance or volume (Simon & Azam 1989). The radioactive label used in conjunction with leucine is tritium (^{3}H), the isotope of hydrogen. Tritium is a weak beta particle emitter able to penetrate only about 6.0 mm of air, and incapable of passing through the dead outermost layer of human skin (Nucleotide data safety sheet) making it attractive in terms of safety and handling.

4.2.4 Sampling Design

The first full suite of sampling, which included all 12 MCs, plus a lake sample was initiated on 5 July 2010. Chlorophyll and bacterial productivity samples were taken every week while light and dark bottle assays were performed every two weeks thereafter. Equivalent procedures were used for lake samples on all parameters tested within the MCs and were taken at random locations near the MCs at the same depth. Sampling ran from July 5th (week 1) until September 19th (week 11).

Chlorophyll *a*

Water samples for chlorophyll analysis were collected from the middle of each MC at a depth of 50 cm with a Nalgene bottle fixed to a graduated metal rod. Samples were kept cool and dark until our return to the lab in Inuvik where samples were filtered through GFC filters that were then folded and frozen in tin foil. At the end of the experiment, all samples were shipped to the University of Calgary for analysis. Chlorophyll *a* concentrations (corrected for phaeophytin) were obtained after extraction in 90% ethanol, by measuring absorbance at 440 and 680 nm with a Quantech fluorometer (Thermo Fisher Scientific).

Light and Dark Bottle Measurements

Pelagic primary production of each MC was assayed with one dark bottle and two light bottles. Bottles were 500 ml glass BOD bottles with glass stoppers, dark bottles were identical to the light bottles except covered with aluminum tape (Figure 4.2) while tin foil was used to insure that no light entered through the stopper. One light bottle and the dark bottle were suspended with a wooden “T” frame at a depth of 50cm while the other light bottle rested at the bottom of the MC. Only one dark bottle was used, as it would not be subjected to light variation with depth like the light bottles. Each bottle was quickly submerged to its resting depth to insure it was filled primarily of water from that depth. After the bottles were filled, they were brought back to the surface where the glass stoppers and tin foil were put into place before being put back to their respective depths for the duration of the incubation. Initial oxygen concentrations were measured with the Fibox within 5 minutes of being filled, incubations lasted approximately 1.5 hours and standardized to hourly rates.

Benthic primary production was assayed with light and dark acrylic tubes (20.3 cm in diameter and 15 cm long) that had a flat cover on the top and open on the bottom (Figure 4.2).

Figure 4.2. Light and Dark bottles with fibre optic cables protruding (top left). Light and dark benthic samplers (top right and bottom). Samplers were pushed into the sediment with the aluminum poll. A spring-loaded stopper was kept open during installation and was closed thereafter. A small (yellow) motor circulated the water just prior to reading.

Using aluminum poles with depth graduation marks, the tubes were pushed into the lake sediment to a depth of 10cm. The tops of the tubes had spring-loaded rubber stoppers that were kept open as the tubes were pushed into the sediment and closed once the tube was set in place. The tubes also had small electric motors that were controlled with a switch at the surface. The motor was run for approximately 10 seconds before the final measurement only. Light and dark tubes were identical accept dark tubes were rendered opaque with black paint. Figure 4.3 shows all the elements of the light and dark bottle procedures within a MC. A total of 4 MCs could be run simultaneously.

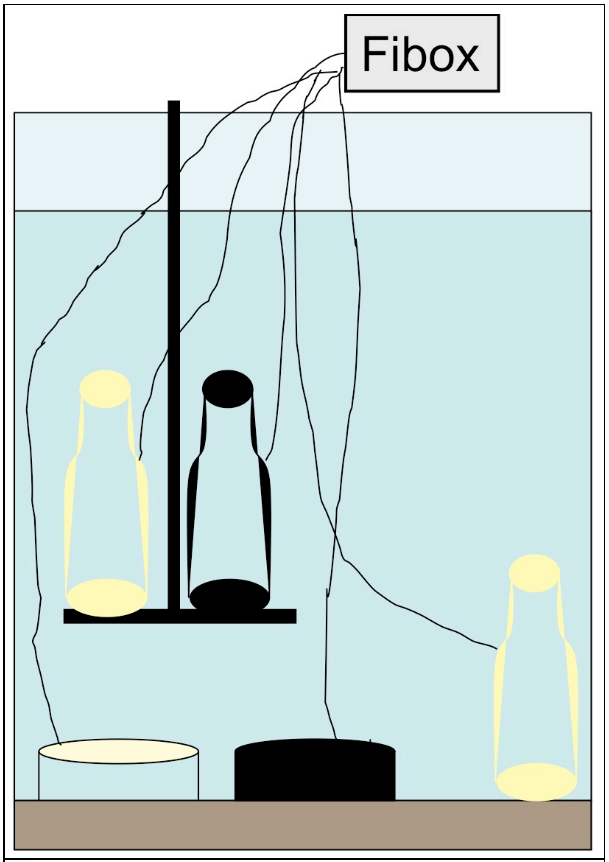


Figure 4.3. All elements of the light and dark procedure within a mesocosm (not to scale).

Net production (NP) results were calculated from the clear containers as final $[O_2]$ – initial $[O_2]$ and therefore negative results indicate a net depletion of oxygen while positive results indicate a net production of oxygen.

Respiration (R) from the dark containers is calculated as initial $[O_2]$ - final $[O_2]$ and since oxygen concentration will decrease from respiration over the period of the incubation, results are positive.

Gross primary production (GPP) is a composite variable calculated by adding net productivity and respiration, thus: $GPP = R + NP$.

All results were converted from oxygen to carbon using the stoichiometric relationship of 0.375 mg O_2 x =1mg carbon derived from the photosynthesis mass balance equation (Wetzel & Likens 2000).

Bacterial Production (BP)

Pelagic: Water samples for pelagic bacterial production (BP_{pel}) were collected from the middle of the MC and integrated from between the surface and 50cm depth with a tube sampler. Samples were put into a pail and poured into a 250ml Nalgene and stored in the dark and on ice until our return to the lab then stored in a refrigerator until processing the following morning. A modified version of the $[^3H]$ leucine incorporation method described by Smith and Azam (1992) was used to measure bacterial production. Four samples of 1.7 ml of unfiltered water from each MC and one lake sample were incubated in darkness in micro-centrifuge tubes in a electronically regulated temperature bath at 17°C for 60 min. For controls (2 replicates per MC), 89 µL of 100% trichloroacetic acid

(TCA) was added before the addition of the isotope and otherwise processed identically to the samples. 35 µL of 50 nM [^{3}H] Leucine (specific activity 5.70 TBq/mmol) was added to all tubes. Incubation was terminated by adding 89 µL of 100% TCA, the samples were vortexed and let sit at room temperature for 20 minutes. Samples were then centrifuged for 10 minutes at 16 000 rcf, and the supernatant discarded. The samples were rinsed by the addition of 1.5 mL of 5% TCA, again vortexed, centrifuged, and the supernatant discarded. Liquid scintillation cocktail (0.5 ml; Ultima Gold XR, Perkin Elmer) was added and the vials vortexed. The ^{3}H activity was measured with a Beckman LS 6500 scintillation counter. Scintillation counts were converted into carbon units according to Simon & Azam (1989). Control values were subtracted from the sample values and were typically less than 10% of the sample value. The concentration of 50nM of [^{3}H] leucine used in the assays was derived from preliminary experimentation using a range of concentrations to ascertain the maximum incorporation of the isotope. Bacterial carbon production was calculated assuming a 7.3 mol percentage leucine in total protein, and a carbon to protein ratio of 0.86 (Simon & Azam 1989).

Benthic: Sediment samples for benthic bacterial production (BP_{ben}) were collected at a random location in the MC with a mini-coring device made from a 60ml syringe from which the tip had been sawn off. The resulting tube (~2cm diameter) and plunger were affixed to a 2x2 piece of lumber and a string attached to the plunger. As the sampler was gently pushed into the sediments (~3 cm) the string attached to the plunger was pulled suctioning the sample into the syringe. The samples were placed into a Ziploc bag and placed into a cooler with ice then placed in the refrigerator upon our return to Inuvik. Samples were processed the following morning. Samples were mixed within the original Ziploc bag. The sediment procedure is a modification of the methods described in Ask *et al*. (2009b). 2g of sediment were placed in a small clean petri dish and 1ml of pure water was added. The sample was stirred to make a uniform slurry. 100 µL of this slurry was added to 1.5ml of pure water, incubated and processed as described for the pelagic samples except with one added wash with 80% ethanol. Results from that assay were extrapolated to the volume of the entire plug, which had a surface area of 3.14 cm$^{2.}$ Final results were subsequently extrapolated to a meter squared. Due to some technical difficulties with the method, benthic sampling started from week three.

4.2.5 Benthic Versus Pelagic and Autotrophy Versus Heterotrophy

The comparison of benthic vs. pelagic and autotrophy vs. heterotrophy, was carried out on an areal basis (m^2) assuming a 1m depth. Pelagic values were multiplied by 1000 (essentially yielding m^3) while benthic values were kept in m^2. Daily rates for autotrophic production were extrapolated from hourly rates multiplied by 12. The mean hours of sunlight over the course of the experiment was 18 hours, 12 hours is roughly 68 % (the probability space within one standard deviation above and below the mean in a normal probability plot) of 18 hours. For heterotrophic production, hourly rates were multiplied by 24.

4.3 Results

4.3.1 Autotrophic Primary Production (PP)

Pelagic: Sediment additions were associated with decreases in rates of PP in the pelagic zone. Probability values from the three parameter mixed effects model including treatment, time and treatment-time interactions are presented in table 4.1 and percentage change relative to the control are presented in table 4.2. Decreases in PP were apparent in decreased concentrations of chlorophyll *a* (Figure 4.4), decreased rates of NP (at both depths) (Figure 4.5) and $GPP_{0.5}$ (“0.5”=at a depth of 0.5m) (Figure 4.6). Rates of GPP_{bot} (“bot”= at bottom) were generally lower than $GPP_{0.5}$ but no significant treatment effect was found.

GPP was weaker than respiration, leading to negative values of NP in all treatments (Figure 4.5). NP and GPP decreased with depth. In the control MCs, the difference between $NP_{0.5}$ and NP_{bot} was not significantly different from the difference between $GPP_{0.5}$ and GPP_{bot} (t-test, t=0.68, p=0.50). In contrast, these differences were significant in the treated MCs (t-test, t=2.23, p=0.028) indicating that decreases in GPP accounted for the decreases in NP in the control but not in the treated MCs. This suggests that respiration rates increased with depth in the treated MCs although they did not vary significantly with treatment (Table 4.1).

There was a significant interaction of time and treatment ($p<0.001$) in chlorophyll *a* concentration (Figure 4.4). This interaction resulted from the control and low treatments increasing in levels throughout the experiment (though low is subdued relative to the control), while the medium and high treatment levels did not vary with time and remained at low levels.

NP_{bot} increased significantly over time while the increase in $NP_{0.5}$ was marginally non significant (p=0.051) (Figure 4.5). Neither GPP nor respiration varied significantly over time.

Benthic: No significant treatment effects were found in NP_{ben}, GPP_{ben}, or R_{ben} however they all changed significantly over time (Figure 4.7).

4.3.2 Bacterial Production (BP)

Pelagic BP decreased significantly with sediment addition and benthic BP increased with sediment additions (Figure 4.8, 4.9). Both pelagic and benthic BP changed significantly over time (Figures 4.8, 4.9).

Table 4.1. Summary table of probability values from a series of three-parameter mixed-effects models for primary productivity and bacterial productivity. The model included. treatment level, time in weeks and an interaction term of treatment and time. Significant p values ($p<0.05$) are shaded with grey. For parameters that varied over time, the direction of the change is in parenthesis after the p value. The final column represents the direction of the trend with increasing treatment level for each parameter.

Para-meter	**Fig. #**	**Significance of Time**	**Contrasts Relative to Control**			**Trend**
			Low	**Medium**	**High**	
Chl'a	4.4	<0.0001 (+)	<0.0001	<0.0001	<0.0001	-
$NP_{0.5}$	4.5	0.051	0.98	0.28	<0.0015	-
NP_{bot}	4.5	0.0017 (+)	0.47	0.022	0.017	-
$GPP_{0.5}$	4.6	0.48	0.62	0.033	0.035	-
GPP_{bot}	NA	0.47	0.89	0.12	0.55	NA
R_{pel}	NA	<0.0001 (-)	0.44	0.80	0.40	NA
NP_{ben}	4.7	<0.0001 (+)	0.24	0.92	0.82	NA
R_{ben}	4.7	<0.0001 (-)	0.34	0.85	0.53	NA
GPP_{ben}	4.7	0.035 (-)	0.53	0.29	0.81	NA
BP_{pel}	4.8	<0.0001 (-)	<0.0001	<0.0001	<0.0001	-
BP_{ben}	4.9	0.0165 (+)	0.027	0.0020	<0.0001	+

Table 4.2. Treatment effect expressed in mean percentage change relative to the control. Calculated as: Treated – Control / Control. Significant changes ($p<0.05$) are shaded with grey.

Process	**Mean % change relative to the control**		
	Low	**Medium**	**High**
Chl'a	-38	-46	-46
$NP_{0.5}$	3	-59	-174
NP_{bot}	-28	-83	-87
$GPP_{0.5}$	-16	-58	-70
BP_{pel}	-37	-46	-51
BP_{ben}	44	112	498

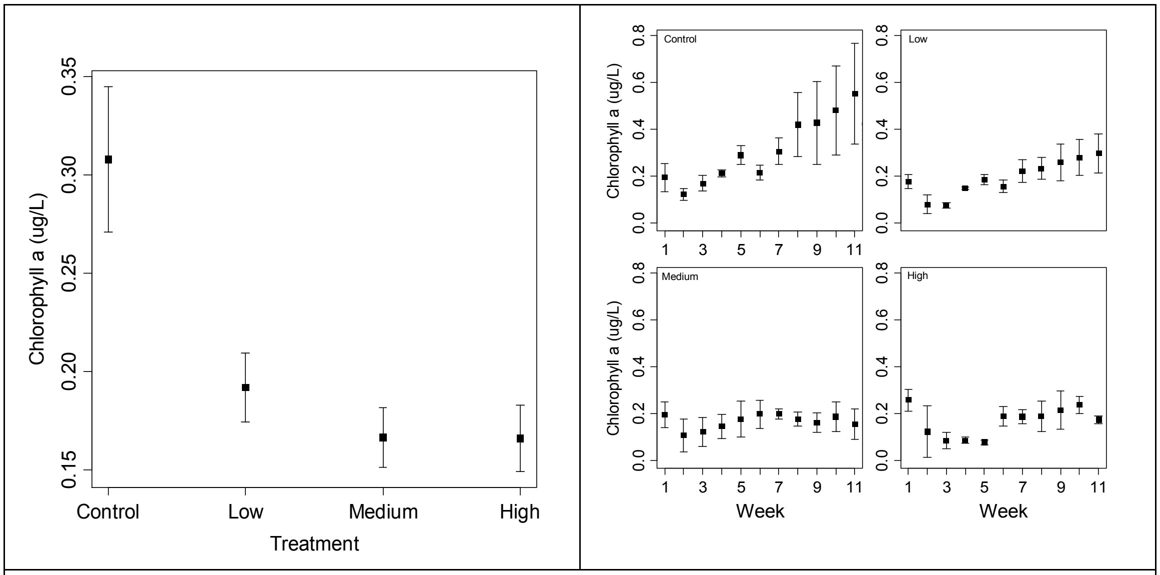


Figure 4.4. Mean concentration of chlorophyll *a*. by treatment level (left) and by treatment level over time (right). All treatment levels decreased significantly relative to the control (p<0.0001). There was a significant interaction between treatment level and time (P<0.05) derived from both the control and low treatment level increasing significantly over time while medium and high treatment levels did not. *Error bars represent the standard error of the mean.

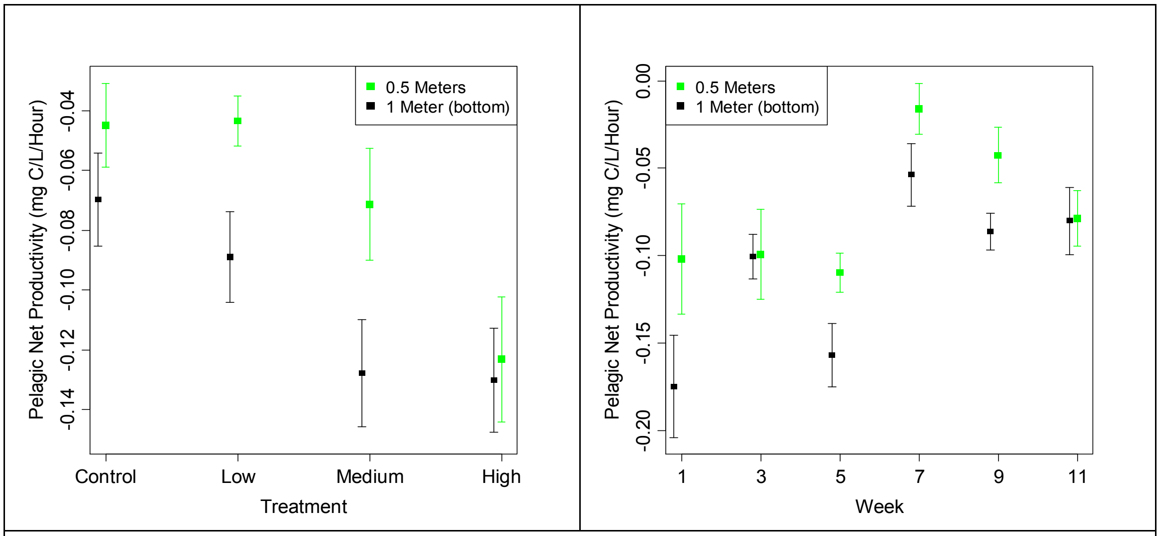


Figure 4.5. Mean net productivity at 0.5 m ($NP_{0.5}$; green) and at bottom (NP_{bot}; black) by treatment level (left) and over time (right). In NP_{bot}, both medium (p=0.022) and high (p=0.017) treatment levels were significantly lower than the control while for $NP_{0.5}$, only the high (p=0.0015) treatment was significantly lower than the control. The increase over time was significant for the NP_{bot} (p=0.0017) but marginally non-significant for $NP_{0.5}$ (p=0.051). *Error bars represent the standard error of the mean.

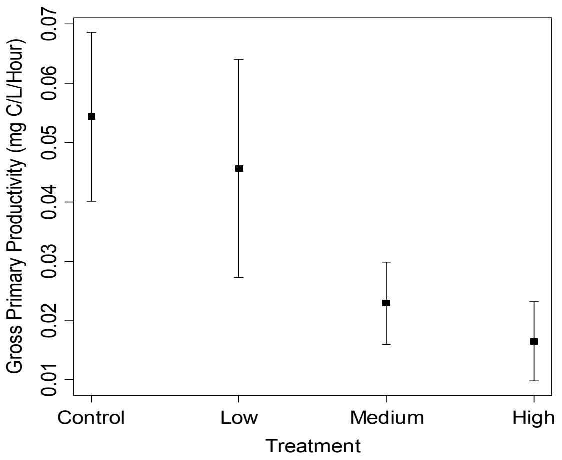
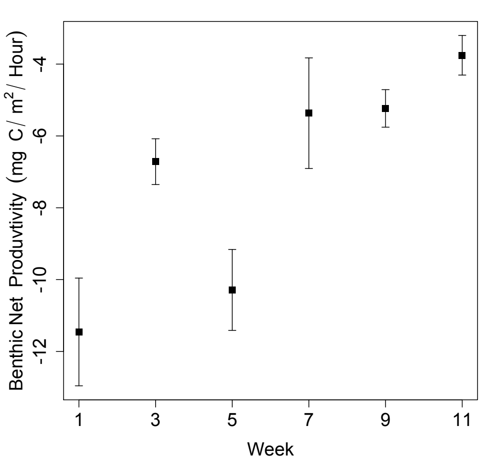
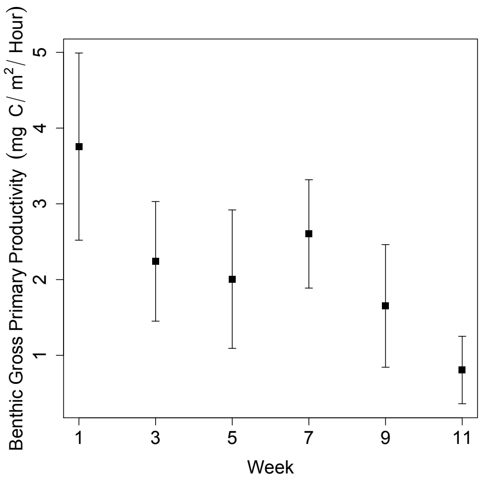


Figure 4.6. Mean rates of gross primary productivity at 50 cm by treatment level. Both the medium (p=0.033) and high (p=0.035) treatment levels were significantly lower than the control. *Error bars represent the standard error of the mean.





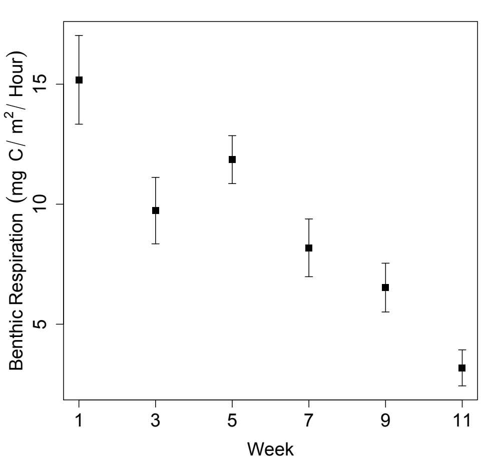


Figure 4.7. Benthic net productivity (top left), benthic gross primary productivity (top right) and benthic respiration (bottom left) changed significantly over time ($p<0.05$). No significant treatment effects were found in these benthic parameters. *Error bars represent the standard error of the mean.

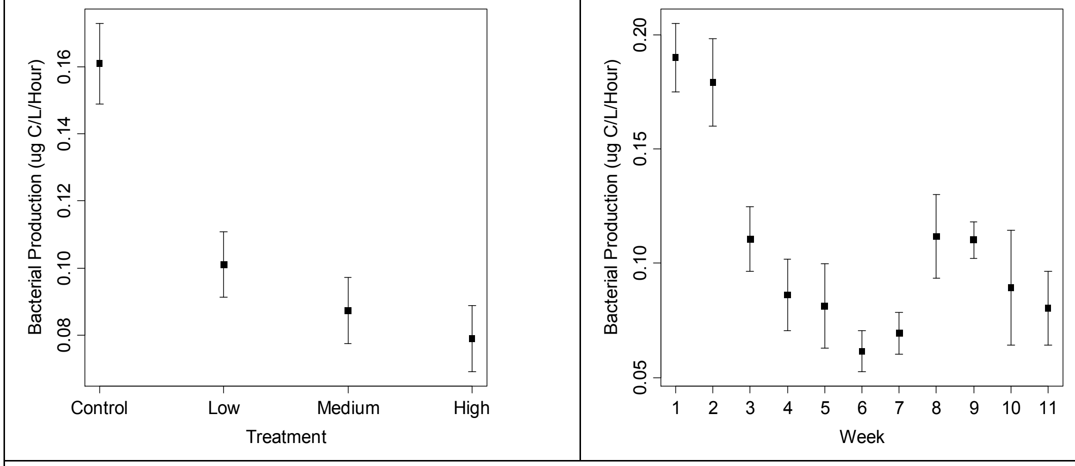


Figure 4.8. Pelagic bacterial productivity at a depth of 50 cm by treatment level (left) and over time (right). All treatment levels were significantly depressed relative to the control ($p<0.0001$). *Error bars represent the standard error of the mean.

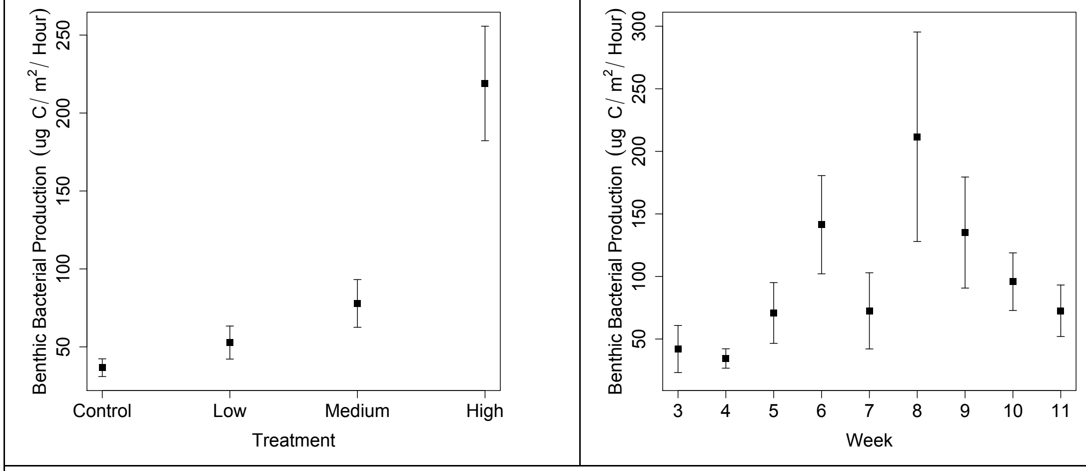


Figure 4.9. Benthic bacterial productivity by treatment level (left) and over time (right). All treatment levels were significantly greater than the control ($p<0.05$). Benthic sampling started on the third week. *Error bars represent the standard error of the mean.

4.3.3 Benthic Versus Pelagic and Autotrophy Versus Heterotrophy

Tables 4.3 and 4.4 summarize primary and bacterial production on an areal basis assuming a 1 meter depth. Autotrophic production was greater than heterotrophic production in both the benthic and pelagic zones regardless of treatment. Pelagic-based autotrophic processes were greater than benthic-based autotrophic processes. In heterotrophic production, pelagic production increased with treatment and surpassed pelagic processes in the high treatment.

Table 4.3. Areal means and standard error of a) pelagic and b) benthic light and dark bottle results. Results are by square meter at one-meter depth.

a) Pelagic

Treatment	**Control** (µ±s.e.) **(mg C/M^2/Day)**	**Low** (µ±s.e.) **(mg C/M^2/Day)**	**Med.** (µ±s.e.) **(mg C/M^2/Day)**	**High** (µ±s.e.) **(mg C/M^2/Day)**
R_{pel}	1355.6 ± 166	1098.7 ± 177	1266.5 ± 196	1598.1 ± 244
$NP_{0.5}$	-538.3 ± 167	-521.9 ± 100	-855.9 ± 224	-1478.4 ± 252
NP_{bot}	-836.8 ± 186	-1067.5 ± 182	-1533.6 ± 215	-1562.4 ± 210
$GPP_{0.5}$	652.6 ± 171	547.5 ± 220	274.8 ± 83	197.6 ± 80
GPP_{bot}	390.3 ± 165	372.3 ± 179	52.9 ± 28	116.8 ± 77

b) Benthic

	All levels pooled (µ±s.e.) **(mg C/M^2/Day)**
R_{ben}	110.6 ± 8.7
NP_{ben}	-86.0 ± 6.5
GPP_{ben}	27.0 ± 4.5

Table 4.4. Bacterial productivity as measured by the radiolabelled leucine incubations.

Treatment	**Control** (µ±s.e.) **(mg C/M^2/Day)**	**Low** (µ±s.e.) **(mg C/M^2/Day)**	**Med.** (µ±s.e.) **(mg C/M^2/Day)**	**High** (µ±s.e.) **(mg C/M^2/Day)**
BP_{pel}	3.9 ± 0.3	2.4 ± 0.2	2.1 ± 0.2	1.9 ± 0.2
BP_{ben}	0.9 ± 0.1	1.3 ± 0.2	1.9 ± 0.4	5.2 ± 0.9

4.3.4 Mesocosm Effects

Table 4.5 lists the dependant variables for which a significant difference was found between lake and control means, potentially indicating a MC effect. All parameters were tested using a two-sample t-test. Significant MC effects were found in the heterotrophic processes of BP_{Pel} and BP_{Ben}. No MC effects were found for any of the autotrophic processes.

Table 4.5. Parameters for which there were a significant differences between lake samples and control MCs.

Parameter	**Lake** (μ ± s.e.)	**Control** (μ ± s.e.)	**P value**	**Effect**
BP_{Pel}	0.043 ± 0.006 ug C/L/Hour	0.16 ± 0.01 ug C/L/Hour	<0.001	+
BP_{Ben}	12.7 ± 3.2 ug C/M^2/Hour	3.7 ± 0.6 ug C/M^2/Hour	0.033	-

4.4 Discussion

4.4.1 Treatment Effects

The results from this experiment provide an improved mechanistic understanding of the potential impacts of thermokarst disturbance on the basal components of the aquatic food web in Arctic tundra upland lakes. Both heterotrophic and autotrophic processes were affected by thermokarst disturbances. In the pelagic zone, both heterotrophic and autotrophic production was negatively impacted by sediment additions. In contrast, benthic heterotrophy was stimulated with increasing sediment addition. No significant treatment effects were detected in benthic autotrophic production. The systems showed little resilience with significant impacts from the lowest treatment level in chl'a concentrations and all BP parameters while significant impacts to the rates of primary production were significant at the medium treatment level. Thermokarst treatment effects were large, with mean chl'a concentrations and GPP down by up to 46% and 70% respectively at the high treatment level. The largest treatment effects were to benthic BP, enhanced by almost 500% relative to the control mesocosms. Except in chl'a concentration, where there was a significant treatment by time interaction, significant time effects likely represented seasonal patterns.

Pelagic: Water chemistry analysis revealed that pelagic P (phosphorus) concentrations increased with treatment. The decreases in pelagic productivity, both autotrophic and heterotrophic, concurrent with nutrient increases suggests that either nutrients are becoming less bioavailable with increased treatment or factors other than nutrients are controlling the overall productivity of these systems (or both). There is significant evidence that humic substances and ions may alter the bioavailability of nutrients through binding and complexing (Hessen & Tranvik 1998). Adsorption of P anions to negatively charged humic substances readily occurs in the presence of cations such as Ca2+ and Mg2+ that are required to overcome electrostatic repulsion between the anions (Tulonen *et al.* 1992). Chapter 3 showed that Ca2+ and Mg2+ were abundant and also positively correlated with treatment. The binding of P to humic substances occurs more readily in lakes with high concentrations of humic substances and in the presence of the correct chemical species (Tipping 2002). Such binding could limit the P availability for both phytoplankton and bacterioplankton (Jones 1992; Waiser & Robarts 1995). For example, prairie lakes with high DOC and ionic concentrations are known to have low chlorophyll relative to their P concentrations (Salm *et al.* 2009). Salm *et al.* (2009) and Waiser & Robarts (1995) found depressed bacterial production for the P concentration of their study lakes. Both studies attribute the lower than expected production to the lack of bio-available P due to binding.

Reductions of heterotrophic productivity might also be attributed to the binding of DOC, their main source of carbon. Similarly to P described above, humic matter (DOC) readily binds to excess cations likely rendering them biologically unavailable as a carbon source (Jones 1992; Tipping 2002). DOC concentrations in this study did not decrease with sediment treatment level. The predictions of decreasing DOC with increasing sediment treatment levels in this study were based on the slump area-DOC relationships observed by Kokelj *et al.* (2005) whose study included old and active slumps. However, given the short time period of this experiment, any newly formed DOC complexes were likely still in suspension.

A possible physical factor that may influence both heterotrophic and autotrophic processes is light. Sediment treatments were associated with increased turbidity and light attenuation coefficients (chapter 3). While the effects of reduced light on autotrophy requires no additional explanations, its effects on heterotrophy are less known. Sunlight is important for heterotrophy in humic lakes because photolysis is required to reduce humic substances to a bioavailable source of carbon (Hessen & Tranvik 1998; Cole 1999) as well as breaking down non-bioavailable nutrient complexes containing P and N (Moran & Zepp 1997). These processes were likely impaired by the increases in turbidity and light attenuation that accompanied increasing sediment additions, further contributing to decreases in pelagic productivity with treatment level.

Benthic: Though an analysis of the sediments from the MCs was never performed for this experiment given the destructive nature of sampling, Mesquita (2008) found that sediment sulfate ion (SO_4^{2-}) concentration was greater in disturbed lakes. It is likely to be the case here as these anions were positively correlated to treatment in the pelagic zone. SO_4^{2-} may stimulate microbial productivity in the sediment by acting as the final electron acceptor in the absence of oxygen (Forsberg 1989). SO_4^{2-} may also spur oxidative bacterial productivity by replacing P as the element adsorbed to Fe which is known as a process by which P is made biologically unavailable (Kalff 2001; Mesquita 2008). With a higher affinity for Fe, an abundance of SO_4^{2-} leaves P available for biological processes within the sediment matrix (Kalff 2001). Bacteria are known to respond dramatically to changes in their chemical environment. Duff & Triska (2000) found that nitrogen and carbon input from vegetated regions into freshwater sediments stimulate aerobic, anaerobic, and chemolithotrophic microbial activity. Similarly, variation in nutrient levels has been found to have strong effects on the species composition of aquatic sediment-dwelling algae (Pringle 1990; Rosemond 1994 reviewed by Palmer *et al.* 2000). Bacterial activity in the sediment contributes to the decomposition of organic matter, which in turn influences remineralization rates and nutrient availability to phytoplankton and macrophytes (Palmer *et al.* 2000). Bacteria also may serve as a direct food source to smaller invertebrates (Bott & Borchardt 1999). Heightened microbial activity in the sediment and resulting nutrient cycling and invertebrate activity may be an important precursor for the dominance of submerged aquatic vegetation as observed in disturbed lakes by Mesquita (2008) and Thompson (2009).

The absence of a significant treatment effect in benthic primary productivity was puzzling in that any existing autotrophic processes would have been suppressed, at least initially by the addition of sediments. If the treated MCs were to recover over time, a significant time by treatment interaction would have been expected. The absence of any significant effects suggests that either benthic primary productivity had recovered by the first sampling date after treatment or random error within the system overwhelmed the detection of a treatment effect. The latter is particularly plausible given the low productivity, even in the control. The recovery of benthic primary productivity would have had to be fast since the first light and dark incubations were two weeks after the treatment was applied. While there were some macrophytes, particularly in block 1, no uniform growth was observed across all the MCs. Further exploration of the impacts to benthic primary productivity with longer incubation times and perhaps a different methodology is required and would likely necessitate a multi-year experiment to allow for the potential colonization of higher order submerged vegetation and invertebrate community.

4.4.2 Benthic vs. Pelagic and Autotrophy vs. Heterotrophy: Addressing the Hypothesis

The hypothesis that the MCs would shift from a heterotrophic-pelagic dominated food web to an autotrophic-benthic dominated food web with increasing sediment addition was not supported by the findings since a heterotrophic-pelagic dominated state was never found in this experiment. On the contrary, pelagic GPP was two orders of magnitude greater than BP in the control. This is likely because the supposition of the dominance of pelagic heterotrophy was based on whole lake estimates where both primary and heterotrophic production were integrated throughout the water column in lakes much deeper than the MCs (Jansson *et al.* 2000; Karlsson *et al.* 2008; Ask *et al.* 2009a). These studies found that heterotrophic production was greater than autotrophic production, particularly in lakes with high concentrations of DOC (this experimental lake would be considered middle to high concentration).

Given that heterotrophic processes may occur independently from light, integration of production at greater depths would result in an increase of heterotrophic production relative to autotrophic production. Therefore, heterotrophic production is likely under represented relative to autotrophic production in this experiment because the MCs were installed at a shallow depth, completely within the photic zone. The discrepancy between the light bottle at 50 cm depth and the bottom suggest that the photic zone was relatively thin (GPP decreased up to a maximum of 80% in the medium treatment from a depth of 0.5 m to 1 meter, while the overall average was ~40%). There was also evidence of increased heterotrophic activity with depth in the treated MCs as a respiration gradient was found between the two depths. Together, this suggests that increased MC depth would increase the integrated estimates of heterotrophic production relative to autotrophic production. However applied to shallow lakes, results of this experiment support early models of lacustrine food webs where primary production is the dominant source of carbon for upper trophic levels.

Negative NPP values across all treatments and control in both benthic and pelagic environments showed that the systems were net heterotrophic. While this seems counterintuitive given the apparent strength of pelagic PP, bacterial efficiency rates may be as low as 1% meaning that bacterioplankton consume a great deal of carbon relative to the amount of carbon used to proliferate (del Giorgio *et al.* 1997). Furthermore, respiration rates that factor into NPP are at the community level and include, among others a large zooplankton community. Pelagic secondary production will be explored in the next chapter.

4.5 Conclusion and Future Recommendations

In general, the addition of thermokarst sediments resulted in decreases in pelagic autotrophic and heterotrophic production while benthic heterotrophic production increased. Furthermore, decreases in pelagic production even as nutrients increased, indicate that factors other than nutrient availability govern the observed reductions in pelagic productivity. These other factors are likely to include the chemical binding of nutrients, DOC and light availability. Because trends were shown to differ by environment (benthic vs. pelagic), how a lake is impacted by permafrost degradation likely depends as much on physical parameters such as depth and volume to benthic area ratios as the geochemical properties of the impacted lake. For example the impact of slumping to shallow lakes, in which benthic production is known to be the most important carbon support for food webs (Vadeboncoeur *et al.* 2003; Rautio & Vincent 2006) will be different than the impact to deep lakes with pelagic-based food webs. The dramatic increase in benthic heterotrophic activity and the absence of any significant changes in benthic primary production were unexpected relative to observations by Mesquita (2008) who reported that slumped lakes had greater benthic primary productivity than unslumped lakes. Results showing stimulated benthic heterotrophic productivity raises the provocative possibility that such increased activity is the first step in a succession leading to the proliferation of benthic production as observed in slumped lakes.

Though a great deal of insight into how lakes may be impacted by retrogressive thaw slumping has been achieved in this study, a longer (inter-annual) experimental period is recommended to better understand how these systems change over time. Reductions in turbidity and the settling of larger particulate complexes in the water column that would likely occur after a season under ice would certainly have revealed a better understanding of the effects of permafrost thaw slumping in these cryospherically dominated systems. Many of the significant time effects found in this study were seasonal, yielding little information of treatment effects over time. It is likely that many of the effects of a major change in such an environment develop over multiple years, especially when the environment is frozen for a better part or the year. For example, the succession of the benthos of new reservoirs is known to be a multi-year process even in climates without ice cover (Voshell & Simmons 1984).

A further recommendation for this study concerns the sensitivity of the Fibox oxygen meter. In some occasions, the difference between the starting oxygen concentration and the final concentration was very close to the precision limits of the machine (15 ppb). It is recommended that longer incubation periods be used to allow for larger differences to establish. Furthermore, given that the Fibox is very sensitive to temperature, a minimum of two Fibox thermometers, one for the benthic and one for pelagic samplers, is recommended. Also in some instances, initial measurements were completely out of line in comparison to the other bottles filled at the exact same time in the same location. It is possible that the bubbling action of the water entering the bottle oxygenates the water or leaves an air bubble on the sensor spot. Given this, it is also recommended to develop a system that allows the water into the bottle without bubbling (a stopper with two tubes- in and out) or allowing a resting period after the bottle is filled to allow oxygen concentrations to equilibrate to environmental levels before capping the bottle and starting the incubations. Further testing of the benthic tube samplers is also recommended. Longer incubation times and the effect of gases trapped in the sediment released as the tube sampler was pushed into the sediments (occasionally observed) should be explored. Proofing the tube method with a C^{14} method is recommended.

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CHAPTER 5: ZOOPLANKTON PRODUCTION

5.1 Introduction

Arctic aquatic ecosystems are highly susceptible to alterations resulting from changes in climate and a key knowledge gap remains in having a mechanistic and predictive understanding of the effects of climatic warming/variability on the structure and function of aquatic food webs (Hobbie *et al.* 1999; Flanagan *et al.* 2003; Wrona *et al.* 2006). A growing range of climate models and scenarios predict an increase in temperature in the western region of the Canadian Arctic (ACIA 2004; IPCC 2007; Lemmon *et al.* 2008), resulting in several corresponding 1st order physical and geochemical effects. These include, for example, increased precipitation, and changes in the cryosphere related to alterations in lake and river ice regimes, distribution of snowpack, and permafrost thawing (Prowse *et al.* 2006; AMAP 2011). Furthermore, such 1st order impacts at the landscape level are predicted to affect nutrient, carbon and other geochemical inputs to freshwater systems from the terrestrial surroundings (Rouse *et al.* 1997; Wrona *et al.* 2006), resulting in changes in primary and/or bacterial production within aquatic systems and having cascading implications on higher trophic levels. Flanagan *et al.* (2003) examining nutrient-productivity relationships in North American lakes predicted that arctic lakes could take a significant leap in productivity if these systems increased in temperature and nutrient concentrations as predicted by climate models.

Understanding trophic-level and ultimately ecosystem-level responses to changes in the physical and chemical environment requires an integrated approach. Determination of the processes and mechanisms associated with the trophic impact of “top-down” vs. “bottom-up” control (i.e., the trophic cascade hypothesis *sensu* Carpenter *et al.* (1985) on lake productivity requires a combination of empirical and experimental (manipulation) approaches. For example, the effects of physical and chemical changes on primary production (i.e., bottom-up control) may go unnoticed if consumer biomass responds quickly to changes in their resource supply. In a nutrient enrichment experiment in large enclosures, O’Brien *et al.* (1992) found that pelagic primary production as measured by chlorophyll *a* (chl’a) concentrations did not change significantly, while zooplankton densities increased with treatment. This is an example of the “exploitation model” of food web theory, which predicts that changes to a basal resource will affect the top trophic level (Oksanen *et al.* 1981). Furthermore, the model predicts that the biomass of primary producers will increase only in odd-linked food chains (Oksanen *et al.* 1981; Persson *et al.* 1992).

Zooplankton is a critical link to upper trophic levels in aquatic food webs (Wetzel & Likens 2000; Kalff 2001). Some zooplankton feed selectively (i.e., raptorial feeding) while others are filter feeders. Collectively, zooplankton may exert strong grazing pressure on phytoplankton and bacterioplankton and may clear as much as 4 times the volume of a lake in a single day (Porter 1977). Daphnia and other Cladocera typically have the highest clearing rates and can account for 80% of the zooplankton community grazing rate (Porter 1977). Given their potential influence on phytoplankton standing crop, it's not surprising that zooplankton are often the target of biomanipulations intending to decrease phytoplankton density. While much of the early literature focuses on phytoplankton as the main food source for zooplankton (e.g., Pearsall 1930; Pennington 1941), more recent research has also identified bacterioplankton as an important source of carbon for zooplankton either by direct grazing or indirectly via heterotrophic nanoflagelates (Wylie & Currie 1991; Jansson *et al.* 2000).

There has been relatively little work done on assessing the role(s) of Arctic zooplankton in affecting nutrient-productivity relationships. An analysis of Arctic lakes by Swadling et al. (2000) found that chloride, temperature and silica were the only abiotic parameters that significantly affected zooplankton community composition, explaining a total of 25 % of the variation. They concluded that food web interactions were likely responsible for the remaining variation. Thompson (2009) characterized three types of lakes associated with SRTS, lakes with active slumps, lakes with stabilized slumps and lakes unaffected by SRTS. She found that zooplankton abundance was lowest in stable lakes, which also had the highest phytoplankton densities of the three lake types. Unaffected lakes had the highest zooplankton densities with pelagic chl'a concentrations between those of stable and active lakes. In contrast, no difference in bacterioplankton cell density across lake types was found (Thompson 2009). These studies underscore the importance of obtaining an improved understanding of the affects of permafrost melt on nutrient-productivity-zooplankton relationships and the implications to higher trophic levels and ecosystem structure and function.

The objective of this study is to use an experimental (mesocosm) approach to assess the responses, relative importance and role(s) of the zooplankton community (structure, density and biomass) in relation to sediment additions mimicking shoreline retrogressive thaw slumps (SRTS) associated with permafrost melt. Using fishless mesocosm systems, zooplankton are consumers as well as top predators, phytoplankton and bacterioplankton are the producers while nutrients are the resource. A primary hypothesis being tested is whether observed changes in productivity at the basal level of the food web leads to concomitant productivity changes at upper trophic levels, as predicted by the exploitation model (Oksanen *et al.* 1981). Based on results described in Chapter 4, it is also predicted that zooplankton secondary production should decrease with increasing sediment additions as observed for pelagic productivity.

5.2 Methods and Zooplankton Community Composition

Zooplankton samples were taken weekly with a tube sampler measuring 50cm long and a volume of 1 litre. A sample from a mesocosm (MC) consisted of three subsamples taken from random locations in the MC and mixed into a bucket. The sample water was then passed through a 63μm Nitex screen held in place between two pieces of 6 inch PVC pipe. A spray bottle with fresh water was used to remove the filtrate from the screen into a wide-mouth jar. Samples were kept on ice in a cooler until our return to the lab where an equal volume of 11% formalin was added to the sample. Samples were transferred to a 70% ethanol mixture for identification down to species according to Brooks (1957, 1959). All individuals in the sample were counted, results were divided by 3 to obtain a per litre density estimate.

The length of Copepoda and Cladocera were measured using a Leica M205 microscope with digital camera and accompanying Leica software. Lengths were converted to body mass (dry weight) using species-specific length to body mass regression coefficients as per McCauley (1984) and Culver *et al.* (1985). As length to body mass coefficients for *Daphnia middenorffiana* were not found in the literature, coefficients for *Daphnia pulex* were used instead as D. *pulex* has a similar range of body mass as D. *middenorffiana* (Peterson, Hobbie, & Haney 1978). Rotifer size was not measured due to limited time and resources therefore no body weight or biomass data are available for this taxonomic group.

5.3 Results

5.3.1 Changes in Composition

Zooplankton were categorized into three broad taxonomic groups: Cladocera, Rotifera and Copepoda. A multivariate analysis of variance (MANOVA) on the percentage composition of taxon density (individuals per litre) within each group was conducted to determine if group composition changed significantly with treatment. Data were arcsine transformed to deal with the bound nature of percentage data (Crawley 2007). A significant result ($p<0.05$) for a given species (last column of Table 5.1) indicates that the species composition changed significantly with treatment. The p-value for the overall MANOVA (last row of each group, shaded in grey) indicates whether or not overall changes in taxonomic composition with treatment were statistically significant for the group.

Table 5.1. Dominant zooplankton groups and breakdown of composite taxa including their overall percentage by density within the group as well as their percentage by treatment. The table includes probability values from a MANOVA performed on each group. The right column indicates the significance of a single taxon change with treatment while the last row in each group (shaded in grey) indicates the significance of the taxon changes for that group.

Group	**Taxon**	**Group %**	**Treatment level %**				**MAN-OVA P Value**
			control	**low**	**med.**	**high**	
Cladocera	Daphina mid.	80	56	91	84	85	0.001
	Bosmina longirostris	11	10	7	15	12	0.80
	Polyphemus pediculus	9	34	2	1	3	<0.001
MANOVA model of species composition for Cladocera: P=0.0001							
Rotifers	Kellicottia longispina	57	50	70	60	52	0.20
	Asplancha spp.	25	14	14	27	16	0.047
	Keratella cochlearis	18	36	16	13	32	0.50
MANOVA model of species composition for Rotifers: P=0.13							
Copepoda	Nauplii	62	61	65	55	71	0.053
	Diacyclops thomasi	20	18	20	22	21	0.90
	Lep. Pribiolofensis	10	13	8	12	5	0.17
	Cyclops scutifers	8	8	7	11	3	0.043
MANOVA model of taxonomic composition for Copepoda: P=0.14							

Within the Cladocera assemblage, percentage taxon composition changed significantly with treatment including D. *middenorffiana* in which the control appears depressed relative to the treated MCs and P. *pediculus* where all the treated MCs are depressed relative to the control. Taxonomic composition of rotifers and Copepoda did not change significantly with treatment ($p > 0.05$), though some individual taxa did change significantly with treatment (i.e., *Asplancha spp., Cyclops scutifers*). However, these taxa did not exhibit any consistent trends with treatment suggesting that treatment effects are not likely responsible for the observed differences.

5.3.2 Density/Biomass/Body Weight

Mixed-effects model analyses were conducted as described in section 2.3 ("Statistical design and analyses"). To conform to assumptions of normality, density data were log +1 transformed. Results of the mixed-effects models were performed on density, biomass and body weight and are summarized in Table 5.2.

Density: The density of both Copepoda and Cladocera increased significantly with treatment (Table 5.2, Figure 5.1), with densities in the medium and high treatments significantly greater than the control. Rotifers showed no consistent pattern with treatment and no significant treatment effects were found. It was also observed that the average density of all groups decreased significantly over time.

Biomass: Although Copepoda remained the most abundant taxa throughout all treatments, Cladocera average biomass was greater (Figure 5.2). Cladocera biomass increased significantly with treatment, while Copepoda biomass showed no significant trend (Table 5.2, Figure 5.2). Both Cladocera and Copepoda average biomass decreased significantly over the 12 week period of the experiments.

Body Mass: Cladocera in all sediment treatments had greater mean body mass compared to the control. In contrast, for the Copepoda, treatment was associated with decreased body mass (Table 5.2, Figure 5.3). The body mass of Cladocera increased significantly over time while the body mass of Copepoda decreased. The right panel of Figure 5.3 shows the treatment impact to body mass in units of standard deviations of the control. Calculated as:

$$x - \bar{x}_{Control} \big/ Std_{Control}$$

Treatment effects are also presented in percentage change relative to the control in Table 5.3.

Table 5.2. Summary table of probability values of zooplankton density, biomass and body mass that were tested with a three-parameter mixed-effects model. The model included: treatment level, time in weeks and an interaction term of treatment and time. Significant p values (p<0.05) are shaded with grey. The direction of the change over time is in parenthesis after the p value in the time column. The "Trend" column indicates the direction of the trend with increasing treatment level.

Group	**Fig. #**	**Significance of Time**	**Contrasts Relative to Control**			**Trend**
			Low	**Medium**	**High**	
Density						
Cladocera	5.1	<0.0001 (-)	0.85	0.0037	0.0017	+
Copepoda	5.1	<0.0001 (-)	0.32	0.018	0.0030	+
Rotifers	5.1	0.0001 (-)	0.28	0.94	0.52	NA
Biomass						
Cladocera	5.2	<0.0001(-)	0.15	0.0020	0.0027	+
Copepoda	5.2	<0.0001(-)	0.75	0.16	0.054	NA
Body mass						
Cladocera	5.3	0.026 (+)	0.0003	0.0034	<0.0001	+
Copepoda	5.3	0.0015 (-)	0.026	0.063	0.27	-

Table 5.3. Treatment effect expressed in mean percentage change relative to the control. Calculated as: (Treated – Control) / Control. Significant changes (p<0.05) are shaded with grey.

Group/parameter	**Mean % change relative to the control**		
	Low	**Medium**	**High**
Density			
Cladocera	-3%	76%	110%
Copepoda	-1%	55%	52%
Biomass			
Cladocera	55%	132%	199%
Copepoda	-1%	43%	46%
Body mass			
Cladocera	145%	82%	243%
Copepoda	-27%	-20%	-14%

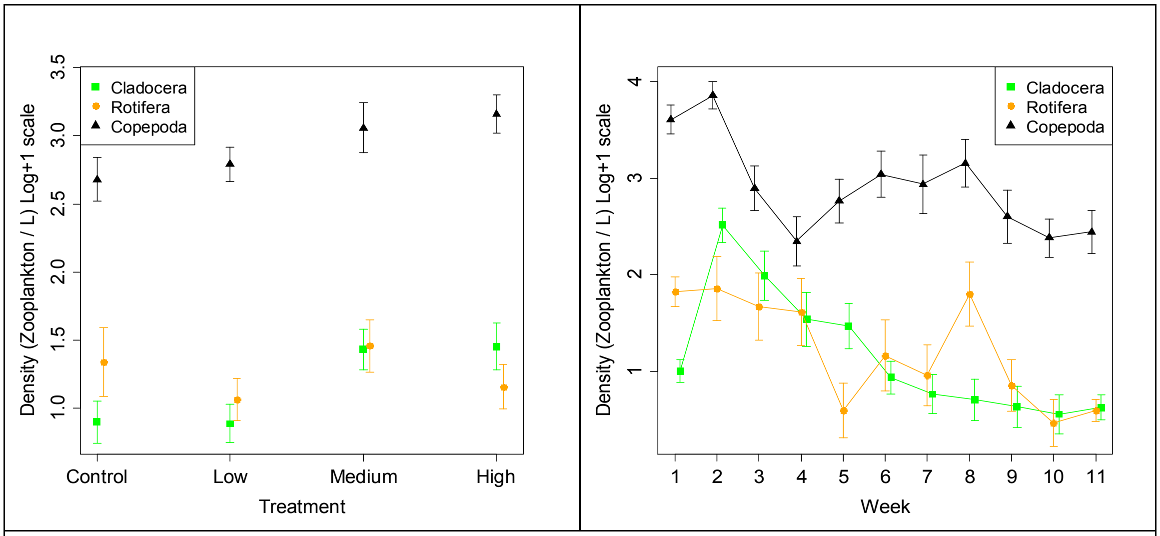

Figure 5.1. Mean density of 3 zooplankton groups by treatment level (left) and over time (right). For the Cladocera and Copepoda, the density in both the medium and high treatment levels were significantly greater than the control ($p<0.05$). There were no significant treatment effects on rotifer density. The density of all groups declined significantly over time. *Error bars represent the standard error of the mean.

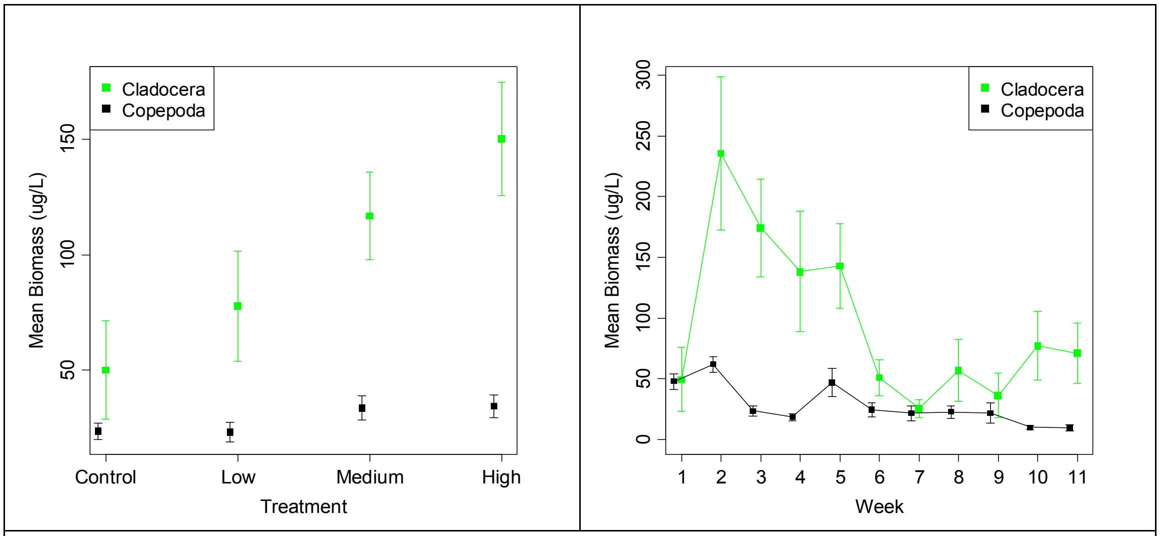

Figure 5.2. Mean biomass of Cladocera (green) and Copepoda (black) by treatment level (left) and over time (right). For the Cladocera, both the medium and high treatment levels were significantly greater than the control ($p<0.05$). There were no significant treatment effects on Copepoda biomass. Biomass in both groups declined significantly over time. *Error bars represent the standard error of the mean.

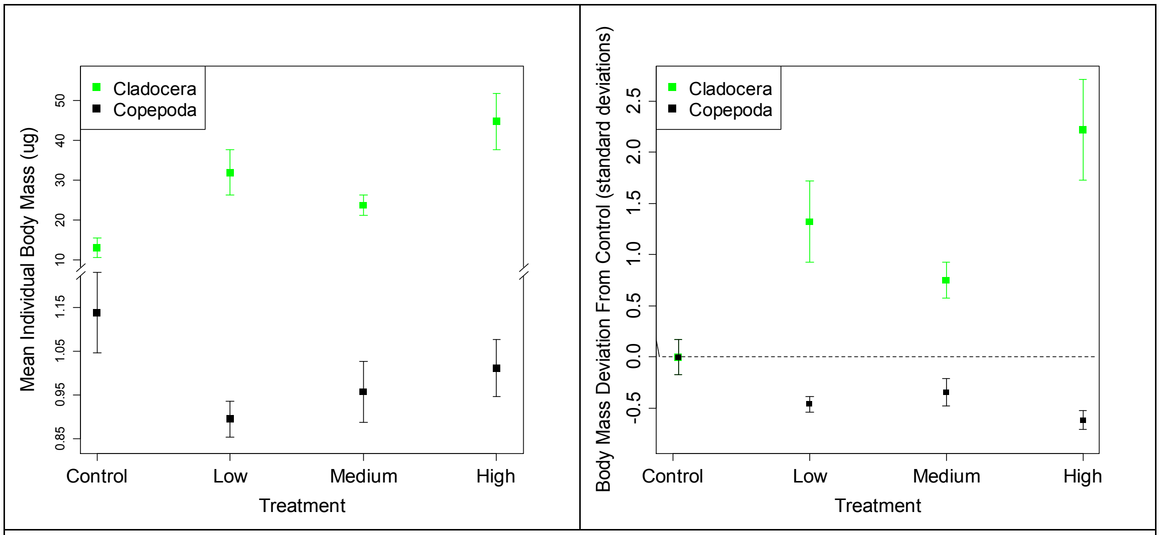

Figure 5.3. Left: Mean body mass for Cladocera (green) and Copepoda (black). For Cladocera, all treatment levels were significantly greater than the control. For Copepoda, the low and medium treatment levels were significantly smaller than the control. *Note the broken axis. **Right**: Changes in body mass relative to the control in standard deviations of the control for Cladocera (green) and Copepoda (black). *Error bars represent the standard error of the mean.

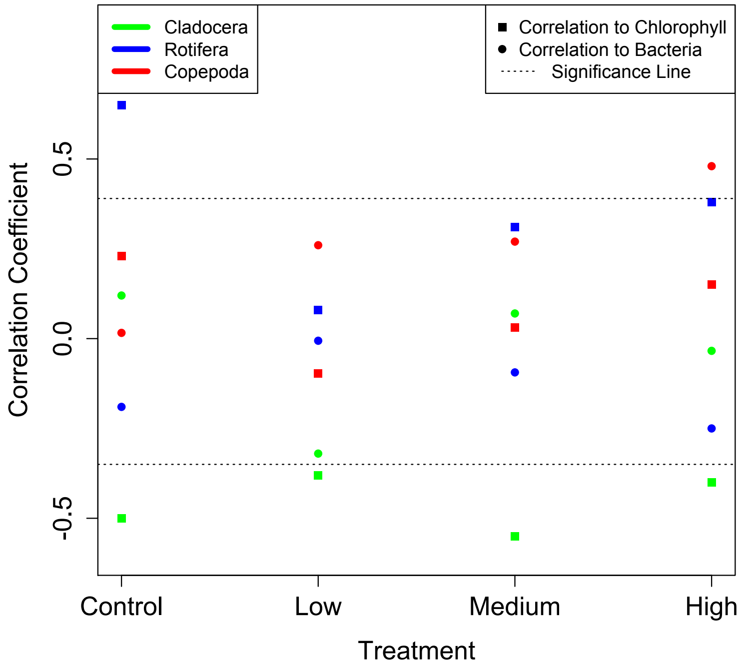

Figure 5.4. Pearson's correlation coefficients of zooplankton density and their potential resources. Correlation coefficients of zooplankton with chlorophyll'a are represented by squares while circles represent correlations between zooplankton and heterotrophic production. Zooplankton groups are colour coded. Correlation values more extreme than +/-0.38, marked by the black dotted line, are statistically significant ($p<0.05$).

5.3.3 Correlation to Potential Resources

Figure 5.4 shows Pearson's correlation coefficients (r) between zooplankton density and their potential resources in the pelagic zone. Correlation coefficients with autotrophic resources are represented by squares while circles represent correlations with heterotrophic production. Correlation values more extreme than +/-0.38, marked by the black dotted line, are statistically significant ($p<0.05$).

Chlorophyll a (Chl'a): Cladocera density was negatively correlated to water column chl'a levels across all treatments. Rotifer density was significantly positively correlated to chl'a levels in the control MCs, but not in any of the sediment treatment levels. Copepoda density was not significantly correlated to chl'a levels in either the control or treatment MCs.

Bacterial production (BP): The correlation between Copepoda and pelagic BP increased with treatment and was significantly correlated in the high sediment treatment. There were no other apparent trends with pelagic BP with the other groups.

5.4 Mesocosm (MC) Effects

Student t-test between the control MCs and the lake showed MCs to have a significant positive effect on Cladocera density ($t=2.15$, $p= 0.041$). Average density of Cladocera in the lake was 0.71 individuals per litre compared to 2.2 individuals per litre in the control MCs. Specifically these differences were the result of significantly lower densities of *Polyphemus pediculus* and *Bosmina longirostis* in lake water samples, while no significant differences were found in *Daphnia middenoriffina* density or biomass. No other significant MC effects were found for any of the other zooplankton groups of for chl'a ($p>0.05$).

5.5 Discussion

The addition of permafrost-related sediments from the terrestrial landscape had a significant effect on the zooplankton community structure and secondary production. The density of Cladocera and Copepoda increased with increasing sediment treatment, and average Cladocera biomass also increased. Cladocera biomass was greater than Copepoda biomass across all treatments and constituted ~70% of the total zooplankton biomass. Treatment was also associated with changes in mean body mass. Cladocera mean body mass increased significantly with treatment while Copepoda mean body mass decreased.

The prediction that secondary production would decrease with increasing treatment was based on the supposition that a decline in primary productivity was related to the deterioration of nutrient bio-availability and environmental (chemical/physical) conditions with increasing treatment. The experimental results do not support this tenant since average zooplankton biomass was found to increase with sediment treatment levels. This suggests that grazing pressure from the Cladocera is principally responsible for the observed decrease in chl’a concentrations rather than nutrient limitation or other abiotic factors inhibiting primary productivity. While deteriorating environmental conditions may also be proposed as a factor that depressed primary productivity with treatment, it cannot be considered the primary factor since zooplankton biomass would also have decreased. This food web dynamic is an example of a trophic cascade. Trophic cascades can be defined as “reciprocal predator-prey effects that alter the abundance, biomass or productivity of a population, community or trophic level across more than one link in the food web” (Pace & Cole 1994).

Evidence of trophic coupling has been documented in other studies between Cladocera and chl’a, Rotifers and chl’a and between Copepoda and bacterial density (Dolan & Gallegos 1991; Berninger *et al.* 1993; Ware & Thomson 2005). A negative correlation between Cladocera and chl’a has been described by McCauley *et al.* (1988), Beisner *et al.* (1997) and others and reflects the strong grazing pressure that Cladocera can exert on the edible phytoplankton community. The coupling remained strong regardless of treatment indicating that environmental factors that influence phytoplankton growth are likely to cascade and affect Cladocera with proportionate impacts. For Rotifera, density was positively correlated to chl’a in the control but was not in any of the other treatment levels suggesting that the trophic coupling between the two was undone by the addition of sediments. Conversely, a weak correlation between Copepoda and BP observed in the control mesocosms increased with increasing treatment, resulting in a strong positive correlation with BP at the high treatment level.

5.5.1 Cladocera

The Cladocera community was numerically dominated by the species *Daphnia middenorffiana* (D.mid), and also accounted for 80% of the species assemblage.

Interestingly, the various Cladocera species were affected differently by the sediment treatments. D. mid. density increased positively with increased sediment loading, while *Polyphemus pediculus* displayed a negative association with increasing sediment loading, and B*osmina longirostris* showed no effect. In terms of biomass, *P. pediculus* and *B. longirostris* collectively comprised less than 1% of the Cladocera group as their mean body mass is approximately 1/25th that of D.mid.

There are several possible explanations as to why D. mid body mass increased with increased sediment loadings. The majority of the literature surrounding zooplankton body size focuses on the effects of "top-down" control, in particular, planktivorous fish that target large-bodied zooplankton (Carpenter & Kitchell 1996; Hershey *et al.* 1999). However, since the experimental lake and MC treatments were fishless and no other invertebrate predators were observed, "top-down" control does not appear to be a plausible explanation for the observed responses. The alternative is a "bottom-up" explanation. Perhaps the physical and chemical environment of the treated MCs has changed the community composition, size structure and/or edibility, and energetic quality of the phytoplankton, which in turn favours larger Daphnia species. In addition, inter-specific competition within the Daphnid assemblage could also have resulted in a suppression of smaller-bodied species. Regardless of the cause, the observed shift in size structure can have ecosystem-wide consequences as exemplified by Vanni (1987), Crowder et al. (1987) and others, highlighting the importance of thermokarst activity in affecting aquatic ecosystem productivity, trophic status and state.

Larger body-sized Daphnia have disproportionally greater clearance rates and are able to consume larger particles (Brooks & Dodson 1963). The presence of increasingly large Daphnia with treatment extends a potential "top-down" explanation for the decreased concentrations of chl'a with treatment in this experiment (Chapter 4). Moreover, the significant negative correlation between Daphnia and chl'a across all treatments further supports this explanation.

As well as consuming phytoplankton, Daphnia are known to be strong planktonic bacteriovores due to their ability to filter a large spectrum of particle sizes (Jurgens 1994). Bacterioplakton are at the lower boundary of ingestible particle sizes for Daphnia and the retention of small particles depends on the species and size of the animal (Jurgens 1994). This suggests that as individual body mass of Daphnia increases, their efficiency as bacteriovores would decrease. This may also have ecological consequences that could cascade up and down the food web. The effect of the release of bacteria from grazing pressure could include a greater abundance of bacterioplankton and increased consumption of bacterial resources such as dissolved organic carbon (DOC) or the proliferation of other bactivorous zooplankton. However, in this study, there is no evidence of correlation between Cladocera density, biomass and body size with pelagic BP.

5.5.2 Copepoda

The Copepoda community was dominated by nauplii (~65% of Copepoda biomass) and as a group, responded more uniformly to sediment treatment levels than observed for Cladocera. Copepoda density increased with increasing treatment level, while mean body mass decreased, indicating a possible bioenergetic trade-off (Townsend & Calow 1981). Evidence of a bioenergic trade-off is further supported by the observation that the decrease in body mass was counterbalanced by the increase in density and resulted in a maintenance of biomass across treatments.

The changes observed in Copepoda density and biomass associated with increased sediment additions are likely not as influential to the ecosystem compared to Cladocera given the large difference in biomass especially with respect to secondary impacts to higher trophic levels. However, they are numerically dominant and due to their smaller body size, have greater specific energy requirements per unit of biomass than Cladocera (Kalff 2001). As such, Copepoda likely exert considerable “top-down” pressure on the microbial component of the food web and may represent a significant allochthonous carbon outlet to upper trophic levels (Ederington *et al.* 1995).

5.5.3 Potential Implications For Higher Trophic Levels

The exploitation model states that the number of trophic levels increases with productivity (Oksanen *et al.* 1981; Fretwell 1987). Results from this chapter suggest that permafrost related sediments represent a source of enrichment. As such, slumped lakes are more likely to host higher trophic levels including fish where colonization is possible. Apart from a direct enrichment effect, increases in the size structure of Cladocera, the dominant zooplankton group, may also increase the potential of an aquatic ecosystem to host fish. A number of studies have linked fish recruitment success with the size of available zooplankton (Crowder *et al.* 1987; Mills *et al.* 1989; Miller *et al.* 1990; Bremigan & Stein 1994). In these studies, the presence of large-bodied zooplankton was found to directly increase recruitment success of fish. Bremigan and Stein (1994) proposed a more subtle effect. They found that lakes dominated by large-bodied zooplankton differed in dominant fish species from lakes dominated by small zooplankton. They experimentally determined that this was a "bottom up" affect resulting from the differential success of larval foraging of different fish species on zooplankton of different size. This suggests that zooplankton size may not only influences recruitment success but ultimately determine the community composition of fish.

5.6 Conclusions

Additions of permafrost-related sediments were associated with

- increases in secondary production-in particular via increases in Cladocera
- shifts in the size structure of the zooplankton community
- dietary shifts for Copepoda and rotifers.

These results likely reflect fundamental shifts in the basal components of the food web and suggest that the addition of permafrost related sediments may have far-reaching effects on the structure and function of affected aquatic ecosystems.

The results presented here underscore the importance of investigating multiple trophic levels when exploring questions of productivity. As such, studies should tailor their sampling regime to their specific questions and include all trophic levels that may surround the specific questions. For example in this study, trophic interactions as a cause for the decreases in BP with increasing treatment cannot be ruled-out because a group of protozoan, called heterotrophic nanoflagelates (HNF), who feed on bacteria (Kalff 2001) were not assessed. It is therefore recommended that HNF be included in future studies particularly when knowledge surrounding the fate of allochthonous carbon is sought.

Future studies should also include Amphipoda as they have been observed to be numerically abundant in numerous upland Arctic lakes in the Mackenzie Delta (Fred Wrona, personal communication). Amphipoda are known detritivores and their diet also includes bacteria, algae and fungi as well as non-living substances (Hargrave 1970). Amphipoda represent an important outlet of carbon to higher trophic levels as exemplified in temperate lakes (Schindler & Scheuerell 2002) as well as in northern systems such as the Mackenzie River basin (Hesslein *et al.* 1991).

5.7 References

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CHAPTER 6: SUMMARY AND CONCLUSIONS

A general working hypothesis of this study was that the input of permafrost-related sediments was responsible for the observed shift from heterotrophic/pelagic-dominated energy pathways in undisturbed upland Arctic lakes to autotrophic/benthic-dominated pathways in disturbed lakes (Mesquita 2008; Kokelj *et al.* 2009a; Thompson 2009). To address the hypothesis, four questions set within the theoretical framework of alternate stable state theory (ASST) were postulated. These questions are revisited here along with the conclusions based on the results from the experiment. It is important to note in addressing these broad-scale questions that the biological end points in this study differ from those of the synoptic studies quoted throughout this thesis such as Thompson (2009), Mesquita (2008) and Kokelj et al. (2005; 2009). This mesocosm study investigated a transition state, which does not represent lakes with older slumps, or steady-state/equilibrium conditions that may result in lakes representing multi-year recovery from an initial thermokarst slump event. However, the results of this study provide an improved mechanistic understanding of how the basal trophic components of upland Arctic lakes are affected by early stages of thermokarst slumping events.

Question 1 **- Does the relative importance of benthic- and pelagic-based processes change as a result of shoreline slumping events?**

Results from this study suggest that pelagic-based processes dominate regardless of the level of shoreline slumping. Pelagic autotrophic and heterotrophic production decreased with increasing sediment treatment; however, analysis of secondary production showed that Cladocera biomass, which accounted for ~75% of total zooplankton biomass, increased ~200% over the control in the high sediment treatment. In combination with results showing a strong negative correlation between chlorophyll *a* concentration and Cladocera abundance, this suggests that the decrease in autotrophic primary production was largely related to grazing from pelagic zooplankton.

While no significant changes in benthic primary production were found associated with increasing sediment treatment, a 500% increase in benthic heterotrophic production raises the possibility that such increased activity could be the first step in ecosystem succession leading to the increased importance of benthic primary production observed in many slumped lakes in the western Canadian Arctic.

Question 2 - Does the relative importance of heterotrophic and autotrophic processes change as a result of shoreline thermokarst slumping?

Ratios of autotrophic and heterotrophic productivity vary with lake depth (Jones 1992; Pace & Cole 1994). As such, comparisons of differences in pelagic heterotrophic and autotrophic production based on this study apply most appropriately to shallow lakes similar in depth to the experimental enclosures. Ratios between pelagic autotrophic and heterotrophic production ranged from approximately 170:1 in the control to 100:1 in the high sediment treatment. Correspondingly, significant differences were also found in the benthic zone, where ratios between autotrophic and heterotrophic production ranged from approximately 27:1 in the control to 5:1 in the high sediment treatment.

These results suggest that autotrophic production is a significantly greater source of carbon into the upper pelagic food webs compared to heterotrophic production, regardless of the level of shoreline slumping.

Question 3 -How does the relative importance of heterotrophic and autotrophic processes in the benthic and pelagic environments change over time starting from the initial slumping event?

The duration of this study somewhat limits the potential to draw inferences regarding temporal trends that may result from multi-year responses to thermokarst disturbance. While most physical, chemical and biological parameters were in flux throughout the experiment, a multi-year experiment would be required to differentiate between seasonal trends and trends specific to the treatment. Given that turbidity and light attenuation coefficients did not change significantly over time, and that these parameters were higher in this experiment than in most slumped lakes in the same geographical area (Kokelj *et al.* 2005; Thompson 2009), it seems probable that the duration of ice-cover is an important physical factor in affecting the rates of deposition of the fine particles to the sediments. Certainly, different light conditions would impact the heterotrophic-autotrophic balance as well as the benthic-pelagic balance. Time may also be required for a complete exchange from the sediments to the water column. For example, conductivity and the concentrations of major ions such as calcium, magnesium and sulfate were lower in this experiment than in most slumped lakes in the same geographical area (Chapter 2), suggesting that ions continue to leach from slump material for considerable time after the initial slumping event.

Question 4 - Does the magnitude of a slumping event affect the differences observed between slumped and undisturbed lakes?

Results of this study suggest that slump magnitude has significant affects to water geochemistry as well as the physical and biological parameters of thermokarst disturbed Arctic lakes. Trends and patterns with increasing sediment treatment level were apparent in many water quality parameters. The particular response to treatment did however vary among the parameters. For example, phosphorus, ammonia, potassium and sodium increased positively with sediment treatment. In contrast, calcium, magnesium, sulfate and conductivity followed a pattern where the intermediate level of sediment treatment had the highest concentrations/levels of these parameters. Sediment treatment level did not influence dissolved inorganic carbon or alkalinity and the response to sediment addition, while significantly different from the control, did not vary with sediment treatment level. Calcium, magnesium and sulfate concentrations were significantly greater in the treated mesocosms compared to the control across all treatment levels. In contrast, nutrient concentrations were generally non-significantly different from the control at low sediment treatment, but significantly different from the control in the medium and high treatment levels. pH in the sediment treated mesocosms differed significantly from the control at the high sediment treatment level only.

Bacterial production and zooplankton density and biomass had a positive, linear relationship with increasing sediment treatment, while chlorophyll *a* followed the shape of a logarithmic decay curve.

It is important to note that the total inputs of slump material in natural systems is multi-dimensional and includes a temporal dimension as well as a frequency and magnitude dimension. In this experiment, all sediments were added at once thus collapsing the temporal and frequency dimensions and leaving only magnitude. As such, questions pertaining to the frequency and duration of slumping events could be the pursuit of future studies.

6.1 Results in the Context of Alternate Stable State Theory (ASST)

Shifts from a clear state to a turbid state in temperate lakes typically involve elevated allochthonous inputs from the surrounding landscape (Scheffer *et al.* 2001; Jackson 2003). As a result of allochthonous inputs, nutrient availability spikes and leads to an increase in primary production. With a large biomass of phytoplankton and often, the increased turbidity associated with the allochthonous material, macrophytes become light-limited and as a result, retract or die completely thus initiating a turbid state. Because macrophytes play an important structuring role in aquatic environments by competing with phytoplankton for nutrients and preventing the resuspension of nutrients and seston from the sediment, their loss reinforces the turbid state (Scheffer *et al.* 1993, 2001; Jackson 2003; Bayley *et al.* 2007). Given that prolific phytoplankton growth is the most important factor contributing to shifts from the clear to turbid state (Scheffer *et al.* 1993; Jackson 2003; Bayley *et al.* 2007), factors which suppress the proliferation of phytoplankton contribute to the resilience of the clear state. Resilience is the strength of the feedback mechanisms, biotic or abiotic which maintain an ecosystem in a given state (Holling 1973; May 1977). In temperate lakes, allochthonous inputs reduce the resilience of the clear state by increasing nutrients for phytoplankton growth, which reduces light availability to the benthos.

Results from this study show that allochthonous inputs in Arctic lakes of the Mackenzie Delta uplands have the opposite effect of what is predicted from ASST theory. Allochthonous inputs from sediment additions led to a suppression of primary productivity; and this suppression was attributed to a trophic-cascade effect from an intensification of grazing pressure from the Cladocera community. In particular, Daphnia increased in biomass and body size with treatment. There was also evidence that sediment treatment also caused rotifers and Copepoda to change their diets as correlation coefficients between food sources changed with treatment.

It is unknown whether extreme or continued inputs could overwhelm the “top-down” feedbacks that seem to structure the nutrient-productivity relationship in slump-affected systems. Currently, the dominance of macrophytes in slumped lakes as observed by Mesquita (2008) suggests that with time, allochthonous inputs cause a shift from lakes characterized by their tea coloured water and low productivity to what resembles a temperate clear state. Furthermore the shift is thought to involve further chemical interactions that reduce water colour and improve the suitability for benthic primary productivity (Mesquita 2008; Thompson *et al.* 2008). Improvements in the light environment and benthic growth are elements reinforcing the clear state.

Results of this study suggest that when investigating the phenomenon of alternate states, it is critical to consider the correct metrics. The concept of allochthonous inputs leading to phytoplankton proliferation clearly does not apply across all input types-even when the input enriches nutrient concentration. Thus lake and watershed managers considering ASST must investigate the biological effects as well as the chemical and physical effects allochthonous inputs may have on the ecosystem.

6.2 Synthesis

Using an experimental mesocosm approach, this study shows that additions of permafrost-related sediments significantly impacts several key basal components of an arctic upland lake food web thereby having important implications to how primary, bacterioplankon and pelagic secondary production will respond to current and future climate variability and change. The basal components of aquatic food webs assessed in this study are presented in Table 1.1 and include both autotrophic and heterotrophic production in the benthic and pelagic environments.

Pelagic autotrophic primary production was found to be the dominant energy pathway for carbon into the food web regardless of sediment treatment level. Autotrophic primary production decreased with increasing treatment level while the biomass of Daphnia, which represented the majority of the zooplankton biomass, increased with increasing addition of sediments. An increase in pelagic secondary productivity with increasing sediment treatment indicates that the overall effect of thermokarst disturbance is an enrichment of the system, and supports the hypothesis that a "top-down" predator-prey interaction is primarily responsible for regulating the abundance of phytoplankton in these systems.

Figure 6.1 summarizes the observed interaction between changes in pelagic water column phosphorus concentration, phytoplankton abundance (as measured by chlorophyll *a* concentration) and Cladocera biomass. The pattern is exemplary of a trophic cascade, which is defined as "reciprocal predator-prey effects that alter the abundance, biomass or productivity of a population, community or trophic level across more than one link in the food web" (Pace & Cole 1994). This food web dynamic was originally proposed by Hairston *et al*. (1960) as part of the Green World Hypothesis and expanded in the Exploitative Ecosystem Hypothesis by Oksanen *et al*. (1981) and Fretwell (1987). The theory predicts that nutrient inputs set the potential productivity levels and that deviations from the potential are related to food web effects (Carpenter & Kitchell 1996). An alternate explanation for the observed trophic pattern in Figure 6.1 is that deteriorating environmental conditions were responsible for the observed depression in pelagic primary productivity with increasing sediment treatment (i.e., increasing sediment levels having a negative effect on light and/or nutrient availability. However, this is likely not a primary factor since zooplankton biomass would have also decreased, which was not the case.

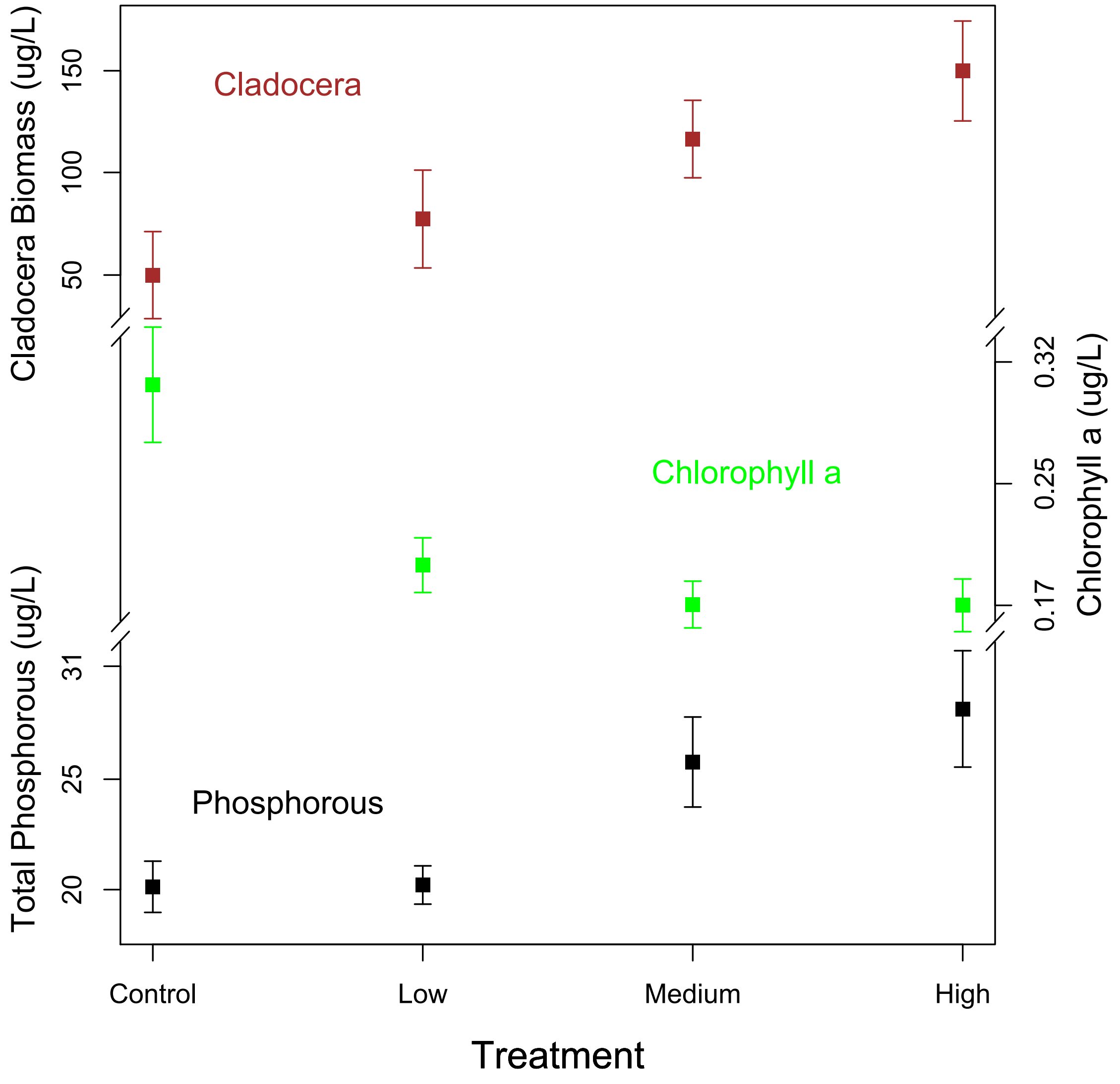

Figure 6.1. Summary of relationships between total pelagic phosphorus concentration, pelagic primary production as measured by chlorophyll *a* concentration and Cladocera abundance with increasing sediment treatment. Results support a trophic-cascade mechanism of phytoplankton regulation as outlined by Carpenter & Kitchell (1988, 1996). *Error bars represent the standard error of the mean.

6.3 Mesocosm (MC) Effects

Student t-tests between lake and control enclosure samples were used to test for potential effects the experimental enclosures may have had on experimental results. Parameters with a significant difference between lake and control samples are considered to have been impacted by a mesocosm effect. The mesocosm effect always drove the parameter in the direction of the sediment treatment trend. Thus for all water chemistry parameters as well as for benthic bacterial production, the effect was positive while for pelagic bacterial production it was negative. The significant difference in Cladocera density was related to the absence of the less common species from the lake samples. Only one lake sample was taken compared to three control MC samples per sampling trip. Thus the difference is likely the result of random sampling error due to the low abundance of rarer Cladocera species. For most parameters with a significant MC effect, the effect was small relative to the treatment effects. As such, the only parameters of concern are those in the cross section of parameters where MC effects were present and yet no treatment effects were found. There were only two such parameters: dissolved organic carbon and total dissolved nitrogen. It is therefore possible that there were significant treatment effects in these parameters but due to the MC effect, they were not picked up. Further studies with modified methods would be needed to fully elucidate the issue.

6.4 Predictions

Climate models predict increasing mean temperatures for the majority of the globe with disproportionate increases in Arctic Polar regions (ACIA 2004; IPCC 2007) (Solomon *et al.* 2008). Unsurprisingly, incidences of permafrost degradation are also predicted to increase (Hobbie et al. 1999, Wrona et al. 2006, Laybourn-Parry and Vincent 2008). Results of this study suggest that the productivity of tundra lakes will increase with increasing thermokarst activity. Following predictions from the exploitation model, increased productivity should increase the number of trophic levels that can be supported within the system (Hairston *et al.* 1960; Fretwell 1987). As such, slumped lakes are predicted to have more suitable habitat conditions conducive to hosting higher trophic levels including fish. Furthermore, increases in the size structure of Cladocera as observed here, may also increase the potential of an aquatic ecosystem to host fish as fish recruitment success is positively correlated with the size of available zooplankton

(Crowder, McDonald, & Rice 1987; Mills, Sherman, & Robson 1989; Miller, Crowder, & Binkowski 1990; Bremigan & Stein 1994).

6.5 Recommendations and Future Directions

Though a great deal of insight into how lakes may be impacted by retrogressive thaw slumping has been achieved in this study, a longer (inter-annual) experimental period is recommended. A multi-year experiment would be required to differentiate between seasonal trends and trends associated with the treatment. Many of the particles in suspension may require the stillness afforded by ice cover to allow them to complex and settle. Reductions in turbidity and the settling of particulate complexes in the water column that would likely occur after a season under ice would certainly have revealed a better understanding of the effects of permafrost thaw slumping in these cryospherically dominated systems. It is likely that many of the effects of a major change in such an environment develop over multiple years, especially when the environment is frozen for a better part or the year. For example, the succession of the benthos of new reservoirs is known to be a multi-year process even in climates without ice cover (Voshell & Simmons 1984).

As described in chapter 4, there were some issues surrounding the fibre-optical oxygen reader: the Fibox. Longer incubation periods as well as methods to insure that bubbling of air into the bottle or, for the benthic samplers, trapped gasses from the sediments do not skew the results. Furthermore, given that the Fibox is very sensitive to temperature, a minimum of two Fibox thermometers, one for the benthic and one for pelagic samplers, is recommended.

Changes in zooplankton size structure and diet as observed in this experiment suggest that sediment additions affect the edibility and size structure of the phytoplankton community. These changes may explain the unique nutrient-production relationships triggered by allochthonous inputs in these systems and should therefore be investigated. Furthermore the inclusion of heterotrophic nanoflagelates and amphipods is also recommended for future work. The inclusion of these key trophic levels would allow a more complete map of how carbon flows through these systems and clarify how thermokarst degradation affects Arctic food webs.

It has been proposed that Arctic food webs are distinct from temperate food webs in a few different ways. In particular, their simplicity (Kling, Fry, & O'Brien 1992) their high secondary productivity despite an oligotrophic water column (Rautio & Vincent 2006) and their unique zooplankton community assemblage (O'Brien, Buchanan, & Haney 1979) to name a few. The ultimate question which remains despite the considerable advancements in our understanding of the impacts of thermokarst inputs gained by this study is whether the counter-intuitive responses of Arctic lakes to allochthonous inputs are due to the nature of the sediments or due to the unique nature of Arctic food webs. To investigate this question, the identical mesocosms experiment could be repeated in a temperate lake with permafrost-related sediments sourced from the same thermokarst-affected Arctic lake as this experiment. Results between experiments could then be compared. Furthermore, to better understand the effects of slumping on predator-prey relationships, selective filtering of zooplankton could mimic predation on zooplankton. This study has contributed greatly to our mechanistic understanding of the impacts of thermokarst degradation to Arctic lakes on the Uplands of the Mackenzie Delta. This experiment supports Drenner and Mazumder's (1999) statements defending the use of mesocosms as an applicable method in aquatic ecology and demonstrates that a multi-faceted approach which includes both phenomenological and experimental methods yields the greatest advancements into complex questions.

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APPENDIX A: MESOCOSM CONSTRUCTION AND INSTALLATION

A.1 Construction

Each Mesocosm (MC) consists of two “short sides” and two “long sides” constructed with 2 x 2 spruce lumber. Figure A.1 shows all dimensions and construction details. Each side is joined at the corner to the adjacent side using four bolts and wing nuts along the length of the frame. It is critical that the predrilled holes are perfectly centered at precisely the correct height. Failing this, the holes from the two frames will not align and the bolt will not pass through making the sides impossible to join. The use of a full length jig is recommended.

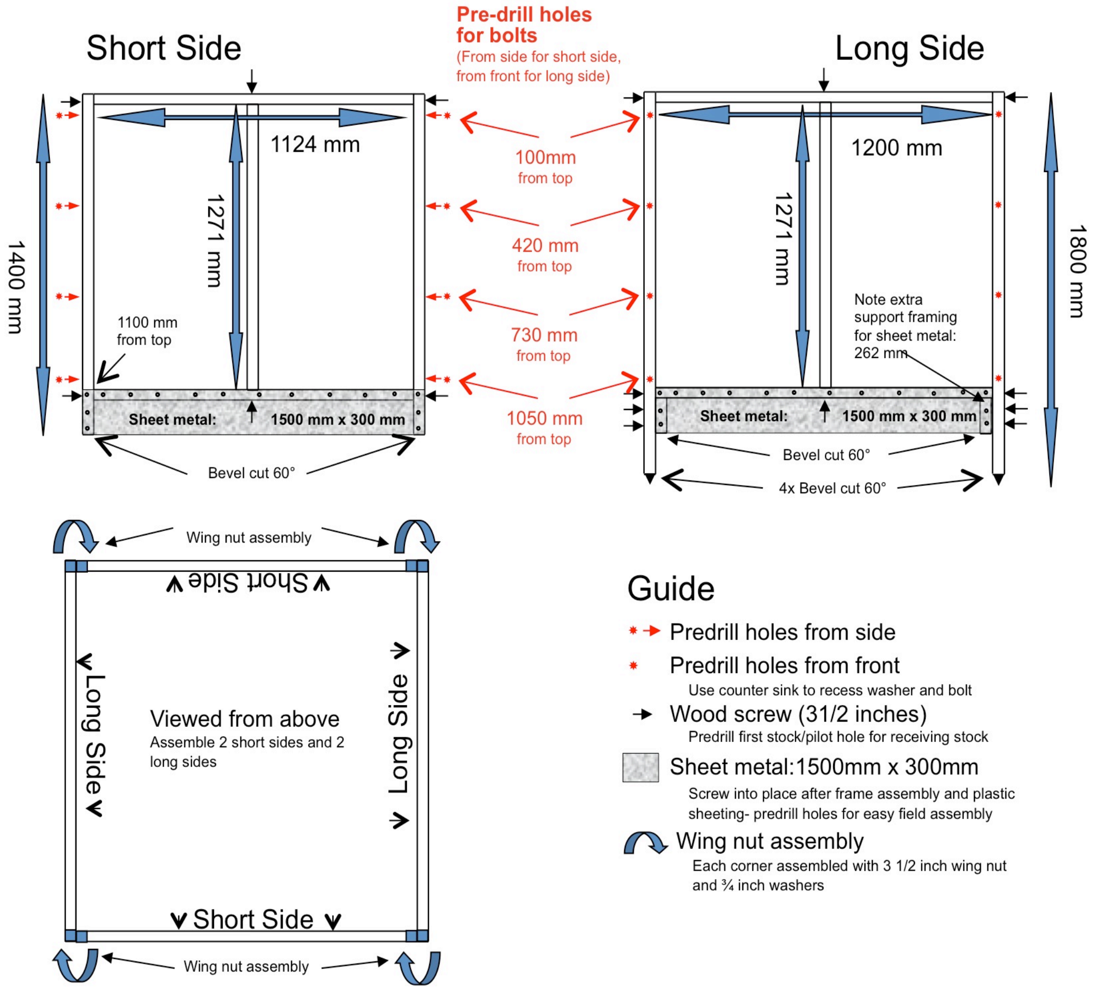

Figure A.1. Mesocosms are built from 2 x 2 spruce, reinforced plastic sheeting and sheet metal. To assemble the mesocosms, the wood frames are joined at the corner with bolts and wing nuts prior to placement of plastic sheeting and sheet metal bottoms.

A.2 Assembly

Fully constructed wood frames, plastic sheeting (16.5 feet x 5 feet), sheet metal (predrilled) and all fastening hardware are brought into the field where the MCs are assembled. Assembly should proceed in this order:

1. Pre-constructed wood frames (two short and two long sides) are joined with wing nuts and bolts (Figure A.2, Top).
2. Plastic sheeting is wrapped and fastened around the wood frame.
3. Sheet metal is screwed onto wood frame and over the plastic sheeting (Figure A.2, Bottom).
4. Thin wood lathing is screwed to the outside of the MC to prevent the plastic sheeting from moving
5. Two "U" brackets are screwed onto each corner. One positioned high near the top of the mesocosm, the other, low, just above the metal sheeting. The two brackets must be vertically aligned for the rebar to pass through (Figure A.3, Bottom left).
6. Eight foot pieces of rebar are threaded through the "U" brackets and duct-taped into place flush with the bottom of the MC. Tapping is required to hold the rebar in place during positioning (Figure A.3, Top).
7. MCs are positioned at 1 meter depth (Figure A.4, Left).
8. Rebar is pounded into place with hammers until flush with the top of the MC (Figure A.3, bottom right).
9. MCs are dosed with sediments.

Figure A.2. Top and bottom: Assembly of mesocosms before installation.

Figure A.3. Top: Four 8-foot pieces of rebar, one in each corner are used to affix the mesocosms to the lake floor. **Bottom left:** Rebar treaded through two aligned “U” brackets. **Bottom right:** Rebar is pounded with a sledgehammer until flush with top of the mesocosm. Note use of recessed washer and bolt as well as wood lathing to prevent the plastic sheeting from moving.

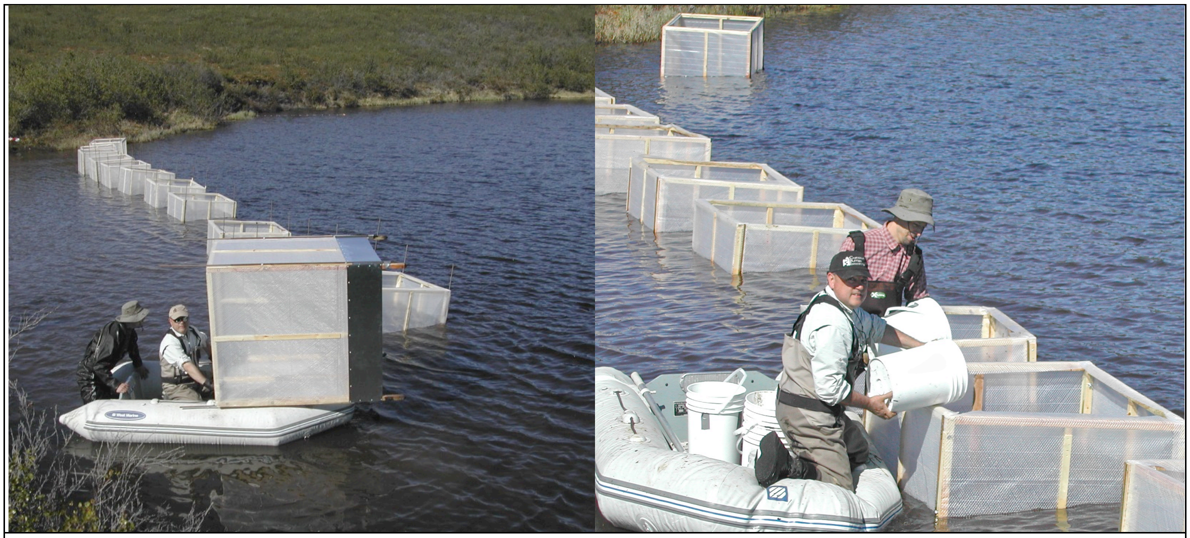

Figure A.4. Left: Mesocosms were positioned by boat. **Right:** Mesocosms being dosed with sediments from a slumped lake.

A.3 Sourcing of plastic sheeting

Plastic sheeting was purchased from Thor Tarp, the product name is “950 ThoroShield-Clear”. See company website for details and contact information: www.thortarp.com.