

The impact of permafrost degradation on the pelagic water chemistry
and biota of small tundra lakes

by

Megan Shera Thompson
B. Sc. University of Calgary, 2003

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Abstract

Up to 59 small tundra lakes were sampled in the uplands east of the Mackenzie Delta, NWT, Canada, in order to assess the impact of permafrost thaw on pelagic nutrient concentrations and biota. Permafrost thaw did not affect the concentrations of nitrogen, phosphorus or organic carbon in the water column of the study lakes. Instead, nitrogen and organic carbon concentrations were positively related to relative catchment size, and phosphorus concentrations were negatively related to maximum lake depth. Lakes affected by permafrost thaw did have lower water colour. In lakes not affected by thaw, where plankton production could have been light limited due to high water colour, the TP-chlorophyll *a* relationship was weaker than in lakes affected by thaw, where light limitation was probably weaker. A model selection analysis for chlorophyll *a* concentration indicated water colour as the best predictor variable in unaffected lakes, but nitrogen and phosphorus as the best predictors in thaw-affected lakes. This result, in particular, suggested a significant shift in the processes governing productivity in thaw-affected lakes.

In a smaller subset of lakes, chlorophyll *a* concentrations were lower in lakes affected by actively degrading permafrost than in lakes affected by stabilized thaw scars or in unaffected lakes. In contrast, zooplankton abundance was lowest in lakes with stabilized thaw scars. Bacterioplankton abundance was not different across the gradient of permafrost thaw. The differences in phytoplankton and zooplankton abundance between active and stable thaw scar lakes did not display a gradient of response that mirrored the degree of permafrost thaw activity. Because sampling did not include higher trophic levels, including macroinvertebrates and fish, it was difficult to determine how these biomass patterns arose. However, detectable differences existed in the morphometry of the lakes that might have affected habitat conditions for several species. Deep, near-shore lake-bottom pits occurred in lakes affected by permafrost thaw, while unaffected lakes were generally deepest at their centre. The pits increased the effective depth of the thaw-affected lakes, and allowed for thermal stratification where it might not have otherwise occurred. Future research should explore the habitat-related impacts of permafrost thaw on adjacent and higher trophic levels in order to better understand the fundamental shifts in trophic structures that appear in lakes affected by permafrost thaw.

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**Introduction: The limnological characteristics of Mackenzie Delta upland lakes
with special consideration of permafrost hydrology and thaw**

Arctic lakes are generally characterized as low-productivity ecosystems in which primary production is limited by a lack of nutrient availability, low temperatures or a short open-water season, among other factors (Shortreed and Stockner 1986, Flanagan et al. 2003). Particularly where lakes occur atop permafrost, the contributing landscape is thought to be inert and groundwater input is considered to be minimal or nonexistent. It is assumed that nutrients are delivered to these lakes mainly from the active layer, which is usually relatively rich in organics but not in mineral-associated nutrients, particularly phosphorus. This assumption is more or less accurate, but not when permafrost thaws, resulting in a deepening of the active layer or thermokarst development. Once runoff is able to penetrate the previously frozen soil horizons, it can transport solutes that were concentrated in the undeveloped mineral soil. In the case of thermokarst development, the transport of soil into lakes leads to a more a more direct introduction of solutes to lakes.

It has been hypothesized that the release of nutrients (ie. phosphorus, nitrogen and organic carbon) from thawing permafrost will contribute to eutrophication in arctic lakes (Hobbie et al. 1999). However, it is unclear first, whether permafrost could be a significant and universal source of nutrients, and second, what the nature of these permafrost-derived nutrients might be and whether they will have consistent impacts once delivered to low-productivity arctic lakes. Ideally, the study of a whole population of lakes in a variety of environmental conditions would provide an estimate of the “average” impact of thawing permafrost occurring in the catchments. However, there are many challenges to gathering such data in the Arctic.

Part of the difficulty in quantifying the impacts of thawing permafrost on any freshwater

system is that the detection of thawing permafrost generally requires adequate records of ground temperature. Such records, although benefiting from an international network of long term monitoring sites (i.e., Global Terrestrial Network for Permafrost), are generally rare, especially across several small, relatively homogeneous lake catchments or at several sites in larger, complex catchments that would lend themselves to limnological investigations.

The lack of a comprehensive understanding of the factors limiting biological production in arctic lakes also complicates investigations of the impacts of permafrost thaw. In particular, the relative importance of light, temperature and nutrient limitation for primary producers across arctic lakes is unknown. Certainly, phytoplankton biomass in arctic lakes has been found to respond positively to an increase in nutrient supply (Schindler et al. 1974, O'Brien et al. 2005), but there is some evidence that nutrient-chlorophyll *a* relationships in arctic lakes are weaker than those found in temperate lakes (Flanagan et al. 2003), perhaps due to co-limitation by light, temperature or both.

With the spatially patchy data available for the identification of both permafrost thaw and limnological conditions across arctic lakes, it would be convenient to measure the impacts of a readily identifiable form of permafrost thaw in several catchments of relatively homogeneous lakes in order to make preliminary investigations of permafrost thaw impacts on lakes. The occurrence of highly visible shoreline retrogressive thaw slumps on several small, first-order lakes located on continuous permafrost in the western Canadian Arctic provided just such an opportunity. This study focuses on these shoreline thaw slumps as a proxy for permafrost thaw in general, and on the resulting impacts on the pelagic zone water chemistry and biota as a

limnological starting point. The following introduction provides background about 1) permafrost hydrology, geochemistry and retrogressive thaw slumping; 2) nutrient dynamics, primary and secondary production and catchment influences over arctic lake trophic status; dissertation objectives arising from the current state of knowledge; and 4) the study area chosen to evaluate these objectives in terms of the impacts of permafrost thaw in lake water chemistry and pelagic biota.

1.1 Permafrost

1.1.1 Permafrost Hydrology and Geochemistry

The presence of permafrost in a catchment can influence water chemistry, generally by restricting runoff to the shallow active layer. In areas where the active layer is comprised of well-developed organic-rich soils, runoff can transport significant amounts of humic material to lakes and streams. For example, in a comparison of two Alaskan stream catchments, streamflow in a catchment with a high percentage of permafrost cover had almost twice the concentration of dissolved organic carbon, higher fluxes of dissolved inorganic and organic nitrogen and lower stream-water ionic concentration than in a catchment with lower percentage of permafrost cover (53% vs. 3% areal coverage, respectively) (MacLean et al. 1999). Soil water sampled in the rooting zone in both catchments was high in dissolved organic carbon, and ionic solute concentrations were higher in groundwater sampled from springs in the same area (MacLean et al. 1999). This was considered support for the hypothesis that permafrost confines runoff to the organic horizon in the active layer where it is enriched with dissolved organic carbon, rather than

infiltrating further to the mineral soil horizons (MacLean et al. 1999). If active layer depths increase in the future, infiltration to mineral horizons will lead to ionic dissolution, and to adsorption and loss of DOC (after MacLean et al. 1999).

Differences in solute concentration between the active layer and the underlying permafrost partly reflects the differential leaching of these soils via infiltrating runoff (Péwé and Sellman 1973, Keller et al. 2007). This leaching occurs in the active layer as it thaws during summer, but is restricted in the permafrost, which acts as an aquitard. Furthermore, historical aggradation of the permafrost table resulting in entrapment of solutes from the active layer and movement of water and solutes downwards to the permafrost table during deep thaws can lead to concentration of solutes in the near-surface permafrost (Kokelj and Burn 2003). This contrast between leaching processes and solute concentrations in permafrost vs. active layer is an important factor in predicting the potential impacts of permafrost thaw and thermokarst processes such as hillside slumping or streambed failure. If the permafrost table moves downward due to deeper thaw, permafrost becomes a source of solutes and melt water to the active layer and to infiltrating runoff (Kokelj et al. 2002).

1.1.2 Retrogressive Thaw Slumping

Permafrost degradation in the Arctic is expected to result from a change in average air temperature (Rouse et al. 1997, Walsh et al. 2005). In areas rich in ground ice, permafrost thaw can lead to the formation of retrogressive slumps that may be several hectares in size and often occur adjacent to small tundra lakes (Rouse et al. 1997, Kokelj et al. 2005). The surface-water

runoff from the slumps, along with the soil that they deliver to the lake, may alter the water chemistry of the water column. Significant potential implications for aquatic organisms have been demonstrated by Hobbie et al. (1999), Kokelj and Lewkowitz (1999), Kokelj et al. (2002), and Kokelj et al. (2005).

Given the influence of ionic solutes supplied by degrading permafrost on lake water chemistry, and the assumption of generally high concentrations of nitrogen and phosphorus in permafrost, nutrient enrichment in these lakes may be a possible outcome of permafrost thaw. In terms of the potential for eutrophication in arctic freshwaters, permafrost degradation and associated runoff has been linked to significant phosphorus introduction in Toolik Lake, Alaska (Hobbie et al. 1999). Nutrients are expected to enter rivers, lakes and wetlands along with sediments and other solutes as permafrost thaws. The potential release of nutrients is significant, as algal and bacterial growth and production in most northern lakes appears to be limited in part by the poor supply of nitrogen, phosphorus or both (Shortreed and Stockner 1986, O'Brien et al. 1992, Levine and Whalen 2001). If algal growth in lakes is enhanced by the addition of these nutrients, major ecosystem shifts may occur, for example in the case of an increase in edible algae in the water column. An increase in such algal growth may create more food for higher trophic levels, including fish, but may also result in large algal blooms with negative effects on oxygen levels in the lakes and general water quality, with implications for the entire food web (Hobbie et al. 1999). An increase in inedible algae or submerged plant biomass may also occur, with impacts expected to affect food availability through the food web, water oxygen levels under ice, and even transport, since submerged plants can impede navigation of rivers and lakes.

In lakes affected by thaw slumps, abiotic influences on nutrient and organic matter availability and dynamics may be as significant in determining the outcome of enrichment as those related to biotic uptake and recycling of nutrients. Kokelj et al. (2005) assessed the water chemistry of 22 small tundra lakes north of Inuvik, NWT with and without shoreline permafrost slumps. Major ion concentrations (Ca, Mg and SO₄) were eight to twenty times higher in lakes with slumps than in unaffected lakes. Kokelj et al. (2005) also found extremely high sulphate concentrations in lakes with lakeshore permafrost slumps (mean 219.9 mg/L in slump affected lakes vs. 17.4 mg/L in unaffected lakes). In addition, dissolved organic carbon (DOC) content was lower and the water-column surface samples were clearer in lakes with slumps than in unaffected lakes, indicating a negative impact on the delivery of organic material from the catchment. This difference in DOC could be the result of different chemical interactions. The introduction of high levels of sulphate into lakes has been linked to changes in pH, to the sequestering of iron in lake sediments (Giblin et al. 1990, De Haan 1992), and to the modification of bioavailability of humic substances in the water column (De Haan 1992). Base cations can increase the adsorption and flocculation of humic substances from the water column (reviewed in Thomas 1997). In bicarbonate dominated freshwaters, precipitation of calcium carbonate can incorporate a significant amount of phosphorus, resulting in a loss of that nutrient through subsequent sedimentation (Wetzel 2001).

These observed water chemistry effects of thaw slumps have been related to the extent and activity of the slumps in the catchment. The elevated major ion concentrations in the slump-affected lakes were related to the percentage of the lake catchment affected by slumping (Kokelj

et al. 2005). This indicates that degrading permafrost is the likely source of solutes, which supports earlier findings that permafrost is enriched in ionic solutes relative to the overlying active layer in the same region (Kokelj and Burn 2005). In lakes with old (estimated at several decades) or small slumps relative to catchment size, the elevated ionic concentrations were still apparent, indicating a susceptibility to long-term effects of slumping in these systems (Kokelj et al. 2005).

1.2 Arctic Lake Productivity

1.2.1 Phosphorus and Nitrogen Sources and Supply

The lake catchment is an important source of nitrogen and phosphorus, especially when a lake is relatively hydrologically isolated without the influence of inflowing streams. While many arctic lakes are nutrient-poor and oligotrophic, naturally eutrophic lakes can occur in catchments dominated by parent material that is rich in soluble nutrients (Downing and McCauley 1992). A survey of lakes in the Yukon and Alaska found that lakes in the western Canadian and American Arctic had higher nutrient (total organic nitrogen, (TON) and total phosphorus (TP)) and major ion concentrations than lakes in other arctic regions (Gregory-Eaves et al. 2000). The authors suggested that this high concentration of solutes was due to the surficial geology, mainly the erodible bedrock that occurs across their study area, and the relatively low precipitation in that region. According to their interpretation of TON:TP ratios, most lakes sampled in the area were more phosphorus limited, rather than nitrogen-limited (Gregory-Eaves et al. 2000). Nutrient and ion concentrations increased from northern arctic tundra lakes to northern forests lakes. This was

attributed to the higher precipitation, lower permafrost cover and breakdown of leaf litter in the forest lakes (Gregory-Eaves et al. 2000). In addition, TP, TON and dissolved phosphorus (DP) were strongly correlated with iron concentration in the western arctic lakes. Iron concentrations were high in the lakes ($>0.5\text{mg/L}$), perhaps due to the presence of permafrost and related poor catchment drainage leading to anaerobic soil conditions (Gregory-Eaves et al. 2000).

There have been preliminary connections made between thawing permafrost and phosphorus release to freshwaters. Hobbie et al. (1999) documented the nutrient enrichment of a small Alaskan stream (the “Milky Way”) in the Toolik Lake watershed and related it to a small patch of degrading permafrost over which the stream was running. The degradation was due to stripping of the overlying organic layer for the purposes of extracting aggregate. The concentrations of ortho-phosphate and nitrate in the stream were considerably higher downstream of the disturbance compared to those in upstream sections (Hobbie et al. 1999). The authors predict that subsequent enrichment of the stream and potential enrichment of the receiving Toolik Lake could lead to a shift in the lake trophic status and/or in primary producer community if widespread thaw occurs.

This prediction has been supported by two more recent studies. Keller et al. (2007) investigated differences in phosphorus concentrations in active layer and permafrost mineral soils in Alaskan glacial till deposits in the foothills of the Brooks mountain range. Along with higher calcium, inorganic carbon and sulfate, phosphorus was generally at higher concentrations in permafrost soils than in active layer soils. The authors suggest using stream water carbonate and strontium levels as indicators of catchment-level permafrost thaw. A separate study of several

Alaskan streams affected by thermokarst in the catchments or along the streambeds reported that ortho-phosphate concentrations were higher downstream of the thermokarst disturbances compared to upstream concentrations (Bowden et al. 2008).

1.2.2 Organic Carbon Sources and Supply

The character and availability of organic carbon as an energy source within a lake is influenced by several factors. Dissolved allochthonous and autochthonous carbon are supplied to lakes via leaching of organic matter in the catchments and from aquatic plant material, respectively. Coloured dissolved organic matter in particular, which is generally allochthonous, reacts with basic cations (especially calcium) and metals (often iron), and therefore may be adsorbed and lost to the lake sediments (reviewed in Jones 1992, Thomas 1997). In addition, the nature of dissolved organic matter can be altered by exposure to UV radiation. Photolysis can degrade high molecular-weight and high-colour organic matter to lower-weight and less coloured forms (Lean 1998). This 'photochemical conditioning' can make DOC a more bioavailable carbon source, especially to secondary producers (Tranvick 1998). The interactions between major ions and DOC (and humic material in general) are also important in terms of nutrient availability because humic matter can affect the concentration of nitrogen, phosphorus and micronutrients in lake systems (Jackson and Hecky 1980, Klug 2005). High molecular-weight humic material can bind phosphorus and metals (including the micronutrient iron), and because of their size, remain relatively biologically unavailable (Wetzel 2001).

1.2.3 Primary and Secondary Producers

The empirical relationship between TP concentration and phytoplankton biomass, as measured by water-column chlorophyll *a* concentration, has been employed for decades to determine and compare the “trophic status” of lakes (Vollenweider and Dillon 1974, Schindler 1978, McCauley et al. 1989, Watson et al. 1992). Although extensively employed in between-lake comparisons, the TP-chlorophyll *a* relationship does not appear to be constant across large latitudinal gradients. Flanagan et al. (2003) conducted an analysis of literature data from North American lakes across a latitudinal gradient from 41 to 79°N, and found chlorophyll *a* concentrations to be significantly positively related to total phosphorus concentration. However, chlorophyll *a* content was also found to be negatively related to latitude, and the slope of the relationship $\log \text{TP} : \log \text{chlorophyll } a$ was found to be less positive in arctic vs. temperate lakes. The suggested explanation was that a combination of abiotic limiting factors, especially water temperature, and nutrient-limited food chain length results in strong bottom-up (nutrient) as well as top-down (predator, or highest food web levels) control of algal biomass in arctic lakes. The authors suggested that a possible increase in air and water temperature due to climate variability could release algae from both forms of control, causing an overall increase in lake productivity in arctic lakes. In other words, nutrient limitation, in conjunction with low temperatures, was found to limit phytoplankton biomass. Therefore, an increase in nutrient availability may not lead to stimulation of phytoplankton growth at the same magnitude as has been established for temperate lakes, possibly because of the damping effect of low temperatures. In addition to low temperatures, strong seasonal shifts in light and UV exposure have been suggested as non-

nutrient limiting factors for primary production in arctic lakes (Hobbie 1980).

There are complicating factors involved in the analysis of permafrost-related nutrient enrichment, especially when employing bioassays meant to determine the extent and nature of algal nutrient limitation in these tundra lakes. In nutrient enrichment experiments conducted *in situ* at Toolik Lake, Alaska, O'Brien et al. (1992) observed that additions of nitrogen and phosphorus increased the water-column nutrient content for the first two seasons of application, after which pelagic concentrations fell. The authors, considering the increasing biomass and production of phytoplankton in the enclosures, concluded that after the second season producers had increased in number and productivity to significantly lower water-column nutrient concentrations despite continued additions. Alternatively, phosphorus can be sequestered from the water column to lake sediments, so that phosphorus additions may have no effect on water-column nutrient concentrations until the storage capacity of the lake sediments is exhausted (Wetzel 2001). For these reasons, if lakes are indeed receiving nutrient subsidies, measuring freely available nutrients in the water column may not allow one to conclusively detect an increase in nutrient loading.

Another important influence on algal growth, particularly in humic lakes, is the limiting role of DOC and its influence on bacterioplankton production, which is known to be a competing process for phosphorus uptake (Currie and Kalff 1984). Coloured DOC compounds may have their most significant impact on primary production through shading, especially photosynthetically active radiation (PAR), that is required for phytoplankton production and growth (Jones 1992, Klug 2002). Due to the influence of light regime on lake thermal structure,

small lakes with high DOC also tend to have shallower thermoclines and less volume for phytoplankton production than those with low DOC (Fee et al. 1996). Beisner et al. (2003) used a model incorporating the effects of phosphorus input, DOC and food web on equilibrium areal chlorophyll and resilience of a clear-water state. For a given phosphorus input or harvest rate, higher DOC concentrations increased resilience of the clear-water state (Beisner et al. 2003). Carpenter et al. (1998) found that a shift from 5 to 17 mg/l DOC in experimental lakes in Wisconsin resulted in a reduction of phytoplankton biomass and production comparable to that caused by a shift in phosphorus input rate from 5 to 0.5 mg/m²/d. It is necessary, therefore, to examine both nutrient supplies and DOC quantity and character to determine whether permafrost-thaw related nutrient release does lead to arctic lake eutrophication.

1.2.4 Zooplankton

Zooplankton communities in arctic lakes are generally not diverse. Brooks (1957) characterized arctic *Daphnia* assemblages, including in the Mackenzie Delta region, as comprised of the large *D. magna* and *D. middendorffiana*, *D. pulex* and the smaller *D. longiremis*. Both calanoid and cyclopoid copepods are common in western Canadian Arctic lakes, and both groups include smaller primary and larger secondary consumers (Swadling et al. 2000).

Abiotic factors such as water chemistry can influence zooplankton community assemblages. A canonical correspondence analysis (CCA) was carried out by Swadling et al. (2000) to investigate the influence of abiotic parameters on zooplankton assemblages. Certain

Cladocera, including *B. longirostris*, were more abundant in lakes with higher ionic concentrations (especially chloride concentrations). Some rotifer and copepod species, but no Cladocera species, were related to the second CCA axis involving water temperature and silica concentration. Only 25% of the variation in zooplankton assemblages was explained by the abiotic factors included in the CCA, and the authors suggest that food web influences including both bottom-up and top-down processes may explain more of the variation.

Water-column light conditions can also influence the fitness and subsequently, the morphs of arctic Cladocera. In an experimental investigation, Luecke and O'Brien (1983) found that *D. middendorffiana* morphs with dorsal pigmented patches were adapted to survive despite high UV exposure in shallow ponds of arctic Alaska. However, the pigmented morphs were thought to be more susceptible to predation by visual predators (Luecke and O'Brien 1983). Finally, the pigmentation in *D. middendorffiana* was lost when individuals were protected from exposure to sunlight (Luecke and O'Brien 1983). This trade-off between UV vulnerability and predation risk may be used to determine controlling influences on plankton abundance, at least in *D. middendorffiana*.

Biological influences can have as important a role in shaping zooplankton communities as physical conditions. It has been proposed that populations of primary producers and secondary consumers (predators), along with decomposers are limited by their food or resource supply, while primary consumers (herbivores) are limited by predation (Hairston, Smith and Slobodkin 1960, Oksanen et al. 1981). This 'exploitation' model of food web complexity predicts that low-productivity systems will contain only primary producers, and that the number of trophic levels

would increase with productivity. These models identify bottom-up (nutrient availability) and top-down (herbivory/predation) control as significant influences on trophic-level biomass, varying in relative importance depending on the number of trophic levels present. System productivity controls the number of trophic levels, that in turn controls the relative biomass at each trophic level.

Highlighting the influence of top-down food web effects on aquatic communities, the size-efficiency hypothesis states that large-bodied zooplankton are more susceptible to predation by planktivorous fish than small-bodied individuals, but are also more efficient at consuming food particles than smaller zooplankton (Brooks and Dodson 1965, Hall et al. 1976, Mazumder 1994). Planktivorous fish additions in Toolik Lake, Alaska were followed by a shift to small-bodied Cladoceran zooplankton (O'Brien et al. 1992). In contrast, invertebrate predation has been found to lead to the relative abundance of large-bodied over small-bodied zooplankton, presumably due to gape-limitation in the predator (Brooks and Dodson 1965, Hebert and Loaring 1980). The potential for size-specific predation, coupled with the size-related feeding efficiencies of herbivorous zooplankton, underlines the role of predation in determining the standing biomass of both zooplankton and phytoplankton communities in tundra lakes.

1.2.5 Landscape-scale Processes

The range in productivity and water chemistry between lakes within the same landscape may be considerable, and it can be difficult to determine how that variability arises when factors such as surficial geology, lake catchment characteristics and morphometry, and climate are

relatively consistent. The geomorphic-trophic model, developed for lake systems in Alaska, is interesting in the context of understanding such between-lake variability (Hershey et al. 1999). The model itself is meant to predict fish assemblage and subsequent trophic structure in a lake, given knowledge of the lake's geomorphic setting as it affects fish immigration rates. In particular, the vertical gradient of connecting streams and lake depth as it affects over-wintering habitat were examined. The major assumptions of this approach are that, in arctic lakes, geomorphic landscape attributes control fish distributions, and that fish control lake food webs (top-down control) (Hershey et al., 1999). Geomorphic barriers to fish movement between Alaskan arctic lakes are considered to be a product of glacial history and postglacial geological processes (Hershey et al., 1999). As a result, some characteristic fish communities have developed, and each community has particular consequences for benthic and pelagic consumers. The assumption of fish-controlled (top-down) trophic systems seems well supported for the Alaska lakes, but bottom-up control may become more important at different spatial scales or in more heterogeneous lake districts (especially if catchment vegetation varies more between systems). Given the possible cascading trophic effects of predation on planktivores and subsequently on planktonic producers, the examination of fish communities in arctic lakes is necessary to obtain a comprehensive understanding of the entire lake ecosystem and therefore to explain variation at all trophic levels. The recent glacial retreat across the Arctic and the resulting geomorphic characteristics of aquatic metapopulations are certainly important historical constraints on current lakes communities, and would undoubtedly have an influence on the response of these systems to future change.

In terms of permafrost degradation at the landscape scale, disturbance theory would suggest that intermediate disturbance regimes would result in the highest possible biodiversity (Connell 1978, Connell and Sousa 1983). However, this may not be the case if connectivity and dispersal between arctic lakes is somewhat restricted, either by physical barriers or by their brief history (Hershey et al. 1999). If potential colonizing species and competitive species are not able to establish themselves after a disturbance for this reason, the patterns of increasing biodiversity may not be fully realized. In addition, the nature of disturbance in some arctic regions can be very extreme. In ice-rich permafrost areas, the size and morphometry of lakes can be highly variable over time as the structuring influence in the landscape, the permafrost, adjusts to fluctuations in climate and other forcing factors (Mackay 1992). Lake systems in such areas may act as hot spots of significant permafrost degradation related to lake enlargement, and may disappear entirely as a result (Smith et al. 2005). In light of the specific requirements formulated by Connell and Sousa (1983) for establishing the stability and resilience of an ecosystem, challenges in determining ecosystem response to such variable and extreme disturbance are significant, and may be linked to processes with time lags on the order of decades. The situation is further complicated by poor historical records of such events across the Arctic, and an incomplete understanding of the landscape and limnological processes involved.

Alternative stable states may also play a role in the status of arctic lakes. The duality between autochthonous and allochthonous energy sources, the complicated interactions between bacterioplankton and phytoplankton, and the variability in macrophyte cover and water clarity found between arctic lakes (Mesquita et al. 2008) all lend themselves to interpretations as

alternatively stable equilibria. However, significant research and long-term records are required to firmly characterize alternative stable states in an ecosystem, and the general lack of such research and records in arctic lakes makes it almost impossible at this time. Certainly, the rapid climatic change currently being experienced across the Arctic compared to general global conditions could cause a shift in the functioning of these lakes, which are generally thought of as climatically-limited (Flanagan et al. 2003).

1.3 Dissertation Objectives

Despite the numerous potential impacts of degrading permafrost on arctic lake ecosystems, few researchers have examined impacts on aquatic biota (but see Hobbie et al. 1999). With the work already being completed towards understanding the chemistry of permafrost and the solute chemistry of lakes affected by permafrost degradation (Kokelj et al. 2005), an expansion into the biological ramifications of this process was considered advantageous and imperative. As already discussed, the implications of changes in water-column chemistry and colour induced by degrading shoreline permafrost for pelagic biota are many. First, if nutrients are delivered to a lake from degrading permafrost, producers may be released from nutrient limitation, and production and/or producer biomass would increase. This enrichment scenario is even more likely if the apparent permafrost thaw-related decrease in DOC translates into a release from light limitation for the producers as well. In addition, bacterioplankton may be negatively affected by a decrease in water-column DOC, and it is not known to what extent these secondary producers function as competitors for primary producers. If production is thus

enriched, an increase in primary consumer biomass may follow, and if herbivory is efficient enough, may indeed exert top-down control on producers. These reactions may be further influenced by the specific communities making up the producer and consumer trophic compartments. If inedible algae or small-bodied zooplankton are favoured by shifts in abiotic conditions, the top-down control of production may be very weak.

The following chapters will present the results of a study involving multiple lakes affected by shoreline retrogressive thaw slumping (SRTS), with the goal of understanding the impacts on water-column habitat quality and planktonic community response. Potential impacts on nutrient chemistry, bacterioplankton, phytoplankton and zooplankton communities will be investigated. The specific areas of interest are (in question form):

A. Relative to other landscape-scale influences, how strongly does shoreline thaw slumping affect the water-column chemistry of tundra lakes?

Are pelagic nitrogen and phosphorus concentrations related to SRTS? Are these nutrient concentrations related to other water chemistry parameters, such as major ion or DOC concentrations? How do the impacts on these water chemistry parameters compare with those of other landscape-scale influences?

B. Is there a significant difference in nutrient concentrations and plankton biomass between slump-affected and unaffected tundra lakes?

Is there a significant difference in nutrient:phytoplankton biomass relationships between

lakes affected by shoreline permafrost slumping and unaffected lakes? Do these relationships reflect existing empirically derived relationships? Is the low [DOC] concentration of the water column in lakes influenced by SRTS significantly positively related to primary producer biomass? Could this reflect a release from light limitation because of high water colour? How is secondary producer (bacterioplankton) biomass related to nutrients and to primary producer biomass?

C. How do the impacts of SRTS on pelagic nutrients and biota relate to the state of SRTS (actively degrading or stabilized and revegetated SRTS)?

Are SRTS-related impacts on nutrient concentrations and plankton biomass greatest in lakes affected by actively degrading thaw slumps and moderate in lakes affected by stabilized thaw slumps, compared to unaffected lakes?

Each of these three questions arose in a stepwise fashion, one from the other, as did the subsequent investigation, which took the form of three lake surveys. The first was a large synoptic survey of 59 lakes that compared the influence of slumping to other catchment and lake characteristics over nutrient chemistry, and involves a multivariate statistical method. The second, smaller, survey was a multi-year survey of 22 lakes, half affected by SRTS and half unaffected. Data from these lakes were used in a direct comparison of nutrient concentrations and the nutrient and light relationship with chlorophyll *a* concentrations. Finally, a set of 9 lakes equally divided between lakes with actively degrading SRTS, stabilised SRTS and unaffected by SRTS

were sampled to characterize conditions across the gradient of SRTS activity using a balanced ANOVA design.

1.4 Study Area - The Mackenzie Delta Uplands

This study involved the sampling of up to 59 small lakes situated in the uplands east of the Mackenzie River Delta, Northwest Territories, Canada. The lakes were located along a roughly north-south transect beginning just southwest of Noell Lake, 12 km north of the town of Inuvik, NWT, to northeastern Richards Island, terminating roughly 15 km south of the Arctic Ocean shoreline. The lakes occur mainly in upland hummocky tundra with little to no modern flooding influence from the nearby Mackenzie Delta river channels. The area is predominantly underlain by glacial till, and much of the surficial geology of the area is classified as rolling and hummocky moraine (Rampton 1988), with pockets of lacustrine, glaciofluvial and alluvial deposits. This lake-rich landscape is the apparent result of a thaw lake formation cycle approx 11.6 to 8.5 ka BP (Dallimore et al. 2000).

The lakes have been described as hydrologically isolated (Mackay 1992, Pienitz et al. 1997, Kokelj et al. 2005), with few and/or ephemeral stream connections between lakes. Spring snow melt within lake catchments represents the most significant annual influx of water to each lake (Mackay 1992). Evaporation during the open water season, coupled with low summer precipitation, is assumed to lead to a gradual seasonal decrease in water level to a minimum in late August/early September (Kokelj et al. 2008). This hydrological isolation was ideal in a study of the between-lake impacts of SRTS. Since it is a disturbance that is confined to a single lake

catchment, the effects of SRTS could be masked by the homogenization of water chemistry in a more hydrologically connected landscape.

The north-south transect of sample lakes in this study was meant to account for climatic and vegetation gradients that occur in the area. The transect crosses the brushline just north of Inuvik on the western shore of Noell Lake. This brush area was burned in a fire in 1968 (Landhäusser and Wein 1993) and now supports willow and alder growth with sporadic black spruce, while the area north of this brushline is tundra. The regional climatic gradient is thought to influence the location of the brushline, as there is a steep precipitation gradient from Inuvik to the Beaufort Sea coast. Annual average precipitation at Inuvik is 248mm and 139mm at Tuktoyaktuk, at the Arctic Ocean. Mean annual temperature is -8.8°C at Inuvik and -10.2°C at Tuktoyaktuk (Environment Canada 2008). Lakes near the coast have shorter open-water periods and may be subject to greater wind-induced mixing than lakes near Inuvik as a result of the climatic and vegetation gradients (Pienitz et al. 1997, M. Thompson, personal observation). The inclusion of these gradients in the study design was meant to allow for identification of existing latitudinal effects that could subsequently be separated from SRTS-related impacts on the study lakes.

The Mackenzie Delta uplands are underlain by continuous permafrost and are affected by active and extensive thermokarst and localized permafrost thaw. Lakes underlain by ice-rich permafrost are susceptible to wind-driven perimeter enlargement or drainage due to warming of the permafrost, especially where ice wedge polygons occur in low-lying areas adjacent to the lakes (Mackay 1992, Smith et al. 2005). The ice content of the permafrost in the study area

ranges from 90 to 100%. Lantz and Kokelj (2008) conducted a survey of 2880 lakes greater than 1 ha in a 3739 km² area in the uplands between Inuvik and the Beaufort Sea and found that 8% of lakes were affected by shoreline slumping. In addition, the authors linked an apparent increase in the rate of thaw slump enlargement to an increase in mean summer and annual air temperatures, and the number of days with maximum air temperatures greater than 20°C (Lantz and Kokelj 2008).

Lakes in the study area have been reported to support nutrient-limited primary producer communities. Upland lakes in the study region were sampled by Pienitz et al. (1997) in their survey of lakes from the southern Yukon to the Beaufort Sea coast. Those authors characterized the 34 lakes near Inuvik and further north to the Tuktoyaktuk Peninsula as oligo- to mesoeutrophic, with low nitrogen and phosphorus concentrations (the mean for lakes above the brushline were 435 µg/L and 11.6 µg/L for total nitrogen and total phosphorus, respectively) and low chlorophyll *a* concentrations (mean 4.0 µg/L in tundra lakes). The total nitrogen to total phosphorus ratio for tundra lakes was high (42:1), indicating potential phosphorus rather than nitrogen limitation of primary production. Low chlorophyll *a* concentration (reflecting algal biomass) also indicated oligotrophic conditions. Chlorophyll *a* concentration was significantly related to total phosphorus concentration, again indicating phosphorus limitation of production ($p < 0.01$). In this light, primary production in lakes near the Inuvik area is likely nutrient limited during the growing season. A somewhat anomalous spike in iron and total phosphorus concentrations and a local peak in dissolved organic carbon concentration (maximum 1.6 mg/L, 48.8 µg/L and 29.9 mg/L, respectively) was also noted in lakes below the brushline near Inuvik,

although no explanation for these peaks was proposed (Pienitz et al. 1997). Kokelj et al. (2005, 2008) suggest that lakes in this area receive significant inputs of terrestrial solutes that are readily available from recently burned areas, where the active layer has deepened into the permafrost.

There is little available information regarding the zooplankton communities of the upland lakes. However, Swadling et al. (2000) found the cladocerans *D. middendorffiana*, *Bosmina longirostris* and *Polyphemus pediculus* and the copepods *Leptodiaptomus pribilofensis*, *Heterocope septentrionalis* and *Cyclops spp.* in their survey of zooplankton species in lakes in the Yukon Territory and lower Mackenzie River catchment, many of which were also included in the lake survey conducted by Pienitz et al. (1997). Swadling et al. (2000) included four lakes in the forest-tundra east of Inuvik, NWT in their survey, where samples collected during July were mostly composed of Rotifera and Copepoda and only one lake had a significant relative percentage of Cladocera. The copepod *L. pribilofensis* and the large cladoceran *D. middendorffiana* were found in the forest-tundra lakes.

Most of the study lakes are capable of supporting some perennial fish communities, although the current fish communities have not been assessed. Ice cover begins to form in early September on lakes near the coast and in late September on lakes near Inuvik. Lake ice thickness measured in seven study lakes during March 2007 ranged from 1.55 m in a lake on northern Richards Island (lake 29B) to 0.54 m in a lake near Inuvik (lake 2B). Dissolved oxygen measurements taken at six lakes in March 2005 indicate that the lakes did not achieve anoxia under ice, although there is a depression in oxygen content near the sediments, ranging from 42.5% to 75% oxygen saturation. In lakes that do not freeze to the bottom (maximum depth >

maximum ice depth), planktivorous fish may be present. Small shiner-type fish have been observed in some of the study lakes (M. Thompson, personal observation). In addition, larger piscivores may occur in sample lakes, especially in lakes deeper than 5m that may stratify in the summer and provide cold-water refuges (Dallimore et al. 2000). For various reasons, especially logistical, no formal attempts to sample fish were made in these study lakes, and no previous investigations in the small lakes under study are known to the author. Larger lakes near many of the study lakes support local fish camps.

1.5 References

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The influence of landscape characteristics and thawing permafrost on nutrient concentrations in tundra upland lakes, Mackenzie Delta region, Canada

Abstract

Data from a survey of 59 tundra lakes were explored using principal components analysis (PCA) to determine the relative influence of localized permafrost thaw, relative catchment area, lake size and depth, catchment vegetation and fire history, and lake order on pelagic concentrations of phosphorus, nitrogen and organic carbon. Although it was anticipated that permafrost thaw in the form of shoreline retrogressive thaw slumping (SRTS) would release nutrients from the permafrost to affected adjacent lakes, none of the measured nutrient concentrations varied with the water chemistry indicators of SRTS. Instead, nitrogen and organic carbon varied with relative catchment area, indicating the importance of the catchment in determining their concentration. Furthermore, nitrogen and organic carbon varied inversely with indicators of SRTS, and were likely influenced by the smaller relative catchment size of SRTS-affected lakes. Phosphorus varied inversely with maximum lake depth, which might be explained by the role of lake depth and stratification in restricting the resuspension of phosphorus to the pelagic zone from the lake sediments. Lake order was also linked to phosphorus variables, however the mechanism for such an association was not apparent. Permafrost thaw in the form of SRTS was not associated with an increase in pelagic nutrient concentrations, and in fact may be related to a decrease in their concentrations. However, more comprehensive investigations of pelagic nutrient cycling are required to determine the ultimate fate of SRTS-derived nutrients in tundra lakes.

Keywords: tundra lakes, landscape influence, permafrost thaw, phosphorus, nitrogen organic carbon, conductivity, bathymetry, catchment area, principal components analysis.

2.1 Introduction

Climate change is expected to impact arctic ecosystems earlier and more significantly than at lower latitudes, reflecting the sensitivity of arctic ecosystems to changing environmental conditions (Wrona et al. 2005, Anisimov et al. 2007, Furgal and Prowse 2008). Impacts on the arctic hydrosphere are influenced in particular by the thawing and potential disappearance of permafrost (Frey and McClelland 2009) that is expected to occur as a consequence of increasing air temperatures related to climate change (Rouse et al. 1997, Walsh et al. 2005). In the northern hemisphere, permafrost underlies 13-18% of the exposed land area (Walsh et al. 2005). Projections of permafrost thaw in the arctic region predict anywhere from 20-90% areal loss and 30-100% active layer deepening by the year 2100 (reviewed in Frey and McClelland 2009). Permafrost thaw, therefore, would have far-reaching implications, including physical, biological and socio-economic impacts.

Few impact projections of permafrost thaw have considered the implications for freshwater systems (but see, Prowse et al. 2006 and Wrona et al. 2006). Permafrost is an important structural component of arctic landscapes, controlling the flow and accumulation of surface waters. Thawing permafrost can also serve as a significant new source of solutes to surface waters when, a) the concentrations of solutes in permafrost are enriched with respect to the overlying active layer (Kokelj and Burn 2005), and b) permafrost thaw allows for the infiltration of runoff and the release and transport of these solutes (Kokelj and Lewkowicz 1999, Frey and McClelland 2009). The resulting potential for hydrological and geochemical impacts on freshwater systems is significant.

At the landscape scale, thaw is expected to deepen the active layer (which seasonally

freezes and thaws) and to penetrate the poorly weathered permafrost below (Walsh et al. 2005). In areas where permafrost is ice-rich, thaw may lead to the formation of large retrogressive slumps, in which several metres of previously frozen and solute-rich soil may be transported down a slope (Burn and Lewkowitz 1990). In the western Canadian Arctic, it has been noted that the occurrence of permafrost thaw slumping, often occurring adjacent to lakes, has been increasing in recent years, paralleling a warming trend affecting the area (Lantz and Kokelj 2008). This shoreline retrogressive thaw slumping (SRTS) has significantly affected the water chemistry of small tundra lakes, specifically increasing inorganic ion concentrations (Kokelj et al. 2005). As permafrost thaw is expected to continue with climate change, the impacts of SRTS will become more important in determining tundra lake water chemistry at the landscape scale.

Permafrost thaw-related increases in inorganic nutrient concentrations in arctic streams, particularly phosphorus, have been noted by Hobbie et al. (1999) and Bowden et al. (2008). Nutrient enrichment in lakes and streams could have significant impacts on aquatic biota, but apart from these preliminary results, no comprehensive investigations of permafrost thaw-related nutrient release and within-stream/lake impacts have been conducted. This study expands on previous work by exploring the pattern of nutrient (nitrogen, phosphorus and organic carbon) concentrations among a large population of tundra lakes that are both affected and unaffected by permafrost thaw. Specifically, the objective was to explore the hypothesis that SRTS permafrost degradation influences the concentrations of nitrogen, phosphorus and dissolved organic carbon across a large population of tundra lakes. Additional catchment characteristics, landscape position indicators and lake morphometry parameters that have been shown to influence within-lake nutrient concentrations were analyzed simultaneously with SRTS indicators to account for

between-lake variation nutrient concentrations.

This manuscript is divided subsequently into five main sub-sections: 1) Background, 2) Methods: Study Area and Analysis, 3) Results and Discussion and 4) Conclusions.

2.2 Background

An increase in the supply of nitrogen, phosphorus or carbon to freshwaters can result in their eutrophication, increasing biological productivity with implications for the entire aquatic food web. Hobbie et al. (1999), for example, predicted that permafrost thaw-related lake eutrophication would be associated with decreased dissolved oxygen availability, threatening the persistence of lake trout, a keystone species, in a large Alaskan Lake. Although nutrient concentrations and supply are important in determining the biological productivity of lakes, their water-column concentrations are dynamic and their supply is influenced by several landscape and lake-specific processes. It is therefore still unclear how permafrost thaw, and specifically SRTS, will influence nutrient concentrations in tundra lakes.

In the uplands east of the Mackenzie Delta, Canada, thaw slumps are a common thermokarst feature (Mackay 1963) and have been growing in occurrence and size since 1950, during a period of increased warming (Lantz and Kokelj 2008) (Figure 2-1). Shoreline retrogressive thaw slumping (SRTS), directly adjacent to lake margins, has significantly affected the water chemistry of small tundra lakes in the area. The concentrations of several ions (Ca^{2+} , Mg^{+} , K^{+} , SO_4^{2-}) were significantly higher in SRTS-affected lakes than in unaffected lakes of similar size and lake order (Kokelj et al. 2005). A more recent multivariate analysis of water chemistry data from over 70 tundra lakes revealed that high ionic concentrations and alkalinity

separated the SRTS-affected lakes from those unaffected by SRTS (Kokelj et al. 2009).



Figure 2-1. An actively degrading lakeside retrogressive thaw slump on the shore of a study lake, on the ground (left, note the person for size reference) and from the air (right, Opposite side of the lake on the right).

Along with major ions, allochthonous nutrients, specifically phosphorus and nitrogen, may be delivered to freshwaters in elevated concentrations from thawing permafrost. Analysis of nutrient concentrations in Alaskan streams within the Toolik Lake watershed revealed high concentrations in areas that were either running through areas of degrading permafrost or had thermokarst features in their contributing catchments (Hobbie et al. 1999, Bowden et al. 2008). In the latter case, nitrogen and phosphorus enrichment that occurred immediately downstream of thermokarst features significantly diminished within 1-2 km (Bowden et al. 2008). It was suggested that the decrease in concentration might be due in part to removal via biological uptake (Bowden et al. 2008), although nutrients might also be lost through sedimentation. Thompson et al. (2008) found that the addition of SRTS sediments and melt water to humic lake water decreased the coloured dissolved organic matter (CDOM) concentrations and suggested that CDOM-associated nutrients may have also been removed via sedimentation processes. Thus, both biological uptake and sedimentation might influence the concentration of nutrients in

SRTS-affected lakes.

In the context of a landscape-scale investigation involving many lakes, several non-SRTS related physical parameters can influence within-lake nutrient concentrations. Relative catchment influence, roughly estimated using the ratio of lake area to catchment area (LA:CA), has been related to the delivery of organic matter to lakes. Lakes with large relative catchments had higher concentrations of organic matter (Rasmussen et al. 1989). Lake order is an indicator of hydrological connectivity of lakes, and ionic concentrations have been found to differ by lake order in a large lake survey (Riera et al. 2000). Catchment vegetation conditions influence water-column concentrations of organic matter, which generally decline over the transition from forest-tundra to open tundra (Pienitz et al. 1997, Rühland et al. 2003). Each of these landscape measures has the potential to influence nutrient concentrations in lakes, and are therefore included in the following analysis.

2.3 Methods

2.3.1 Study Area

Study lakes were selected in the tundra uplands east of the Mackenzie Delta that contain small lakes affected by varying catchment, landscape and morphometric conditions. Thousands of these lakes and ponds occur atop ice-rich permafrost in the area (Mackay 1992). A large lake survey was an ideal method for determination of the common and most significant thaw-related impacts on lakes, since the detectable impacts of permafrost thaw can vary between lakes depending on the specific system characteristics. For this reason, an exploratory study involving a few systems would not be readily transferable to the landscape scale. Both SRTS-affected and

unaffected lakes were selected for a general comparison of lake-water nutrient chemistry, with pairs of both “lake types” located close together, to allow for an exploratory comparison of nutrient chemistry impacts between lake type populations.

The study area forms a ~150 km north-south band that is hydrologically separate from the delta to the west and several large marine-influenced lakes to the east. The deep ice-rich permafrost in the area acts to both contain and isolate surface water bodies by restricting groundwater flow, and the study lakes have limited or ephemeral overland connections. Runoff is restricted to the active layer, prohibiting water from reaching the underlying poorly developed permafrost soils. Because of this isolation, the water chemistry of tundra lakes is strongly influenced by lake catchment characteristics, including surficial geology, soil development and terrestrial vegetation (Pienitz et al. 1997; Gregory-Eaves et al. 2000; Rühland et al. 2003).

Fifty-nine remote tundra lakes were sampled between August 24 and September 2, 2005 along the north-south transect stretching between Inuvik, NWT and Richards Island, in the outer Mackenzie Delta (68.4 to 69.4°N) (Figure 2-2). The lakes selected were mostly first order (no inflow streams), with some second and third order lakes (one or two upstream lakes, respectively) connected by small ephemeral inflows and outflows, which generally only flow during spring snowmelt (individual lake data presented in Appendix A). The latitudinal transect covered a meteorological gradient of decreasing annual total precipitation and mean annual temperatures from south to north (mean annual temperature: -8.8°C at Inuvik and -10.2°C at Tuktoyaktuk, annual precipitation: 248 mm at Inuvik and 139 mm at Tuktoyaktuk) (Environment Canada 2008), and included the transition from brush tundra (alder and willow cover) in the south to open tundra in the north.

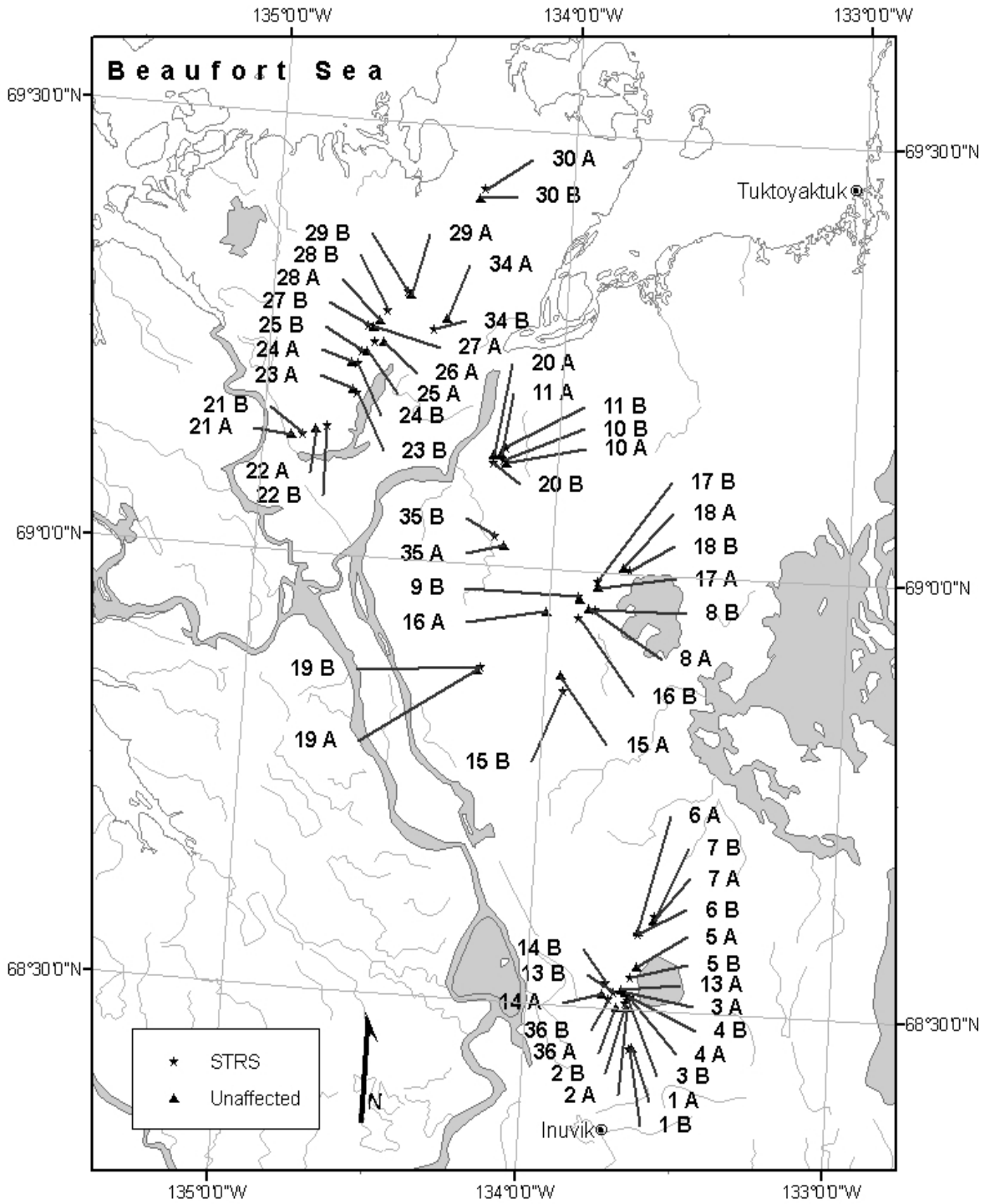


Figure 2-2. Map of sample site locations in the uplands east of the Mackenzie Delta, NWT, Canada.

Approximately half of the study lakes were affected by SRTS, while the remainder were

unaffected. Both of these lake types were spread along the entire length of the north-south transects. In addition, 45 of the lakes were located in areas unaffected by the fire that occurred near Inuvik in 1968 (Landhäusser and Wein 1993), 14 occurred in the area burned by the 1968 fire, and one SRTS-affected lake was in another undated former burn area. The former burn sites were south of the present-day brushline transition or in localized areas of brush vegetation.

The 59 study lakes ranged in depth from 1.5 to 15.3 m, with the mean at 5.4 m (raw data presented in Appendix A). However, since the bottom of several SRTS-affected lakes was found to be irregular (Thompson 2009b), the assumption that the lakes were deepest at the centre may not apply in all cases, and the resulting maximum depths (z_{\max}) determined with a line and sounder could be underestimates.

2.3.2 Lake Sampling

Lake water was sampled from a helicopter on floats positioned near the middle of each lake, where it was assumed the lakes were deepest and vertically mixed. Water samples were collected at 0.5 m below the surface, transported within hours to the Aurora Research Institute lab in Inuvik and air transported for analysis within 24 hours of collection to Environment Canada Laboratories (Saskatoon, Edmonton or Burlington).

Analyses for dissolved organic carbon (DOC) were completed at Environment Canada (EC) in Saskatoon, Canada. Dissolved inorganic carbon was obtained with an Apollo 9000 analyzer (Tekmar-Dohrmann, Cincinnati, OH), and DOC determined as the difference from total dissolved carbon.

Separate water samples were analyzed for soluble reactive phosphorus (SRP), dissolved phosphorus (DP), total phosphorus (TP), ammonia (NH_3), nitrate and nitrite (NO_3NO_2) and total

dissolved nitrogen (TDN = organic nitrogen + NO_3NO_2 + total Kjeldahl nitrogen) at EC National Laboratories for Environmental Testing (NLET) in Saskatoon and Vancouver. Standard methods were followed for all analyses (American Public Health Association 2005, except NH_3 , Technicon AutoAnalyzer Method #329-74W/B). SRP, DP and TP were determined spectrophotometrically after filtration (except TP), digestion (except SRP) and addition of ammonium molybdate. NH_3 was colourimetrically measured after ammonia salicylate complex formation. NO_3NO_2 and TDN were measured spectrophotometrically after digestion, (TDN only), nitrate reduction and azo dye formation.

Water samples for Fe analysis were preserved in the field with nitric acid, further digested with acid if turbidity was > 1 NTU and analyzed via inductively coupled plasma – mass spectrometry (ICP-MS) based on the EPA method 200.8 Revision 5.5.

2.3.3 Statistical Analyses

The nutrient chemistry data collected from the 59 lakes were used in a simultaneous multivariate analysis of C, N and P nutrient concentrations across the populations of SRTS-affected and unaffected lakes. A combination of correlation, principal components analysis (PCA) and analysis of variance (ANOVA) were used to determine how nitrogen, phosphorus and organic carbon concentrations varied with the occurrence of SRTS, catchment fire history, contributing catchment and lake area, lake order and latitude.

Nutrient and related chemistry variables (DOC, Fe, NH_3 , NO_3NO_2 , TDN, SRP, DP, TP) were analyzed together with SRTS-related variables (specific conductivity, SRTS status), lake morphometry variables (contributing catchment area, lake area, lake area:contributing catchment

area (LA:CA), maximum depth (z_{\max}), landscape position variables (latitude, and its correlate water temperature, lake order) and catchment fire history. LA:CA is used here as an indicator of catchment influence on lake water chemistry, where lakes with the lowest ratios experience the greatest catchment influence. Although lake volume and lake volume:catchment area ratios might prove to be additional useful parameters to analyze, the lack of accurate bathymetry for all of the study lakes precludes their use in this analysis. Furthermore, bathymetry data that do exist for several SRTS-affected lakes indicate that these lakes have very irregular bathymetry with numerous deep holes (Thompson 2009b), for which existing methods of estimating volume from lake area and maximum depth alone may not be accurate.

Contributing catchment and lake areas were obtained from digitized air photos of the basins (as described in Kokelj et al. 2009). It is difficult to estimate the error in this method, however if any, it would be associated with the actual digitization or with errors in georeferencing that would apply to all lakes equally. Lake area (LA) averaged 9.4 ha, ranging from 0.8 to 116 ha, although most (45) of the lakes were < 10 ha. Contributing catchment area (CA) ranged from 4.7 to 254.4 ha although, as with lake area, most catchments were small (53 catchments were <100 ha, and 44 were <40 ha). Lake area to contributing catchment area ratios (LA:CA) ranged from 0.05 to 0.58, and were significantly different between lakes affected by thaw slumping (mean 0.25) and unaffected lakes (mean 0.15) ($t = -3.557$, $df = 57$, $p = 0.001$). The lake type-specific difference in LA:CA may be an important factor affecting lake water chemistry and is considered in a subsequent discussion.

Principal components analysis (PCA) and Pearson's correlations were employed to identify the patterns of variation between nutrient and other continuous independent variables.

Data were log transformed (or $\log x+1$ transformed in the case of low-value nutrient variables) before being entered into the analyses, as per Zar (1984). Several values at or below detection limit led to the removal of SRP, NO_3NO_2 and NH_3 from the PCA. Two missing values occurred in the iron concentration data (lakes 16A and 18A), two values were missing for DOC (lakes 2B and 35B), and nutrient data were lacking for lake 23A. All 5 lakes (two SRTS-affected and three unaffected) with missing data were removed from the PCA analysis. The remaining transformed data for 54 lakes, 28 affected and 26 unaffected by SRTS, were entered into the PCA.

The individual PCA lake scores were tested using ANOVA for differences according to the nominal variables: lake order, SRTS status and catchment fire history that could not be included in the the PCA or correlation analyses. All analyses were conducted using SPSS 13.0 (SPSS Inc., Illinois, USA).

2.4 Results and Discussion

2.4.1 Principal component 1: Specific conductivity, LA:CA, DOC, TDN, Fe

The PCA was conducted using the water chemistry correlation matrix (Table 2-1) and produced a three component output. The variable component scores for the PCA are provided in Table 2-2, and individual lake scores for the components are plotted in Figures 2-3 and 2-4. The three components accounted for 72.7% of the variation among the variables. Eigenvalues for these three components after rotation were 3.3, 2.8 and 2.6, which explained 27.8 %, 23.5% and 21.4% of the variation, respectively. A fourth component would have increased the variation explained by < 10%, and was therefore not considered necessary to discern key patterns. Examination of the SCREE plot supported this decision.

Table 2-1. Pearson correlation coefficients (r) between lake physical and chemical variables. Bold and underlined correlations are statistically significant after Bonferroni adjustment (p<0.05).

	LATITUDE	TEMP	LAREA	CAREA	LA:CA	z _{MAX}	Fe	DOC	NH ₃	NO ₃ NO ₂	TDN	SRP	DP	TP	
TEMP	<u>-0.702</u>														
LAREA	<u>0.453</u>	-0.327													
CAREA	<u>0.351</u>	<u>-0.436</u>	<u>0.828</u>												
LA:CA	0.278	0.089	<u>0.502</u>	-0.064											
z _{MAX}	-0.130	0.229	0.005	-0.061	0.085										
Fe	0.022	<u>-0.345</u>	<u>-0.426</u>	-0.103	<u>-0.637</u>	-0.246									
DOC	-0.312	0.100	<u>-0.597</u>	-0.214	<u>-0.732</u>	-0.087	<u>0.558</u>								
NH ₃	0.111	-0.120	0.055	0.115	-0.074	<u>-0.350</u>	0.124	0.150							
NO ₃ NO ₂	0.085	-0.240	0.062	0.110	-0.059	0.022	0.129	-0.193	-0.045						
TDN	-0.174	0.037	<u>-0.490</u>	-0.248	<u>-0.473</u>	-0.294	<u>0.447</u>	<u>0.789</u>	<u>0.389</u>	0.099					
SRP	-0.368	0.014	<u>-0.484</u>	-0.250	<u>-0.503</u>	-0.302	<u>0.704</u>	<u>0.545</u>	0.246	-0.023	<u>0.493</u>				
DP	0.047	-0.325	-0.265	-0.055	<u>-0.376</u>	-0.298	<u>0.760</u>	<u>0.378</u>	0.221	0.140	<u>0.438</u>	<u>0.836</u>			
TP	-0.085	-0.265	-0.022	-0.136	-0.163	<u>-0.341</u>	<u>0.411</u>	<u>0.353</u>	0.101	0.129	<u>0.468</u>	<u>0.463</u>	<u>0.643</u>		
SPCOND	-0.117	0.315	0.226	-0.086	<u>0.540</u>	0.300	<u>-0.794</u>	<u>-0.487</u>	-0.193	0.031	<u>-0.400</u>	<u>-0.532</u>	<u>-0.568</u>	-0.289	

Table 2-2. Variable component scores for the PCAs conducted on data collected from 59 lakes in August 2005. Principal loadings are in bold. Moderate secondary loadings are italicized. Abbreviations are explained in the text.

Parameter	Component 1 Eigenvalue	Component 2 Eigenvalue	Component 3 Eigenvalue
Lake area:Catchment area	-0.923	0.093	0.019
DOC	0.789	-0.379	0.169
Specific Conductivity	-0.744	-0.173	-0.385
Fe	0.729	0.011	<i>0.501</i>
TDN	0.545	-0.342	<i>0.445</i>
Catchment Area	0.155	0.882	-0.222
Lake area	-0.364	0.828	-0.193
Water Temperature	-0.075	-0.729	<i>-0.476</i>
Latitude	-0.284	0.703	0.316
TP	0.162	-0.115	0.796
DP	<i>0.450</i>	0.025	0.732
Z_{\max}	-0.088	-0.106	-0.603

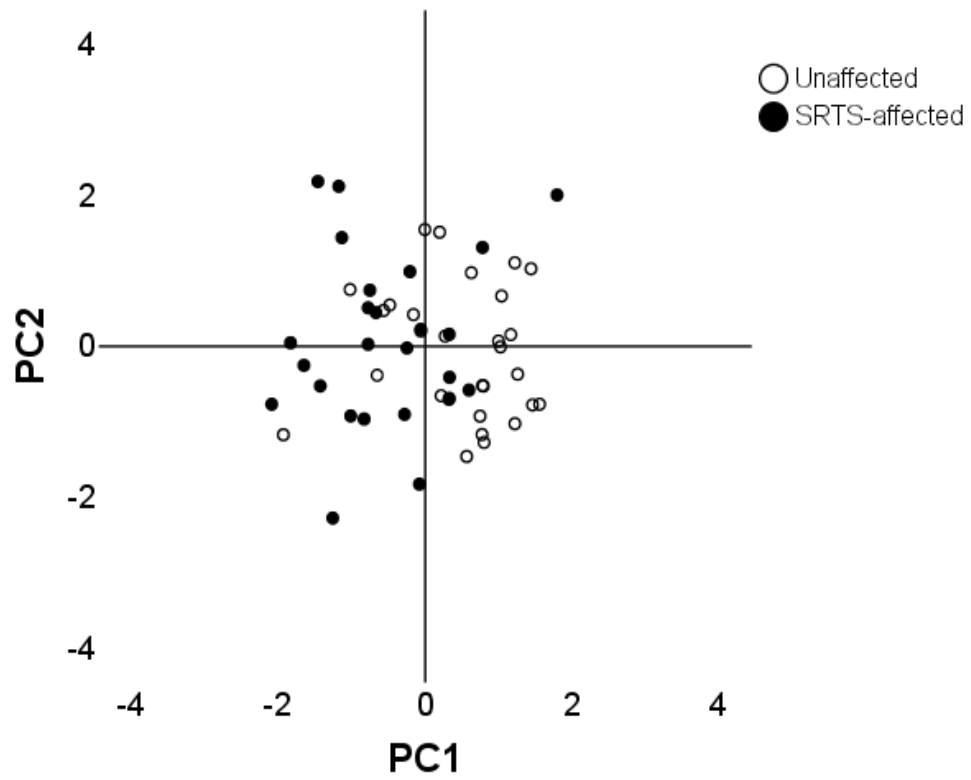


Figure 2-3. Scatter plot of SRTS-affected lake scores for principal component 1 (PC1) and principal component 2 (PC2). Filled circles are lakes affected by SRTS, empty circles are unaffected lakes.

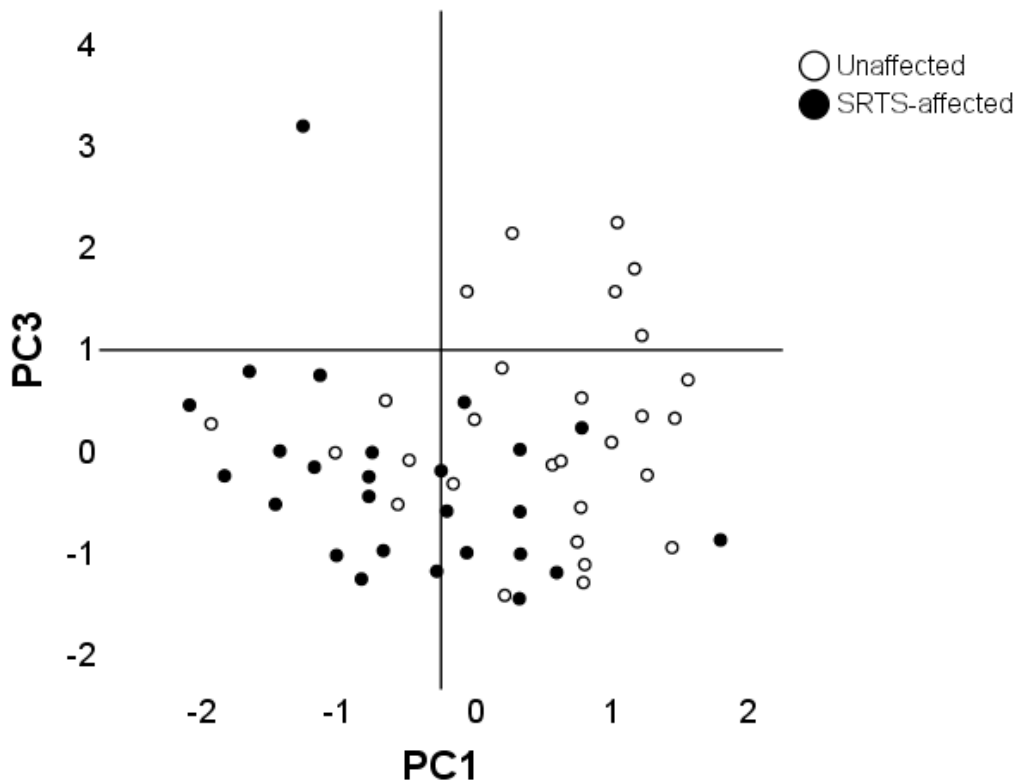


Figure 2-4. Scatter plot of SRTS-affected lake scores for principal component 1 (PC1) and principal component 3 (PC3). Filled circles are lakes affected by SRTS, empty circles are unaffected lakes.

The first principal component (PC1) separated lakes with high specific conductivity and LA:CA from lakes with high DOC, Fe and TDN (Table 2-2). Because of the reported strong pattern of increasing ionic concentrations with slump occurrence and activity and the higher water colour in unaffected vs. SRTS-affected lakes (Kokelj et al. 2005), this component separated SRTS-affected lakes from unaffected lakes. The follow-up ANOVA showed a significant difference ($p < 0.05$) in PC1 lake scores between SRTS-affected and unaffected lakes (Table 2-3). The degree of separation according to SRTS status is illustrated in Figures 3 and 4.

Table 2-3. Results tables for ANOVA analyses conducted on principal component lake scores for each of the separate PCAs. Significant results are in bold. Slump status is SRTS-affected or unaffected. Fire history refers to the location of lakes in catchments near Inuvik burned in 1968, areas where an ancient burn is evident, and unburned areas. Lake order refers to the number of upstream lakes (beginning with 1 – no upstream lakes, 2 – one upstream lake, etc.)

Component	a) Slump Status		b) Burn Unit		c) Lake Order	
	F (1, 54)	p value	F (1, 54)	p value	F (2, 54)	p value
PCA 1	5.303	0.026	0.379	0.541	1.655	0.203
PCA 2	1.072	0.306	16.682	0.000	1.244	0.298
PCA 3	2.547	0.117	0.208	0.650	5.414	0.008

The loading of LA:CA with specific conductivity may reflect the higher LA:CA in the SRTS-affected vs. unaffected study lakes (Kokelj et al. 2009). However, it may also indicate the influence of the catchment as a source of terrestrial humic material for the lakes (Rasmussen et al. 1989, D'Arcy and Carignan 1997), which is supported by the negative loading and correlation with common constituents of humic material (DOC and Fe) (Tables 2-2 and 2-3).

Significant amounts of terrestrial humic material associated with both carbon and nitrogen can be delivered to lakes via export from the catchment (Rasmussen et al. 1989, D'Arcy and Carignan 1997). The significant negative correlation between LA:CA and both DOC and TDN concentrations (Table 2-1) supports the postulate that DOC and TDN are influenced in part by catchment-related processes. Yet specific conductivity was positively correlated with LA:CA since, as was previously mentioned, LA:CA were higher in SRTS-affected lakes. Lake type differences in LA:CA may account for some or all variability in these DOC and TDN concentrations between SRTS-affected and unaffected lakes, simply because the SRTS-affected lakes had higher LA:CA than unaffected lakes. However, the experimental results of Thompson et al. (2008) validate a negative effect of SRTS on coloured dissolved organic matter

concentration.

2.4.2 Principal component 2: Latitude, LA, CA, water temperature

Latitude was also negatively correlated with water temperature, which reflected the latitudinal air temperature gradient, but was not significantly ($p>0.05$) correlated with the C, N and P nutrient variables. Latitude loaded on PC2, which separated lakes by fire history (Table 2-3). This might have been expected since the lakes and catchments located in the previously burned (1968) area were concentrated in the southern portion of the study lake transect (Table 2-3). In general, catchments in burned areas were affected by deepening of the active layer, thawing the near-surface permafrost and subsequently causing an increase in the export of solutes to the lakes (Landhäusser and Wein 1993, Kokelj et al. 2009). In a PCA analysis involving only tundra lakes not affected by SRTS, Kokelj et al. (2009) found that variation in ionic concentrations was related to the occurrence of lakes in previously burned catchments. However, the PCA completed in this study used data from both SRTS-affected and unaffected lakes, and the results indicated that conductivity was predominantly influenced by SRTS-status.

The study lakes located at higher latitudes were larger with larger catchments than at lower latitudes, indicated by the significant positive correlation between latitude, LA and CA ($p<0.05$). However, this result might be skewed by a few large outlier lakes located on Richards Island near the coast (34A, 26B, 34B; Appendix A), rather than reflecting an overall trend (Figure 2-5).

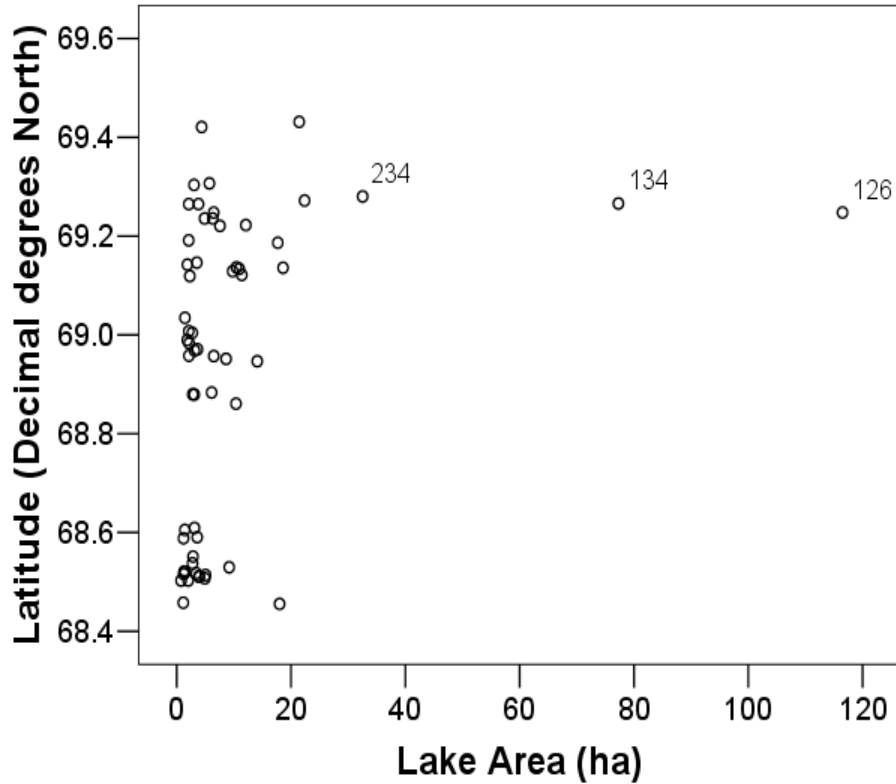


Figure 2-5. Scatter plot of study lake area and latitude. Labeled points are lakes 26B (126), 34A (234) and 34B (134).

2.4.3 Principal component 3: TP, DP, z_{\max}

Dissolved phosphorus concentrations loaded secondarily with SRTS activity (PC1 component score for DP was 0.450), but both DP and TP varied more with maximum lake depth (PC3). Deep lakes (high z_{\max}) were separated along PC3 from lakes with high P nutrient concentrations (DP, TP) (Table 2-2), and z_{\max} was significantly ($p < 0.05$) negatively correlated with TP (Table 2-1). A possible explanation for this relationship is that z_{\max} limits the occurrence of stratification (thermoclines in this area occur between 3 and 6 m depth, Thompson 2009b), while the lack of a thermocline in shallow lakes exposes the sediments to wind-induced turbulent mixing that can release sediment phosphorus to the water column (Zicker et al. 1956).

PC3 scores were significantly different across lake order (Table 2-3). First and third order lakes were shallow, while second order lakes had high phosphorus concentrations. However, post-hoc comparisons found no significantly different subsets according to lake order. Furthermore, the ANOVA interaction term between fire history and lake order was significant (ANOVA, $F=12.629$, $df=54$, $p=0.000$).

The separation of PC3 according to lake order is difficult to explain. In their analysis of systems in Wisconsin lake districts, Riera et al. (2000) found that total phosphorus concentrations were not significantly different across lake order, despite greater ionic concentrations in higher order lakes. The absence of significant post-hoc subgroups in the PC3 ANOVA complicated the interpretation of phosphorus concentrations as they related to lake order. In addition, the significance of the fire history and lake order interaction term indicates that the occurrence of the study lakes in previously burned catchments in conjunction with lake order has an impact on phosphorus concentrations.

2.5 Conclusions

In the PCA analysis, SRTS-affected lakes with high ionic concentrations were separated from low LA:CA lakes with high DOC, TDN and Fe concentrations. Low DOC and Fe in SRTS-affected lakes can both contribute to reported low water colour compared to unaffected lakes (Kokelj et al. 2005). Sedimentation of humic material is a possible explanation for the negative association of DOC, TDN and Fe with conductivity. The experimental additions of sediments from a retrogressive thaw slump to humic lake water (Thompson et al. 2008) produced a decrease in lake water optical absorbance and water colour that was attributed to the removal of humic

material. The proposed mechanism for decrease in absorbance involved the adsorption of humic material to basic cations or sediment particles, especially clay, and its subsequent sedimentation.

Despite the transition from brush tundra to open tundra north of Inuvik, no latitudinal pattern was found in any of the water chemistry parameter concentrations. Instead, water temperature varied latitudinally, reflecting the climatic gradient covered by the study transect. In contrast, in the Yukon and low-arctic lake survey analysis conducted by Pienitz et al. (1997), the first PCA component separated clear, deep oligotrophic lakes from shallow, highly coloured lakes with high nutrient and Fe concentrations that occur mostly in the forest-tundra near Inuvik. The range in catchment vegetation across the considerable latitudinal gradient covered by that study was found to have a significant influence on the nutrient chemistry of the sampled lakes. However, no patterns in water nutrient chemistry were found over the relatively narrow latitudinal gradient covered by this study.

TP in the study lakes varied most with z_{\max} and not with SRTS status, but lake bathymetry does appear to be impacted by SRTS status (Thompson 2009b). The lack of evidence for a relationship between SRTS and TP may also result from any SRTS-derived phosphorus being associated with allochthonous humic material (Jackson and Hecky 1980, Klug 2005), which can be removed from solution in tundra lake water following the addition of SRTS-derived clay sediments with high ionic content (Thompson et al. 2008). Since DOC and Fe are also components of humic material (Perdue 1998, Wetzel 2001), the finding that their concentrations varied inversely with SRTS supports a humic material sedimentation mechanism. However, if TP is delivered to the lakes via SRTS, it may also be removed from the water column through biotic uptake (Bowden et al. 2008). Certainly, the complex evidence for nutrient enrichment in

the lakes raises the question as to whether or not SRTS is a source of nitrogen and phosphorus for affected lakes. However, concentrations of nitrogen and phosphorus in runoff collected from actively degrading slumps in the study area were an order of magnitude higher than concentrations in the adjacent lake water (Thompson 2009a). Further research is required, since measuring only the water-column concentrations in the lakes does not fully account for the loss of nutrients to biotic uptake or to sedimentation processes.

Intense and localized permafrost thaw in the form of SRTS is increasing in activity in the Mackenzie Delta region, and serves as an indicator of the potential impacts that climate variability and change may have on freshwater ecosystems. The results of this study did not support the hypothesis that SRTS would deliver significant amounts of nutrients to adjacent lakes, leading to eutrophication. Instead, water-column nutrient concentrations varied negatively with or were unrelated to SRTS activity. However, further investigation into the possibility of biological uptake, the sequestration of nutrients in the lake sediments and the pattern of relative catchment size in SRTS-affected lakes is required to obtain a more complete understanding of the importance of SRTS in altering nutrient supply. Although the results of this study do not support the eutrophication hypothesis, the impacts of SRTS on nutrient concentrations in the study lake systems remain considerable and merit further study.

2.6 References

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The effects of thawing permafrost on chlorophyll *a*, nutrient and light relationships in small tundra lakes

Abstract

Twenty-two tundra lakes, half affected by shoreline retrogressive permafrost thaw slumping (SRTS) and half unaffected were considered in a comparative analysis to determine whether nutrient concentrations, water colour and chlorophyll *a* concentrations differed between lake types. This analysis was followed by a comparison of the phosphorus-chlorophyll *a* relationship between lake types, and finally by a model selection analysis to determine the best predictors of chlorophyll *a* concentration. Chlorophyll *a*, total phosphorus (TP), total dissolved nitrogen (TDN) and dissolved organic carbon (DOC) concentrations, and water colour were higher in unaffected lakes than in SRTS-affected lakes. The TP-chlorophyll *a* relationship was also different between lake types, with a higher slope in SRTS-affected lakes than in unaffected lakes. Finally a model selection analysis using Akaike's Information Criterion (AIC) indicated that water colour was the best predictor of chlorophyll *a* in unaffected lakes, but the interaction term TPxTDN was the best predictor in SRTS-affected lakes. The results indicate that phytoplankton are limited by light availability related to high water colour in unaffected lakes, but not in SRTS-affected lakes, where nutrients are more limiting. The difference in pelagic light availability means that, for a given TP concentration, SRTS-affected lakes have higher phytoplankton biomass than unaffected lakes.

Keywords: tundra lakes, shoreline retrogressive thaw slump, comparative study design, phosphorus, nitrogen, organic carbon, chlorophyll *a*, AIC model selection.

3.1 Introduction

The impacts of climate change are expected to be particularly significant in the Arctic (Wrona et al. 2005, Anisimov et al. 2007, Furgal and Prowse 2008), and permafrost thaw is expected to occur in those areas predicted to experience an increase in air temperature (Rouse et al. 1997, Walsh et al. 2005). Active layer deepening in the Arctic is projected to increase by approximately 30-100% and the areal extent is expected to decrease by 20-90% by the year 2100 (reviewed in Frey and McClelland 2009). In areas of ice-rich permafrost, retrogressive thaw slumps may form as a result of permafrost thaw, and these slumps can and often do occur along the shoreline of lakes (Lantz and Kokelj 2008). This shoreline retrogressive thaw slumping (SRTS) is increasing in occurrence in concert with an increase in air temperatures in the western Canadian Arctic (Lantz and Kokelj 2008).

Nutrients, along with other solutes, may be delivered to freshwater systems from thawing permafrost. For example, increased nutrient concentrations were observed in Alaskan streams within the Toolik Lake watershed that were running directly over areas of degrading permafrost or had thermokarst features in their contributing catchments (Hobbie et al. 1999, Bowden et al. 2008). Permafrost is estimated to contain more carbon than the current atmospheric supply (Schuur et al. 2008), and permafrost thaw is expected to release this carbon, some of which will be transported to freshwater systems via infiltrating runoff and thermokarst development (Prowse et al. 2006).

SRTS that penetrates the permafrost layer can release concentrated solutes (Kokelj and Lewkowitz 1999, Kokelj and Burn 2005). Thawing permafrost may thus act as a source of nutrients, specifically phosphorus, nitrogen and organic carbon, in addition to the ions that were

released to runoff and receiving lakes with permafrost thaw (Kokelj et al. 2005). Hobbie et al. (1999) predicted that an increased supply of phosphorus resulting from localized permafrost thaw would generally lead to eutrophication through stimulation of algal productivity, potentially leading to an increase in the number of trophic levels in an Alaskan lake. However, in considering the well-documented influence of phosphorus on phytoplankton biomass, Flanagan et al. (2003) found that phytoplankton biomass in arctic lakes did not respond to phosphorus concentrations as strongly as phytoplankton in, for example, temperate lakes. This was thought to be due to the relatively low air and water temperatures in the Arctic. The response of arctic lake ecosystems to increased nutrient availability may therefore depend on other environmental conditions.

The objective of this study was to determine whether SRTS activity and the associated release of nutrients has led to nutrient enrichment in arctic lakes. The hypothesis that intense localized permafrost thaw (as represented by SRTS) will lead to the eutrophication of arctic freshwaters, specifically an increase in nutrient supply and primary productivity, was tested by comparing nutrient concentrations and phytoplankton biomass and size in two lake-type populations (SRTS-affected and unaffected). The unaffected lakes were used as indicators of conditions in SRTS-affected lakes before the thaw-slump disturbance. In addition, the significant factors controlling algal enrichment were compared between lake types in a model selection analysis. As a related aside, and because previous results from SRTS affected lakes have been equivocal (Thompson 2009), pooled runoff from within four SRTS sites were sampled to estimate the potential nutrient supply in SRTS runoff.

3.2 Background

The conditions for pelagic biota in arctic lakes differ from more well-studied temperate lakes in several ways, each of which influence the process and possibility of eutrophication. Arctic lakes have been characterized as low productivity systems (Shortreed and Stockner 1986), and Flanagan et al. (2003) found that, for a given water-column concentration of phosphorus, chlorophyll *a* was lower in arctic lakes ($\geq 60^\circ\text{N}$) than in lakes at lower latitudes. Low temperatures in arctic lakes as well as food web effects, including unrestricted zooplankton grazing pressure in relatively unproductive lakes with few trophic levels, were suggested as possible explanations for the disparity in phytoplankton biomass. Climate warming, and particularly, longer open water periods, were expected to increase the response of phytoplankton biomass to phosphorus in arctic lakes (Flanagan et al. 2003). However, eutrophication of tundra lakes may involve additional controls and mechanisms, outlined below.

Contrary to the prediction of eutrophication (Hobbie et al. 1999), SRTS activity was most related to high concentrations of several major ions across a population of 59 SRTS-affected and unaffected tundra lakes (Thompson et al. 2009). Lake water phosphorus and nitrogen were not related to SRTS, but to maximum lake depth (z_{max}) and lake area:catchment area ratios, respectively (Thompson et al. 2009). This may be explained by the biological uptake of nutrients. Bowden et al. (2008), for example, hypothesized that nitrogen and phosphorus enrichment that occurred immediately downstream of thermokarst features in Alaska was significantly diminished within 1-2 km downstream because of in-stream biological uptake. Although no evidence of nutrient uptake is apparent in thermokarst-affected tundra lakes, macrophyte and benthic invertebrate biomass were significantly higher in SRTS-affected than unaffected lakes in

a small subset of 8 lakes (Mesquita et al. 2008). This high primary producer biomass may be the result of nutrient enrichment, or light subsidies produced by the change in water colour related to SRTS activity (Mesquita et al. 2008). The necessary assumption in both streams and lakes would be that primary producers were highly resource-limited and capable of rapid nutrient uptake once it was made available through permafrost thaw. The sequestering of phosphorus by iron in tundra lake sediments is another, possibly related, process by which phosphorus may be removed from the water column to the sediments (Prentki et al. 1980). Thompson et al. (2008) found that the addition of SRTS sediments and melt water to humic lake water decreased the coloured dissolved organic matter (CDOM) concentrations and hypothesized that CDOM-associated nutrients may have also been removed via the proposed sedimentation process. If SRTS is in fact acting as a source of nutrients, the concentration of these nutrients in the receiving lakes may not reflect SRTS activity due to these competing removal processes.

Light limitation may also cause differences in the primary producer biomass of SRTS-affected and unaffected lakes. The above-mentioned removal of CDOM from the incubated lake water was indicated by lower absorbance and water colour of the humic water (Thompson et al. 2008). Adsorption of CDOM to basic cations and/or clay particles in the slump sediments was thought to be responsible for the shift in water transparency (Thompson et al. 2008). Because humic conditions can lead to light limitation of phytoplankton productivity (Jones 1992, Klug 2002), and because lakes unaffected by slumping have higher water colour and DOC concentrations (Kokelj et al. 2005), light limitation in lakes unaffected by slumping can limit phytoplankton growth. This pattern may be complicated by interactions between major ions and DOM, which affect nutrient availability (Jackson and Hecky 1980, Klug 2005). High molecular

weight humic material can bind phosphorus and metals (including the micronutrient iron), and because of their size, remain relatively biologically unavailable (Wetzel 2001). In addition, organic matter can be a source of nitrogen and phosphorus, depending on its particular source, and DOC can act as an energy source for planktonic bacteria (Williamson et al. 1999, Klug 2005).

Finally, the response of phytoplankton to nutrient enrichment, particularly to TP, can be moderated by a shift in average phytoplankton cell size due to preferential herbivory. Watson et al. (1992) proposed that a sigmoid relationship between phosphorus and phytoplankton biomass resulted from the logistical shift in the ratio of cell size-determined edible vs. inedible algae biomass. They determined that the sigmoid relationship largely reflected changes in inedible algal biomass. Edible algal biomass was dominant where phosphorus $<0.010 \text{ mg L}^{-1}$, but inedible algal biomass became dominant at higher phosphorus concentrations. This pattern can result from preferential herbivory on edible forms by higher trophic levels (Watson et al. 1992). While examination of higher trophic level biomass and herbivory pressure was beyond the scope of this study, measurement of phytoplankton size ratio (i.e., edible vs. inedible) will provide an indication of possible shifts in SRTS-affected and unaffected lakes.

The following analysis will focus on phytoplankton biomass dynamics (estimated by chlorophyll *a* concentration) and will involve water colour, nutrient concentration, cell size ratio and bacterioplankton density data. In particular, each of the possible predictor variables considered in the model selection analysis can influence chlorophyll *a* concentrations in the study lakes as outlined above. TP and TDN are both thought to limit phytoplankton growth in arctic lakes (Shortreed and Stockner 1986, O'Brien et al. 1992, Levine and Whalen 2001) and co-

limitation by nitrogen and phosphorus is common in global lakes. High-water colour lakes are known to have light-limited phytoplankton and DOC may act as both a source of nutrients and as a component of light-limiting coloured humic material (Jackson and Hecky 1980, Jones 1992, Klug 2005).

3.3 Methods

3.3.1 Study Area

The study area is comprised of a band of hydrologically isolated upland lakes that are bordered on the east by large marine-influenced lakes and on the west by the Mackenzie Delta. The area covers a northward gradient of decreasing annual total precipitation and mean annual temperatures (mean annual temperature: -8.8 C at Inuvik and -10.2 C at Tuktoyaktuk, annual precipitation: 248 mm at Inuvik and 139 mm at Tuktoyaktuk) (Environment Canada 2008), and includes the transition from brush tundra (alder and willow cover) in the south to open tundra in the north. This local vegetation transition generally coincides with the extent of an intense fire that occurred in 1968, with the previously burned areas now covered by the brush vegetation.

The tundra uplands area is underlain largely by glacial deposits with carbonate and shale parent material (Rampton 1988), and the underlying permafrost is deep and ice-rich (Mackay 1992). SRTS activity has been found to influence the concentrations of major ions and water colour in the current study lakes (Kokelj et al. 2005), and it was anticipated that the small size and hydrologic isolation of the lakes would maximize potential impacts on nutrient concentrations, making them more detectable.

3.3.2 Lake Sampling

A survey of SRTS-affected and unaffected tundra lakes was undertaken to compare water-column carbon, phosphorus and nitrogen concentrations, and plankton biomass between lake types. Twenty-two lakes were selected along a 150 km north-south transect stretching between Inuvik, NWT and Richards Island on the Beaufort Sea coast, east of the Mackenzie River Delta (Figure 3-1.). Eleven of the study lakes were affected by SRTS while the remaining 11 lakes were unaffected. To control for potential landscape effects (e.g., latitude and catchment vegetation), the study lakes were selected in pairs of SRTS-affected and unaffected systems < 5 km apart along the north-south transect. The lakes were also exclusively first order, which was intended to make the detection of SRTS impacts less complex, since the delivery of solutes to the study systems from upstream lakes and their catchments was eliminated. Water-column conditions were then compared between these populations of SRTS-affected and unaffected lakes.

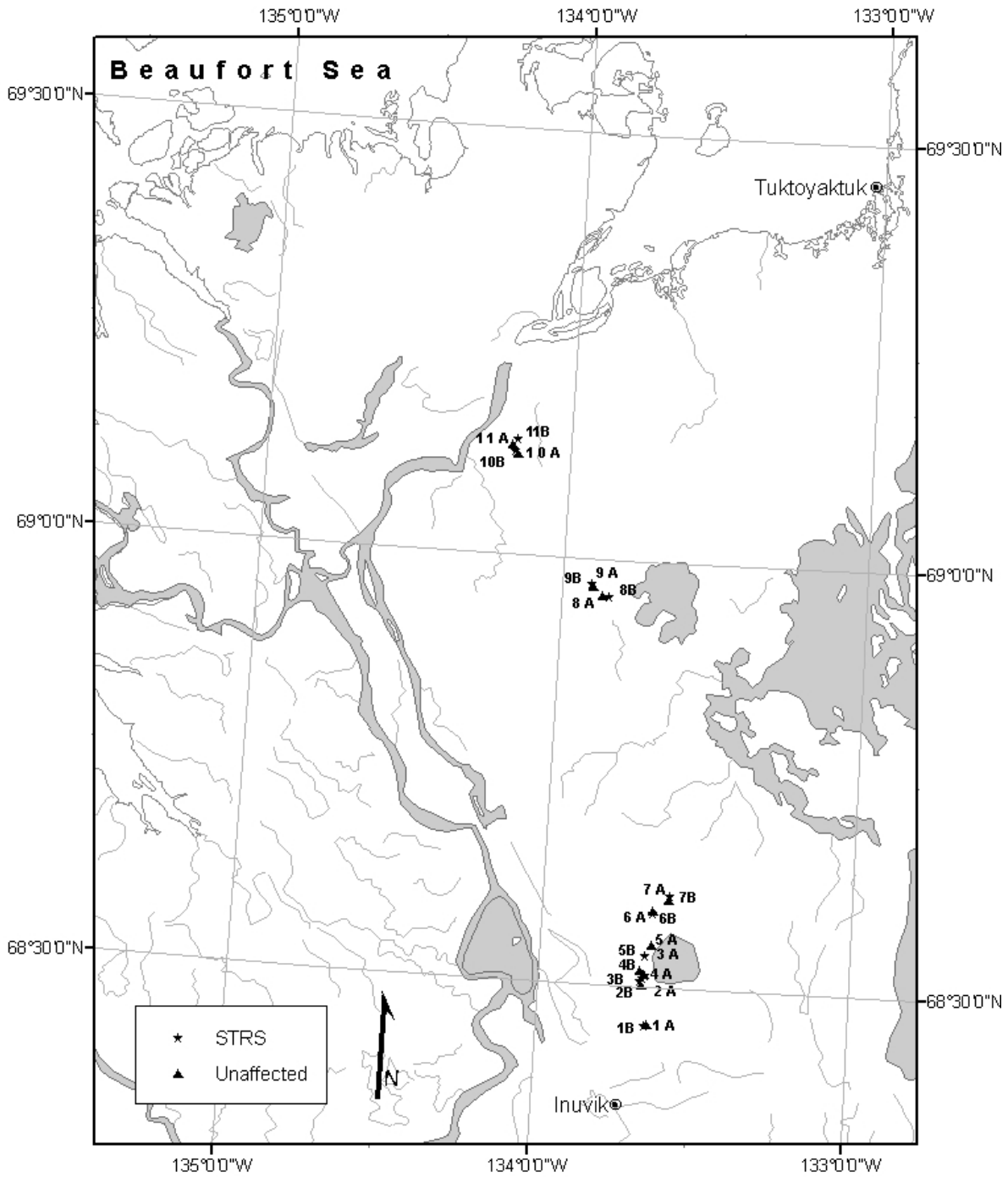


Figure 3-1. Map of sample site locations in the uplands east of the Mackenzie Delta, NWT, Canada. “A” lakes are unaffected by SRTS, “B” lakes are affected by SRTS.

Water-column chlorophyll *a* and nutrient concentrations in the 22 study lakes were

sampled and analyzed during late summer over three years (late August to mid-September, 2005-2007). The sampling regime was subsequently expanded in 2006 to include the analysis of water colour, to better assess the factors limiting plankton growth. This change was made because preliminary analysis of the 2005 data confirmed the finding of Kokelj et al. (2005) that water colour differed between SRTS-affected and unaffected lakes (Jones 1992, Klug 2005). Also starting in 2006, water-column bacterioplankton cell density was measured to account for secondary production that might have been competing with phytoplankton for limiting nutrients. Finally, in 2007, phytoplankton size ratios (<35 µm:whole sample) were measured to better explain phytoplankton response to SRTS. Slump water runoff was also collected in 2007 from some of the study lakes to confirm the potential of the slumps as nutrient sources.

Sampling of the 22-lake set was carried out from a helicopter fitted with floats. Samples were collected from the water column of each lake at 0.5 m below the surface near the middle of the lake, where it was assumed the lakes were deepest. Water samples were shipped for analysis within 24 hours of collection to Environment Canada (EC) laboratories in Saskatoon and Edmonton for analysis of total phosphorus (TP), total dissolved nitrogen (TDN) and dissolved organic carbon (DOC) following standard methods (American Public Health Association 2005). TP was determined spectrophotometrically after digestion and addition of ammonium molybdate. TDN was measured spectrophotometrically after digestion, nitrate reduction and azo dye formation. DOC was obtained with an Apollo 9000 analyzer (Tekmar-Dohrmann, Cincinnati, OH). Additional water samples were collected in 2007 from shoreline slumps on four of the study lakes (lakes 5B, 9B, 10B and 11B). The water was collected when available from pools of standing water within slumped areas that were actively degrading. These samples were analyzed

in EC labs as above for water chemistry parameters only.

Water samples for chlorophyll analysis were filtered through GFC filters at Inuvik, frozen and shipped to EC for analysis. Chlorophyll *a* concentrations (corrected for phaeophytin) were obtained after extraction in 90% ethanol, by measuring absorbance at 665 and 750 nm with a Turner designs 10-AU Digital Fluorometer (Turner Designs, Inc., Sunnyvale, CA) (adapted from Sartory and Grobbelaar 1984). In 2007 only, duplicate water samples for chlorophyll *a* concentration determination were also filtered through 35 µm pore size Nitex mesh before filtering through a GFC filter as above for analysis. This <35 µm fraction was used to calculate the phytoplankton size ratio (<35 µm chlorophyll *a* µg L⁻¹ / whole chlorophyll *a* µg L⁻¹).

Water colour was determined after filtration through GFC glass fibre filters (pore size 1.2 µm) by spectrophotometrically scanning for absorbance from 0-900nm. Absorbance was measured using an Ultrospec 3100 pro spectrophotometer equipped with a 1-cm cuvette (Biochrom, Cambridge, UK). Representative absorbance measurements at 320nm (UV-B, a320nm) and 440nm (photosynthetically active radiation, PAR, a440nm) were corrected for turbidity-related light scattering by subtracting absorbance values at 750nm.

Bacterioplankton enumerations were performed on duplicate lake water samples preserved with formaldehyde. 2-ml subsamples were stained for 5 minutes with 1 ml solution of 10 µgml⁻¹ fluorescent DAPI dye (4',6-diamidino-2-phenylindole) (M.Waiser, personal communication). The subsamples were filtered through black polycarbonate Nucleopore membrane filters. Cells were counted using an epifluorescent compound microscope equipped with an ocular graticule by counting 10 view fields per filter and were averaged before use in statistical analyses (American Public Health Association 1992).

3.3.3 Statistical Analyses

All data were logarithmically (\ln) transformed to obtain normal homoscedastic distributions. The dependent variables TP, TDN, DOC, absorbance at 320 nm and 440nm, chlorophyll *a* concentration, bacterioplankton abundance and phytoplankton size ratios were compared between lake types using two-way ANOVAs, which simultaneously tested the effects of the independent classification variables lake type and sampling year. A further ANOVA analysis was used to determine whether the nutrient (TP, TDN and DOC) concentrations in the water sampled from onshore slumped areas differed from those in the water collected from the adjacent lakes.

The slope of the relationship between TP and chlorophyll *a* was compared between SRTS-affected and unaffected lakes using simple regression on the \ln -transformed data, with a further t-test to compare the regression slope between lake types.

The relationship between chlorophyll *a* concentration and all of the measured predictor variables (nitrogen, phosphorus and dissolved organic carbon concentrations, a combined TDN \times TP concentration term to account for possible co-limitation, and bacterioplankton abundance and absorbance) was explored using Pearson's product moment correlation (significant at Bonferroni corrected $p < 0.05$). Predictor variables that were significantly correlated with chlorophyll *a* concentration were identified and data were pooled across all years. The relationships between chlorophyll *a* concentration and its correlated predictor variables in each lake type were subsequently assessed using Akaike's Information Criterion (AIC). AIC is a model selection method that measures the lack of fit of a given model to the observed data, and

employs a correction factor for the number of parameters in the model (Johnson and Omland 2004). The AIC approach towards model selection was chosen over multiple stepwise regression because AIC makes no assumption of independence between the predictor variables considered. Because the correlations between the predictor variables for each lake type differed (see Results below), using multiple stepwise regression would have required the *a priori* removal of different predictor variables from the analysis for each lake type. In the interest of maintaining a similar starting point for the comparison by lake type of the relationship between chlorophyll *a* and the predictor variables, AIC analysis was used. The availability of an AIC correction for a small sample size (relative to the number of predictors) was also useful in the following analysis.

The AIC for each possible combination of one-predictor through four-predictor variable models (27 in total) using the selected factors was calculated separately for SRTS-affected and unaffected lakes data. Models including TP, TDN and TDN \times TP were excluded due to collinearity between the predictor variables. The AIC correction for small sample size, AIC_c (recommended when sample size/estimated parameters < 40, as in this case) (Burnham and Anderson 1998), was subsequently calculated for all 27 models, and these values were then used to determine the Akaike weight for each model (Johnson and Omland 2004). Finally, the weighted average of each parameter estimate was calculated as the sum of the products of the Akaike weight for every model that included the predictor variable in question and its corresponding regression coefficient (Johnson and Omland 2004). These average parameter estimates for the factors influencing chlorophyll *a* concentration were compared via inspection for SRTS-affected and unaffected lake types.

Post-hoc regression analyses for each lake type were performed using the predictor

variable(s) with the highest Akaike weights. Analyses were completed using SPSS 13.0 (SPSS Inc., Illinois, USA).

3.4 Results

3.4.1 Comparative ANOVAs

Means and standard errors for all variables measured in the pooled 2005, 2006 and 2007 lake surveys are presented by lake type in Table 3-1. Several detection limit values for TP in 2006 led to the removal of data for 6 SRTS-affected and 4 unaffected lakes from the TP ANOVA, correlation and AIC analyses, so that overall $n = 27$ for SRTS-affected lakes and $n = 29$ for unaffected lakes in the TP analysis.

Table 3-1. Mean and standard error values for measured parameters in the 22 lake surveyed from 2005 to 2007, presented by lake type.

Parameter	Units	Unaffected		SRTS-affected	
		Mean	±SE	Mean	±SE
<i>i) Abiotic variables</i>					
Total phosphorus	mg L ⁻¹	4.1 x10 ⁻²	0.6 x10 ⁻²	1.9 x10 ⁻²	0.3 x10 ⁻²
Total dissolved nitrogen	mg L ⁻¹	6.38 x10 ⁻¹	0.37 x10 ⁻¹	4.65 x10 ⁻¹	0.03 x10 ⁻¹
Dissolved organic carbon	mg L ⁻¹	2.11 x10 ¹	0.11 x10 ¹	1.41 x10 ¹	0.09 x10 ¹
Absorbance (UV)*#	a320nm	2.42 x10 ⁻¹	0.24 x10 ⁻¹	0.06 x10 ⁻¹	0.01 x10 ⁻¹
Absorbance (PAR)*#	a440nm	3.23 x10 ⁻²	0.41 x10 ⁻²	0.62 x10 ⁻²	0.11 x10 ⁻²
<i>ii) Biotic variables</i>					
Chlorophyll <i>a</i>	µg L ⁻¹	7.0	0.8	3.9	1.5
Phytoplankton size ratio†	<35µm:whole µg L ⁻¹ chlorophyll <i>a</i>	9.20 x10 ⁻¹	0.40 x10 ⁻¹	9.23 x10 ⁻¹	0.30 x10 ⁻¹
Bacterioplankton density #	cells mL ⁻¹	8.59 x10 ⁵	1.13 x10 ⁵	7.88 x10 ⁵	0.54 x10 ⁵

3.4.1.1 Chlorophyll *a*, TP, TDN, DOC, absorbance

Chlorophyll *a*, TP, TDN, DOC and absorbance at 320nm and 440nm were significantly different between unaffected and SRTS-affected lakes (Table 3-2, Figures 3-2 to 3-5). Mean values for chlorophyll *a*, TP, TDN, absorbance and DOC were all higher in unaffected lakes than in SRTS-affected lakes (Table 3-1). Chlorophyll *a*, TP, TDN and water colour were not significantly different between sampling years (Table 3-2) and are shown pooled across years for all sampling dates in Figures 3-2, 3-3 and 3-5. Both DOC and a440nm were significantly different between years, between 2006 and 2007 for a440nm (Table 3-2) and 2005 and 2007 for DOC (Figure 3-4, Table 3-2).

Table 3-2. ANOVA table for parameters measured in 22 survey lakes from 2005 to 2007. Dependent parameters were tested for differences according to lake type (SRTS-affected or unaffected) and by year of sampling. Results with $p < 0.05$ are in bold. Interaction terms (lake type*year) were also tested but were not found to be significant for any of the parameters ($p > 0.1$ for all) except for bacteria cell density.

Parameter	Sample size	Lake Type (SRTS status)			Year (2005, 2006, 2007)			Post Hoc differences (Tukey's)
		F	df	p	F	df	p	
<i>i) Abiotic variables</i>								
Total Phosphorus	60	11.622	1	0.001	1.390	2	0.258	
Total Dissolved Nitrogen	66	15.094	1	0.000	0.228	2	0.797	
Dissolved Organic Carbon	66	34.915	1	0.000	5.944	2	0.004	2005 vs. 2007
Absorbance (320nm)	43	85.877	1	0.000	2.184	1	0.147	
Absorbance (440nm)	43	62.838	1	0.000	4.524	1	0.040	(only sampled 2006 and 2007)
<i>ii) Biotic variables</i>								
Chlorophyll <i>a</i>	66	24.89	1	0.000	0.103	2	0.902	
Phytoplankton size ratio	22	0.005	1	0.942	-	-	-	(only sampled 2007)
Bacterioplankton density	22	0.078	1	0.782	14.357	1	0.000	(only sampled 2006 and 2007)

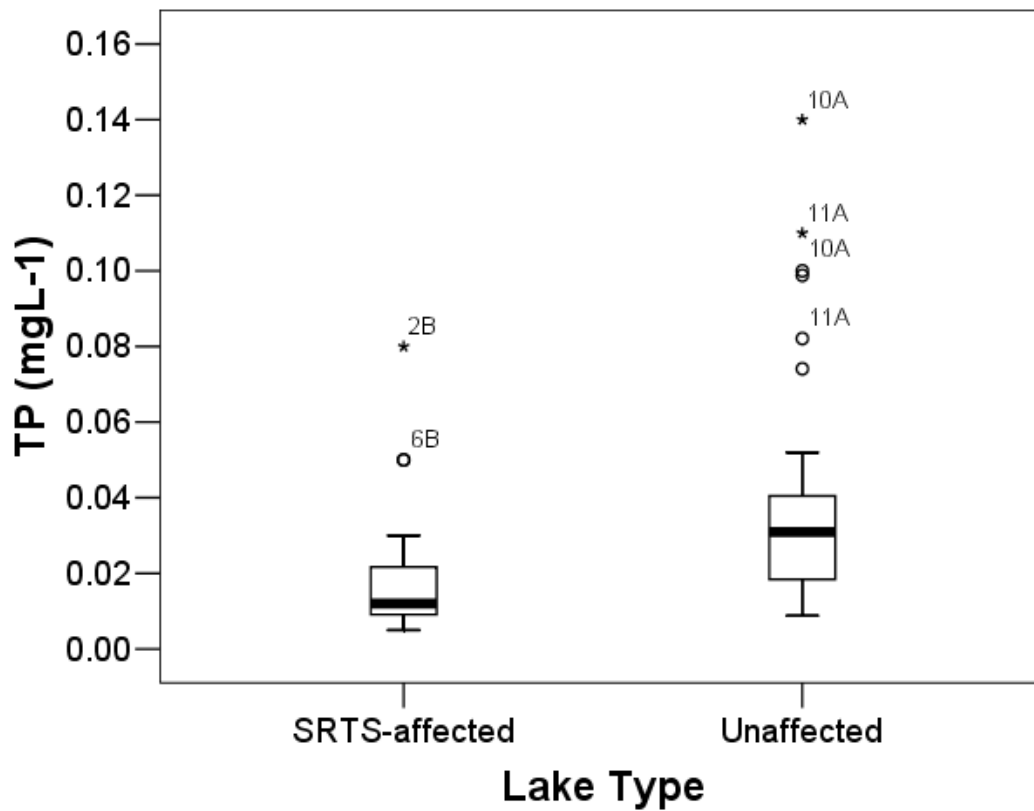


Figure 3-2. Total phosphorus (TP) concentrations in 22 tundra lakes pooled for 2005, 2006 and 2007. The plot is divided into SRTS-affected and unaffected lakes. The box plot shows the median (thick line), the interquartile range (box), outliers (within 1.5 and 3 box lengths of the upper box edge) and extreme values (more than 3 box lengths away from the upper box edge). Outliers and extreme values are labeled with the appropriate lake name.

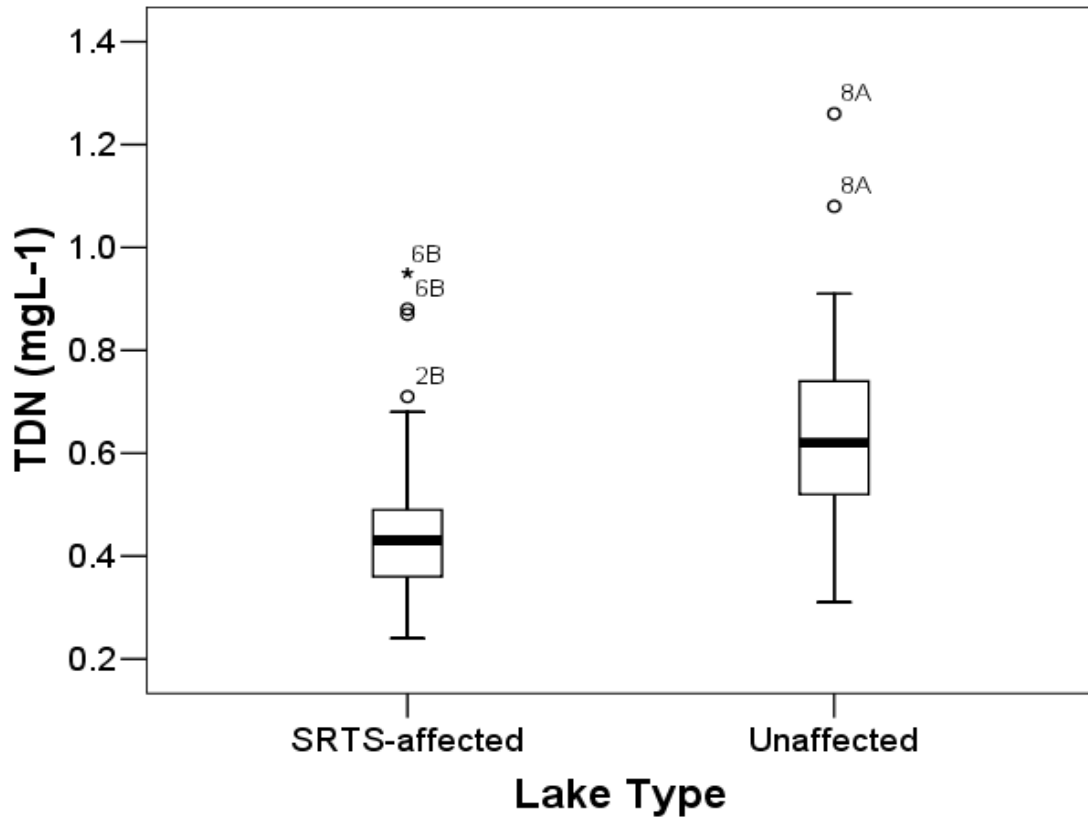


Figure 3-3. Total dissolved nitrogen (TDN) concentrations in 22 tundra lakes pooled for 2005, 2006 and 2007. The plot is divided into SRTS-affected and unaffected lakes. The box plot shows the median (thick line), the interquartile range (box), outliers (within 1.5 and 3 box lengths of the upper box edge) and extreme values (more than 3 box lengths away from the upper box edge). Outliers and extreme values are labeled with the appropriate lake name.

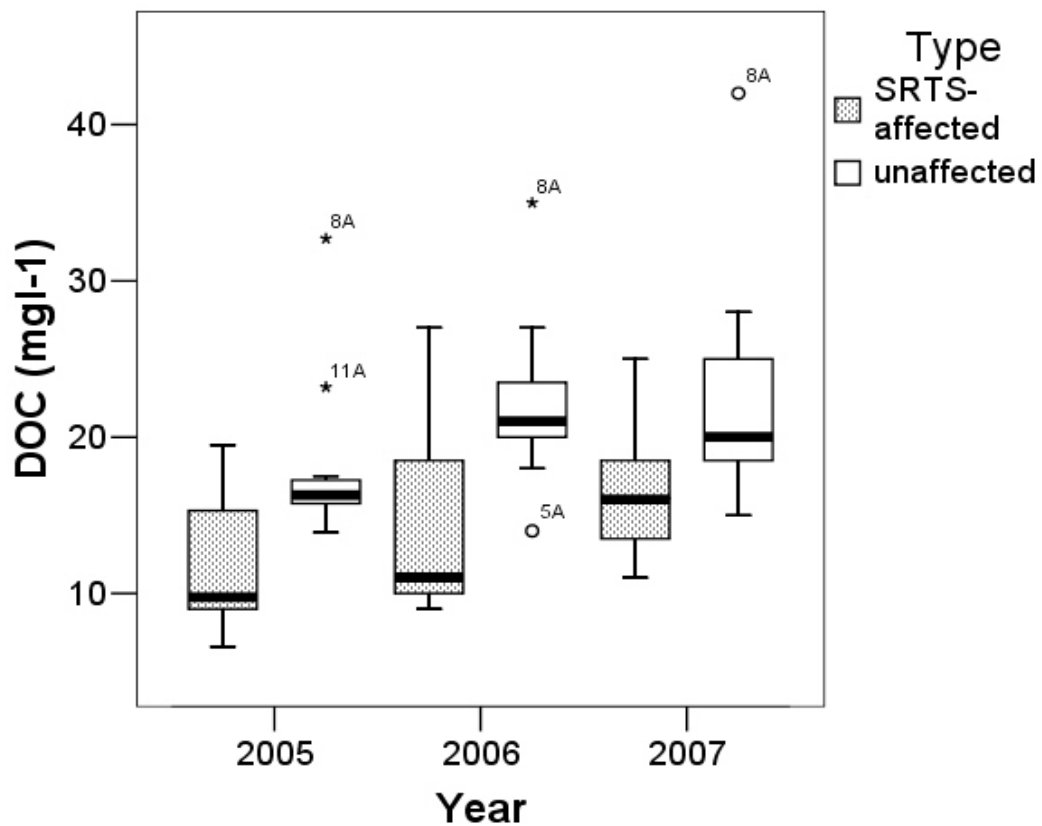


Figure 3-4. Dissolved organic carbon (DOC) concentrations in 22 tundra lakes shown separately for 2005, 2006 and 2007. The annual plots are divided into SRTS-affected and unaffected lakes. The box plots show the median (thick line), the interquartile range (box), outliers (within 1.5 and 3 box lengths of the upper box edge) and extreme values (more than 3 box lengths away from the upper box edge). Outliers and extreme values are labeled with the appropriate lake name.

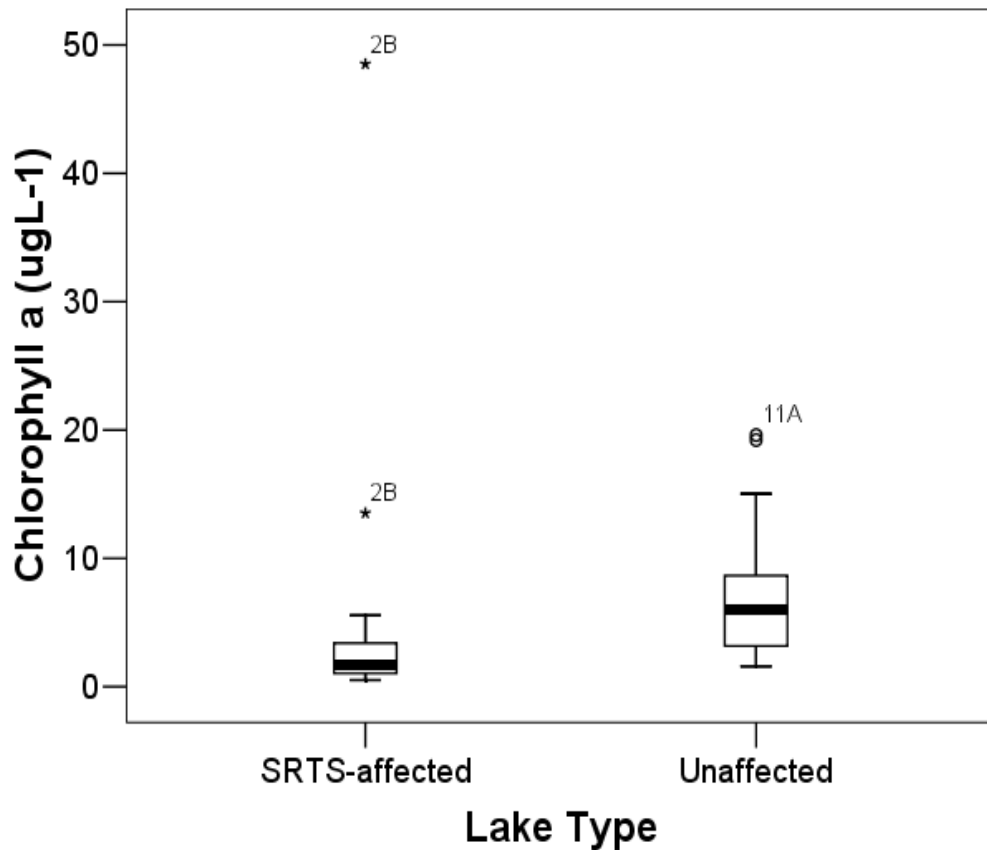


Figure 3-5. Chlorophyll *a* concentrations in 22 tundra lakes pooled for 2005, 2006 and 2007. The plot is divided into SRTS-affected and unaffected lakes. The box plot shows the median (thick line), the interquartile range (box), outliers (within 1.5 and 3 box lengths of the upper box edge) and extreme values (more than 3 box lengths away from the upper box edge). Outliers and extreme values are labeled with the appropriate lake name.

From inspection of the box plots, it is apparent that the concentrations of TP and chlorophyll *a* in the study lakes are highly variable. Outlier high TP values were found in unaffected lakes 10A and 11A from 2005 to 2007 (with the exception of 11A in 2007). Outlier high TP and chlorophyll *a* values were found in SRTS-affected lake 2B in 2005. No reason for these high values is currently known, however the concentration values across all of the study lakes is quite variable. An analysis of equality of variance using Levene's test found no difference in variation according to lake type in transformed TP, TDN, chlorophyll *a* and DOC data ($p <$

0.05). DOC and TDN were also consistently high in unaffected lake 8A. That lake has a small lake area to catchment area ratio (LA:CA = 0.09) that varied inversely with DOC and TDN in a larger lake survey analysis in the study area (Thompson 2009a).

3.4.1.2 Bacterioplankton abundance and phytoplankton size ratio

Bacterioplankton cell counts in 2006 and 2007 were not significantly different between SRTS types (Table 3-2). However, bacteria cell density was significantly higher in 2006 than in 2007 (Figure 3-6), especially in unaffected lakes, as the interaction term between lake type and year was also significant ($F= 4.226$, $df= 1$, $p= 0.046$).

There was no significant difference in phytoplankton chlorophyll *a* size ratio (<35 μ m:whole sample) between the slump-affected and unaffected lakes (Table 3-2).

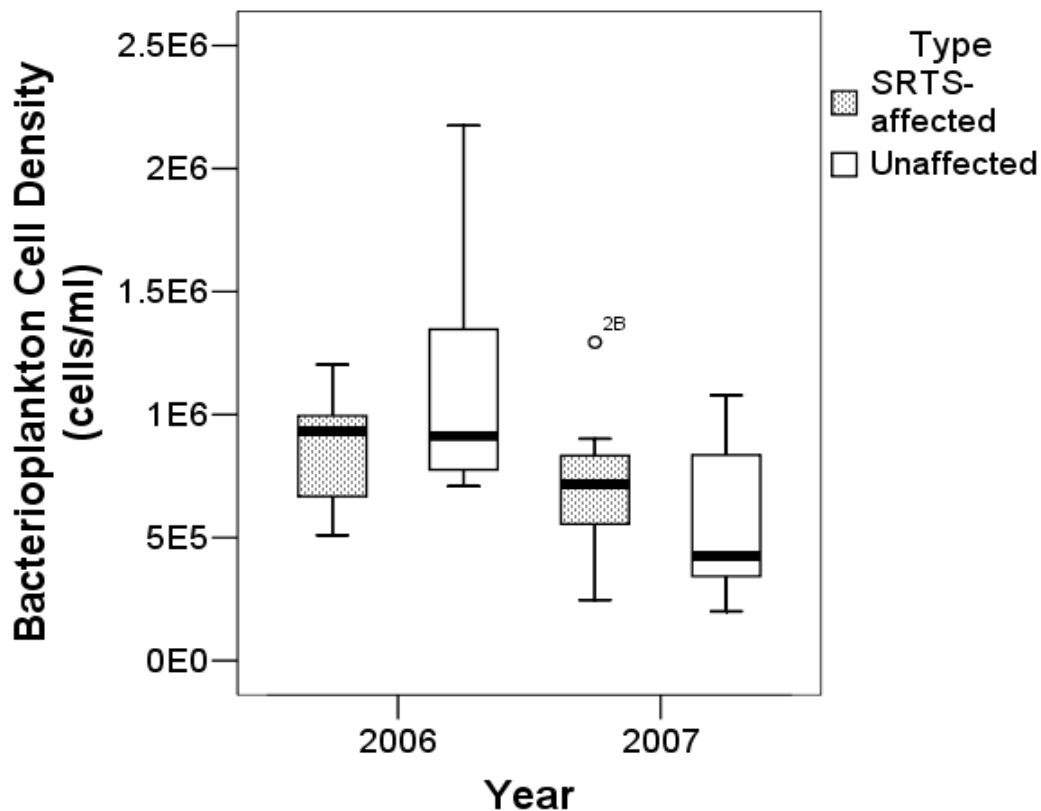


Figure 3- 6. Bacterioplankton cell density in 22 tundra lakes shown separately for 2006 and 2007. The annual plots are divided into SRTS-affected and unaffected lakes. The box plots show the median (thick line), the interquartile range (box), outliers (within 1.5 and 3 box lengths of the upper box edge) and extreme values (more than 3 box lengths away from the upper box edge). Outliers and extreme values are labeled with the appropriate lake name.

3.4.2 Chlorophyll *a* and TP regressions

The regression between logTP and log chlorophyll *a* was significant in both SRTS-affected ($F= 33.813$, $df= 26$, $p= 0.000$) and unaffected lakes ($F= 10.625$, $df= 28$, $p= 0.003$) (Figure 3-7). The regression equation for SRTS-affected lakes was $\log(\text{chlorophyll } a) = 0.569 + 0.758 * (\log(\text{TP}))$, ($R^2= 0.558$) and in unaffected lakes, it was $\log(\text{chlorophyll } a) = -0.062 + 0.531 * (\log(\text{TP}))$ (adjusted $R^2= 0.256$). TP explained more of the variation in chlorophyll *a* in SRTS-affected than unaffected lakes, and the difference between lake type regression slopes was significant ($t=1.990$, $df=55$, $p= 0.052$).

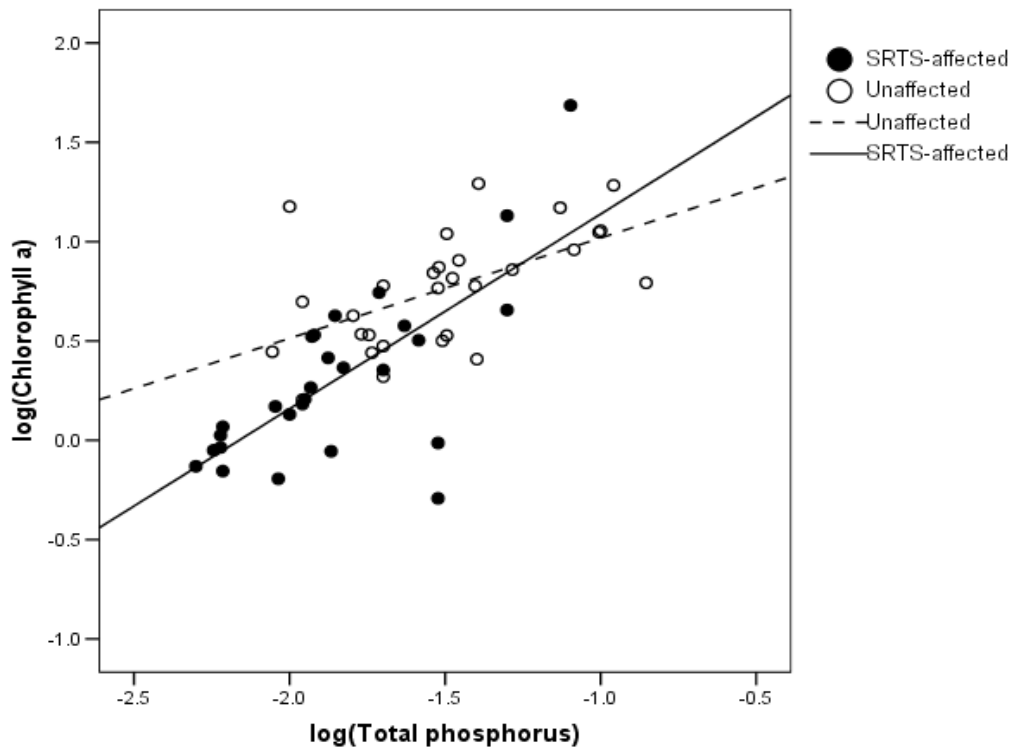


Figure 3-7. Scatter plot of log(Total phosphorus) and log(Chlorophyll *a*) with linear regression lines for SRTS-affected and unaffected lakes. Solid circles and line are SRTS-affected lakes and empty circles and dashed line are lakes unaffected by SRTS. The lake type slopes are significantly different from each other ($p=0.052$).

3.4.3 Correlations

Pearson's product moment correlation matrices for TP, TDN, TDN \times TP, DOC, absorbance, bacterioplankton cell density and chlorophyll *a* were calculated separately for SRTS-affected and unaffected lakes (Table 3-3). Of the significant correlations, chlorophyll *a* was most highly correlated (high *r* value) with $a_{320\text{nm}}$ and $a_{440\text{nm}}$ in lakes unaffected by SRTS. Apart from absorbance, chlorophyll *a* was most highly correlated with TP and DOC. In SRTS-affected lakes, TP, TDN and DOC, in that order, were most highly correlated with chlorophyll *a*. Bacterial abundance and, unexpectedly, TDN \times TP was not significantly correlated with chlorophyll *a* in

either lake type.

Table 3-3. Correlation coefficients (Pearson's r) for five regression factors considered as explanatory variables for phytoplankton and bacterioplankton biomass estimates. Significant correlations ($p < 0.05$ after Bonferroni adjustment) are in bold. For SRTS-affected lakes, TP n = 27, TDN n = 33, DOC n = 33, a320nm n = 22, a440nm n = 22 and bacterial abundance n = 11. For unaffected lakes, TP n = 29, TDN n = 33, DOC n = 33, a320nm n = 21, a440nm n = 21 and bacterial abundance n = 11.

a) SRTS-affected Lakes

	TP	TDN	TDNxTP	DOC	a320nm	a440nm	Bac. Abundance
TDN	0.842						
TDNxTP	0.984	0.925					
DOC	0.598	0.661	0.642				
a320nm	0.413	0.553	0.478	0.687			
a440nm	0.532	0.556	0.560	0.577	0.897		
Bac. Abundance	0.686	0.721	0.724	0.476	0.254	0.287	
Chlorophyll <i>a</i>	0.709	0.617	0.404	0.536	0.293	0.200	0.494

b) Unaffected Lakes

	TP	TDN	TDNxTP	DOC	a320nm	a440nm	Bac. Abundance
TDN	0.413						
TDNxTP	0.957	0.659					
DOC	0.450	0.708	0.597				
a320nm	0.685	0.440	0.703	0.750			
a440nm	0.695	0.485	0.725	0.711	0.971		
Bac. Abundance	0.095	0.117	0.114	0.365	0.338	0.277	
Chlorophyll <i>a</i>	0.562	0.301	0.289	0.421	0.673	0.635	0.289

It is interesting to note the differences in correlation patterns between the lake types. In SRTS-affected lakes, TP and TDN were highly positively correlated ($r > 0.84$) but in unaffected lakes TP and TDN were not significantly correlated. Chlorophyll *a* was also positively correlated with TP, TDN and DOC in SRTS-affected lakes, but in unaffected lakes, chlorophyll *a* was positively correlated with a320nm and a440nm, and not correlated with TDN and DOC. It would appear from these results that chlorophyll *a* is related to TP, TDN and DOC in SRTS-affected lakes, but is more highly correlated with water colour in unaffected lakes.

3.4.4 Chlorophyll *a* model selection

Since TP and DOC were significantly correlated with chlorophyll *a* in both lake types and SRTS-affected lakes, respectively, they were entered into the AIC model selection analysis. TDN and a320nm, which were correlated with chlorophyll *a* in SRTS-affected and unaffected lakes, respectively, were also entered into the AIC analysis. The inclusion of a320nm restricted the AIC analysis to those years in which water colour was sampled - 2006 and 2007.

It was decided not to include a440nm in the analysis, because a320nm and a440nm were so highly correlated ($r = 0.971$) and a440nm was shown to differ between 2006 and 2007 in the ANOVA analysis, making the pooling of data across sample years less desirable. Although the inclusion of five predictor variables (including TDNxTP) with a relatively small sample size negatively affects the adjusted R^2 value of the “global model” (which includes all predictor variables), the exploratory nature of the analysis and the evidence in favour of including the selected predictors justifies their inclusion in the AIC analysis of the chlorophyll *a* model. AIC_c calculations for the two factors influencing chlorophyll *a* included data from 16 SRTS-affected and 18 unaffected “lake years” pooled from the 2006 and 2007 surveys.

The single-model Akaike weights and AIC_c weighted average parameter estimates for the predictor variables are presented in Table 3-4. In unaffected lakes, a320nm had the highest estimate, while in SRTS-affected lakes, the TDNxTP estimate was the highest. Exploratory post-hoc regressions of chlorophyll *a* for each lake type were calculated using the predictor variable(s) with the highest Akaike weight and average parameter estimate. For unaffected lakes, a linear regression with a320nm was significant ($F=13.281$, 17 df, $p=0.002$) and the R^2 was 0.42 (0.45

unadjusted). In SRTS-affected lakes, the linear regression with TDN was significant ($F=6.521$, 15 df, $p=0.023$) and the R^2 was 0.27 (0.32 unadjusted). The significant regression coefficients for each predictor are listed in Table 3-4. The unaffected lakes regression accounted for just under half of the variability in chlorophyll *a*, which indicates the substantial influence of a_{320nm} as a predictor variable in those lakes. In contrast, TDN \times TP accounted for about a quarter of the variation in chlorophyll *a* in SRTS-affected lakes, indicating that other factors might substantially influence chlorophyll *a* concentration. An exploratory regression was undertaken for the SRTS-affected lakes of chlorophyll *a* on TDN \times TP and DOC, which had the second highest weighted parameter estimate. Adding this second predictor variable increased the R^2 for the significant regression ($F=3.977$, 15 df, $p=0.045$) to just 0.38 (0.28 unadjusted), so that adding more of the considered predictors to the SRTS-affected regression does not appear to increase the R^2 to a level comparable with that of the unaffected lakes regression.

Table 3-4. Akaike weights from the single-predictor regression models on chlorophyll *a*, AICc-weighted average parameter estimates from the 27 considered models and post-hoc regression coefficients for the predictor variables used in the chlorophyll *a* model selection analysis.

a) SRTS-affected Lakes			
	W_i (Akaike weight)	Weighted average parameter estimate	Post-hoc regression Coefficient
TDN \times TP	0.50	1.07	0.56
TDN	0.21	0.28	
TP	0.15	0.33	
DOC	0.12	0.39	
CORa320nm	0.02	0.00	

b) Unaffected Lakes			
	W_i (Akaike weight)	Weighted average parameter estimate	Post-hoc regression Coefficient
CORa320nm	0.89	0.71	0.67
TP	0.05	0.34	
TDN \times TP	0.03	-0.10	
DOC	0.02	-0.03	
TDN	0.00	-0.26	

3.4.5 Landscape Geochemistry

Examination of nutrient concentrations in the standing water collected from the slumped areas within four lake catchments (Table 3-5) revealed that they were up to two orders of magnitude higher in the standing water than in the lakes sampled. TP, TDN and DOC concentrations were all significantly different in the onshore slump water compared to in the adjacent lakes (Table 3-5). However, because there was no observed standing water in catchment areas unaffected by slumping that could be analyzed, the relative importance of slump-derived nutrients as part of those delivered from the entire catchment landscape is unknown.

Table 3-5. Mean nutrient concentrations with standard error by sample type for water collected from standing pools

in actively degrading shoreline thaw slump areas and from the corresponding lake surface water in autumn 2007. ANOVA tables are presented for an analysis of logarithmically transformed (*ln*) nutrient concentration data by sample type from 4 SRTS-affected lakes ($n = 4$).

	TP (mgL ⁻¹)		ANOVA Table		
	Mean	±SE of the mean	F	df	p
Slump water	0.465	0.210	19.366	1	0.005
Lake water	0.011	0.002			

	TDN (mgL ⁻¹)		ANOVA Table		
	Mean	±SE of the mean	F	df	p
Slump water	1.640	0.701	19.366	1	0.040
Lake water	0.405	0.036			

	DOC (mgL ⁻¹)		ANOVA Table		
	Mean	±SE of the mean	F	df	p
Slump water	48.0	18.1	7.363	1	0.035
Lake water	16.0	0.8			

3.5 Discussion

Mean TP, TDN and DOC were significantly different in unaffected lakes compared to SRTS-affected lakes. The relatively low DOC concentrations in SRTS-affected lakes agrees with previous observations (Kokelj et al. 2005). The pattern of lower TDN and TP in these lakes does not support the hypothesis that SRTS makes these nutrients more available in the water column of tundra lakes. However, TP, TDN and DOC concentrations were significantly higher in runoff pools within SRTS areas than in the study lakes, which indicates that SRTS could serve as a considerable source of these nutrients to the adjacent lakes. If lakes affected by permafrost slumping were receiving nutrient subsidies from SRTS, this supplemental nitrogen and phosphorus was not detectable in the surface water of the lakes.

One explanation for this apparent paradox is that within-lake sinks, with mechanisms such as biological uptake and loss to sediment sequestration, are removing SRTS-derived nutrients from the water column. For example, additions of nitrogen and phosphorus to enclosures in an Alaskan lake increased the water-column nutrient content for the first two years of application, after which pelagic concentrations fell (O'Brien et al. 1992). Phytoplankton had increased in number and productivity to significantly lower water-column nutrient concentrations despite continued additions. Phosphorus can also be sequestered from the water column into lake sediments, so that phosphorus additions may have no effect on water-column concentrations until the storage capacity of the lake sediments is exhausted (Prentki et al. 1980, Hobbie et al. 1999). Further investigation into the within-lake cycling of nitrogen and phosphorus along with estimates of primary and overall production will be required to determine whether degrading shoreline permafrost is not a significant nutrient source to these tundra lakes.

In addition to the differences in nutrient concentrations between SRTS-affected and unaffected lakes, chlorophyll *a* concentrations were significantly different between lake types. The AIC model selection analysis revealed that chlorophyll *a* was most strongly influenced by TDN \times TP in SRTS-affected lakes, and by water colour measured as $a_{320\text{nm}}$ in unaffected lakes. A possible explanation for the different predictors between lake types is that high water colour in undisturbed lakes inhibits phytoplankton growth, while in the relatively clear SRTS-affected lakes, phytoplankton growth is less related to light availability and more directly reflects nitrogen and phosphorus concentrations.

A significant positive relationship between chlorophyll *a* and TP was expected for lakes in this study area. This well-documented limnological relationship was confirmed by Pienitz et al.

(1997), who conducted a water chemistry survey that included lakes in the forest-tundra and tundra uplands east of the Mackenzie Delta. Total phosphorus and nitrogen concentrations were at low or oligotrophic concentrations in tundra lakes, but were somewhat higher in the forest-tundra zone (Pienitz et al. 1997). The high TN:TP (42:1) and significant correlation between phytoplankton biomass and TP suggested phosphorus limitation of primary production. However, chlorophyll *a* was also at oligotrophic levels (mean 4.0 $\mu\text{g L}^{-1}$ in tundra lakes, 1.4 $\mu\text{g L}^{-1}$ in forest-tundra lakes), in contrast to the relatively high concentrations found in this study for lakes unaffected by slumping ($>7 \mu\text{g L}^{-1}$, Table 3-2). The oligotrophic conditions reported by Pienitz et al. (1997) are similar to those found in the SRTS-affected lakes in this study, the same lakes in which TDN was significantly positively related to chlorophyll *a* concentrations. In addition, the correlations between TDN, TP and chlorophyll *a* were significant in SRTS-affected lakes, but only TP and chlorophyll *a* were correlated in unaffected lakes. This suggests that both TDN and TP limit phytoplankton growth in SRTS-affected lakes, supporting the possibility of TDN \times TP co-limitation.

In contrast, the AIC results indicated water colour-related limitation of chlorophyll *a* in lakes unaffected by SRTS, supported by the TP-chlorophyll *a* regressions that found a stronger relationship between the two variables in SRTS-affected vs. unaffected lakes. Dissolved organic matter (DOM), including DOC, is known to limit the penetration of radiation required for phytoplankton production and growth through the water column (e.g., Jones 1992, Klug 2002). A shift from 5 to 17 mg L^{-1} DOC in experimental lakes in Wisconsin, for example, significantly reduced phytoplankton biomass and production that was comparable to that caused by a shift in P input rate from 5 to 0.5 $\text{mg m}^{-2} \text{d}^{-1}$ (Carpenter et al. 1998). The mean DOC in lakes unaffected by

SRTS (21 mg L^{-1}) was significantly different than in SRTS-affected lakes, supporting the hypothesis of differing light availability between lake types.

Phytoplankton size ratio was not different between slump-affected and unaffected study lakes sampled in 2007. The lack of difference in phytoplankton size ratios between lake types suggests that there is no difference in competition conditions or herbivory according to phytoplankton cell size between lake types, and that the difference in TP-chlorophyll *a* relationships was not related to a shift in phytoplankton community composition. Further sampling would be useful to ensure that this conclusion is consistent over time and across varying levels of herbivory which might be operating in SRTS-affected lakes (Thompson et al. 2009b).

Bacterioplankton biomass was not directly influenced by SRTS activity, since bacterioplankton abundance was not different between SRTS-affected and unaffected lakes. It is unclear whether bacterioplankton may be competing directly or indirectly with phytoplankton in the study lakes. Bacterioplankton and phytoplankton biomass were not significantly correlated with each other, however both were correlated with TP and TDN in SRTS-affected lakes, which suggests competition is a possibility in these lakes.

The effect of bacterioplankton production on phytoplankton growth is complex, and the outcome of competing processes is difficult to project. While bacterioplankton can compete with phytoplankton for phosphorus, DOC use by bacterioplankton can be limited by P availability. Bacterioplankton in humic Swedish lakes were P-limited, while phytoplankton production appeared to be N-limited (Karlsson et al. 2002). The contrasting nutrient limitation between bacterioplankton and phytoplankton might have been partly explained by trophic interactions

between primary and secondary producers. Phytoplankton productivity may be greater than that of bacterioplankton if the phytoplankton community is dominated by phagotrophic flagellates capable of consuming bacteria, despite the inferior ability of phytoplankton to obtain phosphorus (Jansson et al. 1996). Phytoplankton assemblages have yet to be identified in the study lakes, and more extensive sampling of the plankton community is required to investigate the competitive relationship between phytoplankton and bacterioplankton. This should permit the identification or exclusion of bacterioplankton as competitors in nutrient uptake.

Interannual variation in hydrologic conditions did not affect the concentration of nutrients in the study lakes as it was shown to do for major ion concentrations (Kokelj et al. 2008). The relatively wet winters in the study area before the 2005 and 2007 open-water seasons led to more dilute lake water ionic chemistry conditions in late summer, while the relatively dry winter of 2006 led to more concentrated late summer conditions (Kokelj et al. 2008). In contrast, chlorophyll *a*, TP and TDN were not significantly different between the three sampling years, indicating no influence of interannual dilution patterns in either lake type. DOC was significantly different from 2005 to 2007, displaying a pattern of increasing concentration in both slump-affected and unaffected lakes. This is not in agreement with the interannual pattern of relatively dilute ionic conditions in 2005 and 2007, indicating that DOC is not exclusively influenced by supply from the catchment. Indeed nutrients are subject to biological uptake, sedimentation and degradation within the lakes and do not appear to behave as other less labile solutes in these lakes (e.g. major ions, Kokelj et al. 2008).

3.6 Conclusions

Contrary to the prediction of eutrophication in freshwaters influenced by degrading permafrost (Hobbie et al. 1999), phytoplankton in the small tundra lakes east of the Mackenzie Delta does not appear to be affected by nutrients released from SRTS. Despite the apparently abundant supply of nitrogen, phosphorus and organic carbon in runoff pools within SRTS sites, these nutrients are not present in high concentrations in the water column of the adjacent lakes. This does not preclude the possibility of eutrophication in benthic zones of the study lakes, nor the possibility that periphyton, macrophytes, invertebrates and fish (not sampled in this study) are taking up permafrost-derived nutrients from the water column. However, the fate of permafrost-derived nutrients in freshwaters is likely determined by complex within-lake nutrient cycles.

The low water colour in the SRTS-affected study lakes was counterintuitive, considering the amount of sediment and debris that can enter a lake via SRTS activity. Nevertheless, the significant relationship between chlorophyll *a* and water colour in unaffected lakes was not apparent in SRTS-affected lakes. This effect may be analogous to the nutrient subsidies predicted to occur with permafrost degradation, since phytoplankton in SRTS-affected lakes appeared to be released from light limitation that was occurring in unaffected lakes. The weaker relationship between TP and chlorophyll *a* in unaffected compared to SRTS-affected lakes supported the postulate of light limitation in unaffected lakes. In addition, the shift in pelagic habitat conditions in SRTS-affected lakes could be significant in determining overall system productivity and sensitivity to changing environmental conditions, and will require more study to understand its extensive ecological implications.

3.7 References

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**Assessment of a gradient of lake shoreline thaw slump activity:
Impacts on bathymetry, nutrient concentrations and pelagic biota**

Abstract

An investigation using a balanced ANOVA design was conducted to assess how the bathymetry, water-column nutrient concentrations and pelagic community structure of upland tundra lake were affected by a gradient of shoreline retrogressive thaw slump (SRTS) activity. Three levels of SRTS activity were compared: actively thawing slumps, revegetated and stable slumps, and unaffected lakes. The effects of SRTS were predicted to be greatest where slumps were active, intermediate where slumps were stable, and not apparent in unaffected lakes. Lake-bottom “pits” were found to be greatest adjacent to active slumps and were not evident in unaffected lakes. In contrast, affected water chemistry and biotic components of the pelagic zone did not follow the predicted responses associated with the SRTS gradient. Total phosphorus (TP) and chlorophyll *a* concentrations were highest in stable SRTS lakes, and lowest in active SRTS lakes. It is postulated that SRTS may be a source of TP subsidies to tundra lakes, but stratification in active SRTS-affected lakes may be limiting TP resuspension to the pelagic zone. In contrast, there was no difference in bacterioplankton abundance across lake types. Total zooplankton abundance was lowest in stable SRTS lakes and highest in unaffected lakes, possibly indicating a top-down predation pressure in stable SRTS lakes. The incidence of lake-bottom pits might improve habitat conditions for planktivorous and/or piscivorous fish in the SRTS lakes, thereby having implications for the whole food web. Future comprehensive research on production rates and fish communities are needed to provide a more complete picture of the complex effects of SRTS activity.

Keywords: Upland tundra lakes, shoreline retrogressive thaw slump, disturbance gradient, bathymetry, chlorophyll *a*, bacterioplankton, zooplankton, permafrost thaw, ANOVA design.

4.1 Introduction

Warming air temperatures related to climate change are predicted to cause permafrost thaw at high latitudes (Rouse et al. 1997, Walsh et al. 2005). Ice-rich permafrost is particularly susceptible to thermokarst thaw processes (Mackay 1992). A particularly intense and localized form of thermokarst is retrogressive thaw slumping, which frequently occurs on the shoreline of tundra lakes in the uplands of the Mackenzie Delta Region, Canada. Shoreline retrogressive thaw slumping (SRTS) has been found to affect between 5-15% of the lakes in the region (Kokelj et al. 2005). Furthermore, the rate of thaw slump enlargement in the uplands has increased in recent years (Lantz and Kokelj 2008).

The effects of SRTS on lakes include possible impacts on water chemistry and aquatic biota, particularly in the form of eutrophication resulting from elevated phosphorus and nitrogen concentrations found in SRTS runoff (Hobbie et al. 1999, Thompson 2009b). This may be the result of the release of solutes from the exposed thawing permafrost, which has a higher solute content than the overlying active layer (Kokelj and Burn 2003). However, despite the high nutrient concentrations in SRTS runoff, Thompson (2009b) found nutrient and phytoplankton chlorophyll *a* concentrations to be lower in SRTS-affected lakes compared to unaffected systems. Water colour was also observed to be significantly lower when water from an unaffected lake was exposed to SRTS-derived sediments. It was postulated that this was related to the removal of nutrients and humic material from the water column by adsorption to mineral soils introduced to the lakes by the SRTS activity (Thompson 2008). The difference in water colour was greater the higher the sediment:water ratio. These findings suggest that the impacts of SRTS on the water-

column geochemistry and pelagic biota of tundra lakes will vary according to the degree of thermokarst thaw activity.

To test this hypothesis, an ANOVA-based field-study was conducted using nine upland tundra lakes to determine whether water-column nutrient concentrations and planktonic biota abundance differed with the level of observed SRTS activity (i.e., unaffected, stable, or active SRTS). After controlling for landscape and morphometric influencing factors through the lake selection (explained below), it was expected that the effects of SRTS on nutrient concentrations and plankton biomass in the study lakes would be most apparent in systems affected by active SRTS, moderate in lakes affected by stable SRTS, and not apparent in unaffected lakes. Building upon previous findings, active SRTS-affected lakes were expected to have the lowest phosphorus concentrations and algal biomass (Thompson 2009a), but it was unclear how relative catchment area (lake area to catchment area ratio, LA:CA) influenced DOC and nitrogen concentrations would respond along the SRTS gradient.

4.2 Background

Several differences in water chemistry between SRTS-affected tundra lakes and unaffected lakes in the study area have been previously reported. Compared to nearby unaffected lakes, lakes affected by SRTS had higher water-column specific conductivity and ion concentration, and lower dissolved organic carbon concentration and associated water colour (Kokelj et al. 2005). Nitrogen and phosphorus concentrations in SRTS-affected lakes were also lower than in nearby unaffected ones (Thompson et al. 2009b). In addition, phytoplankton

biomass, which was expected to increase with thaw-related nutrient release, was lower in SRTS-affected than in unaffected lakes (Thompson et al. 2009b). It therefore appears that SRTS activity does not lead to nutrient enrichment of the surface water in these upland lakes. However, because phosphorus can be sequestered from the water column to the sediments in tundra lakes (Prentki et al. 1980), and nutrients may also be quickly taken up by nutrient-limited primary producers (Bowden et al. 2008) or consumers, it can be difficult to detect enrichment by measuring nutrient concentrations alone. This is further complicated by the possibility that organic carbon and nitrogen that is associated with humic material can be lost via sedimentation in SRTS-affected lakes (Thompson et al. 2008)

LA:CA and z_{\max} can also influence nutrient concentrations in lakes, especially nitrogen and phosphorus, respectively (Thompson 2009a). Phosphorus varied inversely with maximum lake depth, which was thought to influence concentrations by controlling water-column stratification (Thompson 2009a). Deep lakes had lower phosphorus concentrations than shallower lakes, possibly as a result of sequestration of phosphorus in the sediments due to a lack of water column mixing and sediment resuspension (Thompson 2009a). Both total dissolved nitrogen (TDN) and dissolved organic carbon (DOC) varied negatively with LA:CA, an indicator of catchment influence on the lake. The lower DOC and nitrogen concentrations in SRTS-affected lakes compared to unaffected lakes might have been related to the difference in catchment influence (LA:CA) between lake types (Thompson 2009a).

Investigating algal enrichment can benefit from the consideration of trophic interactions that influence algal biomass in addition to nutrient supply, especially herbivory. Measuring

producer biomass without assessing adjacent trophic levels might fail to detect an enrichment effect, since nutrient enrichment of phytoplankton production can be obscured by an increase in consumer biomass and subsequently, herbivory and predation. The “exploitation” model of food web structure (Hairston et al. 1960, Oksanen et al. 1981) predicts that populations of primary and secondary producers (like phytoplankton and bacterioplankton) and secondary consumers (predators) are limited by their food or resource supply, while primary consumers (herbivores) are limited by predation. Low-productivity systems are predicted to contain only primary producers, and the number of trophic levels within a system increases with productivity that is linked to resource supply. Therefore, system productivity controls the number of trophic levels, which in turn, controls the relative biomass at each trophic level (through herbivory and predation). Accounting for grazing pressure can significantly contribute to an explanation of the primary producer biomass response to nutrient availability.

The roles of nutrient availability and predation in simultaneously controlling primary production was demonstrated by Mazumder (1994). In a comparison of “bottom-up” (resource) and “top-down” (herbivory/predation) influences on phytoplankton biomass, the influence of phosphorus concentration on phytoplankton (bottom-up influence) was apparent across all lakes, but was stronger in lakes lacking planktivorous fish (secondary consumers of zooplankton, top-down influence) (Mazumder 1994). Assessment of these secondary consumers is consequently also important in understanding producer enrichment. In cases where fish are not studied, zooplankton species and body-size data can also provide an indication of dominant planktivory in the system (Mazumder 1994), since large-bodied zooplankton are susceptible to fish predation

(Brooks and Dodson 1965).

Another trophic interaction that can affect phytoplankton biomass is the contrasting feeding habits of copepod and cladoceran zooplankton, which can influence bacterioplankton abundance. Copepods graze on ciliates and flagellates that consume bacteria, and cladocerans graze directly on bacteria (Zollner et al. 2003, Vrede and Vrede 2005). In this way, copepod grazing increases the abundance of bacteria, while cladoceran grazing lowers bacteria abundance. Since bacterioplankton and phytoplankton compete for nutrient resources (Rhee 1972, Klug 2005), grazing on bacterioplankton can affect phytoplankton biomass.

The complex trophic interactions outlined above illustrate why attempting to determine the impacts of SRTS activity on phytoplankton in tundra lakes requires sampling of adjacent trophic levels. At the same time, a comparison of conditions along an SRTS gradient requires the landscape and lake morphometry variables that have been shown to influence nutrient concentrations to be constant across the study lakes as much as possible.

4.3 Methods

4.3.1 Study Area

Nine study lakes were chosen from a set of 59 lakes that were first sampled for nutrient concentrations in 2005 (Thompson et al. 2009a). Lakes were selected as three sets of lake “triplets” (Table 4-1) using digitized catchment and lake area data (Kokelj et al. 2009), and air photos to determine lake order. The selection of lake “triplets” was performed to control for abiotic landscape and lake morphometry influences such as lake area to catchment area ratio

(LA:CA) and maximum lake depth (z_{\max}), both of which were shown to vary with dissolved organic carbon, total nitrogen and total phosphorus (Thompson 2009a). Each triplet included one lake unaffected by SRTS, one lake affected by actively degrading SRTS, and one lake affected by stabilized vegetated SRTS in order to provide a “treatment” gradient of SRTS activity. As much as possible, the variation in LA:CA and z_{\max} were minimized within each triplet. All lakes were first order, although one lake unaffected by SRTS (lake 25A) was later found to be connected via a heavily-vegetated shallow link to a small second basin that is not included in the calculated lake area. The lakes were all situated on glacial moraine surficial deposit except lakes 16B (on a colluvial deposit) and 19B (on a glaciofluvial complex).

Table 4-1. Catchment characteristics and lake morphometry information for the nine study lakes, presented as “triplets”. Abbreviations are: LA - lake area, CA – catchment area, z_{\max} – maximum depth, CA:LA = catchment area to lake area ratio.

Triplet	Lake	Latitude	Longitude	Area	Slump Status	LA (ha)	CA (ha)	Z_{\max} (m)	CA:LA
1	30A	69.42085	-134.31624	Richards Island	unaffected	4.360	22.997	9.9	5.275
	16B	68.94674	-133.89690	Parson's Lake	active	14.095	62.973	16.8	4.468
	19B	68.88338	-134.21645	North Storm Hills	stable	6.105	28.110	10.1	4.604
2	25A*	69.23570	-134.66783	Richards Island	unaffected	4.876	28.484	7.8	5.842
	8B	68.95713	-133.84096	Parson's Lake	active	6.485	32.709	8.4	5.044
	24B	69.22069	-134.69533	Richards Island	stable	7.563	40.260	5.3	5.323
3	22A	69.14230	-134.82175	Richards Island	unaffected	1.871	8.309	4.2	4.441
	29B	69.30672	-134.54274	Richards Island	active	5.719	14.264	7.8	2.494
	22B	69.14630	-134.78548	Richards Island	stable	3.519	11.700	9.4	3.325
Mean						6.066	27.756	8.9	4.535

The study lakes are located in the uplands east of the Mackenzie Delta, ranging from

about 50km north of the town of Inuvik, NWT to the Beaufort Sea coast (Figure 4-1). All of the study lakes occur north of the local treeline, in open tundra underlain by ice-rich permafrost (Mackay 1992, Kokelj et al. 2005). The relatively shallow organic-rich active layer in the uplands area (maximum depth approximately one metre) restricts runoff from reaching the deeper, poorly developed permafrost soils, so that solute input from catchment runoff is a major influence on the water-column chemistry of the small lakes in the area (Pienitz et al. 1997, Gregory-Eaves et al. 2000, Rühland et al. 2003). The region is further described in Thompson et al. (2009a,b).

In June 2006, bathymetric mapping of the nine study lakes was completed using a GPS-depth sounder mounted on the bottom of an inflatable boat with depth soundings recorded along multiple transects. Kriging software was used to interpolate the entire lake bathymetry. Although this was an estimate, many of the most interesting and distinctive features of the lake bottoms (see Results section) were apparent along the sounding transects.

The comprehensive surveys of the study lakes included an assessment of both abiotic water chemistry, including nutrients, as well as planktonic biota, including phytoplankton, bacterioplankton and zooplankton. Lake-water specific conductivity was also measured because of its utility as a conservative indicator of SRTS-derived solute contributions to the lakes. Phosphorus, nitrogen and organic carbon concentrations were measured to assess potential eutrophication, and the planktonic biota were sampled to test for eutrophication after nutrient uptake. Both producers and primary consumers were sampled to assess the possibility of “bottom-down” consumption of nutrient-enriched primary producer biomass.

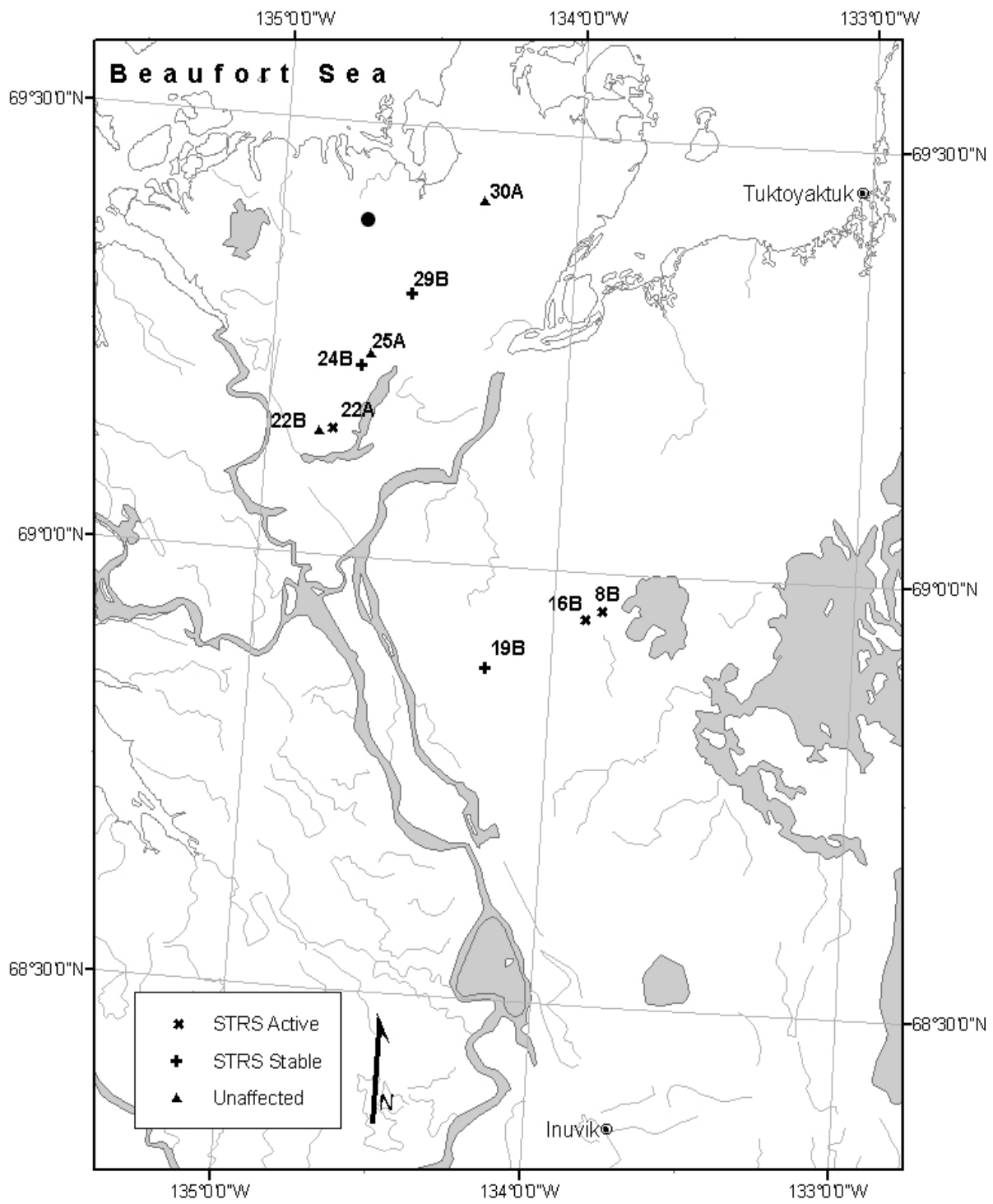


Figure 4-1. Map of sample site locations in the uplands east of the Mackenzie Delta, NWT, Canada.

4.3.2 Lake Sampling

The nine lakes were sampled just after spring ice-off (late June and early July) and in autumn (late August and early September) 2006 and 2007. Water samples were collected from each lake at 0.5m below the surface as a composite of samples taken at 3 locations on each lake. Where a thermocline was evident during the 2007 surveys, hypolimnion water samples were also collected at one site per lake using a Niskin discrete water column sampling bottle. Water-column temperature, dissolved oxygen (DO) and specific conductivity profiles (0.5m increments) were also taken in each lake at the deepest known point with a YSI 556 multiprobe meter (Yellow Springs Instruments, Idaho, USA). After the first sampling in June 2006, replicated surface water sampling for bacterioplankton enumeration was added to sampling program to account for this possibly significant influence over phyto- and zooplankton biomass.

Samples were shipped for analysis within 24 hours of collection to Environment Canada (EC) National Laboratories for Environmental Testing in Saskatoon and Edmonton, Canada for analysis. Water samples were analyzed for total phosphorus (TP), total dissolved nitrogen (TDN) and dissolved organic carbon (DOC). Standard methods for all analyses were followed (American Public Health Association 2005). TP was determined spectrophotometrically after digestion and addition of ammonium molybdate. TDN was measured spectrophotometrically after digestion, nitrate reduction and azo dye formation. DOC was obtained using an Apollo 9000 analyzer (Tekmar-Dohrmann, Cincinnati, OH).

Water samples for chlorophyll analysis were filtered through GFC filters, which were frozen and shipped to EC for analysis. Chlorophyll *a* concentrations (corrected for phaeophytin)

were obtained after extraction in 90% ethanol, by measuring absorbance at 665 and 750 nm with a Turner designs 10-AU Digital Fluorometer (Turner Designs, Inc., Sunnyvale, CA) (adapted from Sartory and Grobbelaar 1984).

Zooplankton were sampled at the deepest known location in each lake using a tow net with 63 μm mesh, pulled vertically from just above the sediments to the lake surface. Samples were preserved in buffered formaldehyde until enumeration and identification. *Daphnia* were identified to species according to Brooks (1957, 1959). Identification to species was performed for *Daphnia* because of the significant size differential and functional difference between larger *D. middendorffiana* and *D. pulex* and smaller *D. longiremis*. Remaining Cladocera were identified to genus. Copepods were identified as either adult calanoid or cyclopoid, and all nauplii were combined for enumeration. The body length of 20 randomly selected individuals from each of these identification (ID) groups in each sample was measured using stage and ocular micrometers, and averaged to obtain body length estimates.

Beginning in autumn 2006, duplicate lake water samples were collected, preserved with formaldehyde and stained for bacterioplankton enumeration. 2-ml subsamples were stained for 5 minutes with 1 ml solution of 10 μgml^{-1} fluorescent DAPI dye (4',6-diamidino-2-phenylindole). The subsamples were then filtered through black polycarbonate Nucleopore membrane filters. Cell counts were completed using an epifluorescent compound microscope equipped with an ocular graticule by counting 10 view fields per filter and were averaged before use in statistical analyses (American Public Health Association 1992).

4.3.3 Statistical Analyses

Lake water chemistry variables, bacterioplankton abundance, chlorophyll *a* concentration and zooplankton assemblage data were analyzed as dependent variables for differences according to the two independent variables lake type (active, stable or unaffected) and sampling season (spring or autumn) using two-way general linear model ANOVAs. Variables analyzed using ANOVA were log-transformed to obtain normal, homoscedastic distributions, with the exception of specific conductivity, which is discussed in the results section. In the case of TDN, *ln*-transformation was required in order to obtain a normal homoscedastic distribution. All significant ANOVA results are $\alpha \leq 0.05$. All analyses were completed using SPSS 13.0 (SPSS Inc., Illinois, USA).

4.4 Results and Discussion

4.4.1 Observational Variables

4.4.1.1 Water temperature and stratification

Surface water temperatures in spring (June and July) ranged between 12°-18°C, but were cooler in autumn (August and September), ranging between 10°-12°C. In the spring, there was a gradient of 6°C from the southernmost to the northernmost study lakes, but the temperature gradient was only about 1°C in autumn.

In terms of thermal stratification, the study lakes range between dimictic and polymictic during the ice-free season. Most of the lakes affected by active SRTS were thermally stratified during all sampling periods. The exceptions to this were lake 8B in June and August 2006 and

lake 22B in autumn 2006; however, the June measurement was made at a depth of 3.5 m, instead of at the maximum of 8.4m, before bathymetry data was available. Of the stable SRTS-affected lakes, only lake 19B (the deepest of the stable lakes) was thermally stratified at each sampling period. Lake 29B was stratified in spring, and lake 24B (the shallowest stable lake) was not thermally stratified during sampling. The only unaffected lake that was thermally stratified during any of the sampling periods was lake 30A (the deepest unaffected lake), and then only in June of 2006. A representative autumn 2007 temperature profile of a stratified active SRTS-affected lake (8B) and unstratified stable SRTS-affected and unaffected lakes is presented in Figure 4-2. Since all three lakes have approximately the same z_{\max} , the location of lake 8B further south than the other two lakes along the regional north-south temperature gradient is probably the determining factor in their stratification status. Because of the regional climatic gradient, the lakes further north are generally slightly cooler and, if they stratify, turn over earlier than the more southern lakes.

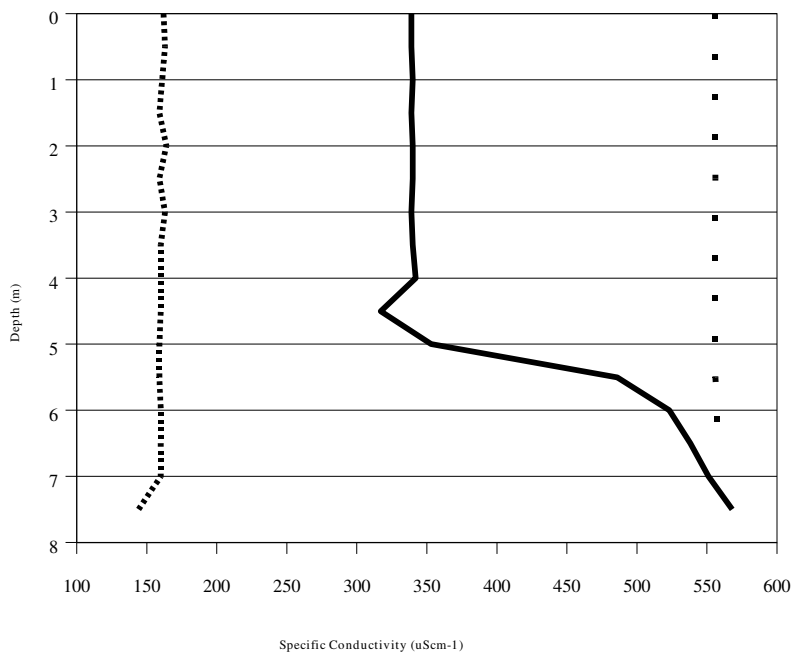
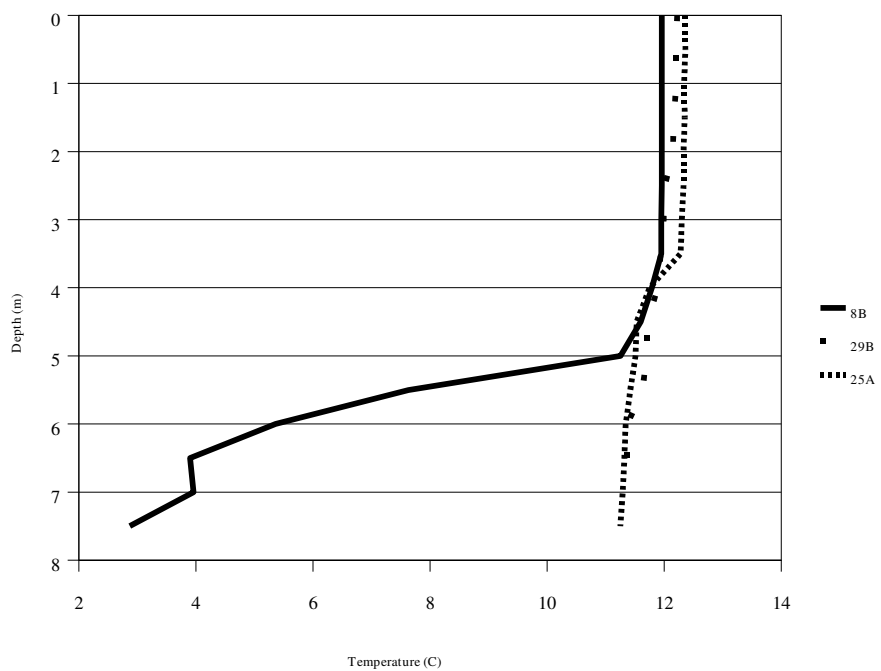


Figure 4-2. Autumn 2007 profiles of active SRTS-affected lake 8b, stable-SRTS affected lake 29B and unaffected lake 25A. Temperature profiles are presented on the top and specific conductivity profiles on the bottom.

4.4.1.2 Bathymetry

The results of the bathymetric surveys revealed unexpected and important morphometric characteristics of the study lakes. SRTS-affected lakes, especially those affected by active slumps, contained localized pits that were significantly deeper than the average of the lake bottom. In addition, these pits were not necessarily located near the centre of the lakes, but were generally located in the areas immediately adjacent to the SRTS-affected shoreline. In lake 8B the majority of the lake bottom was between 2 and 3.5 m deep. However, in the area adjacent to SRTS, the lake was up to 8.4m deep (Figure 4-3). The deepest pit found was over 16m and was in lake 16B, which was affected by SRTS around nearly its entire shoreline. Pits were found in five of the six SRTS-affected lakes (lake 22B was the exception). In contrast, the bottoms of the three unaffected lakes were gradually sloped towards the deepest point near their centre (e.g., lake 30A, Figure 4-4).

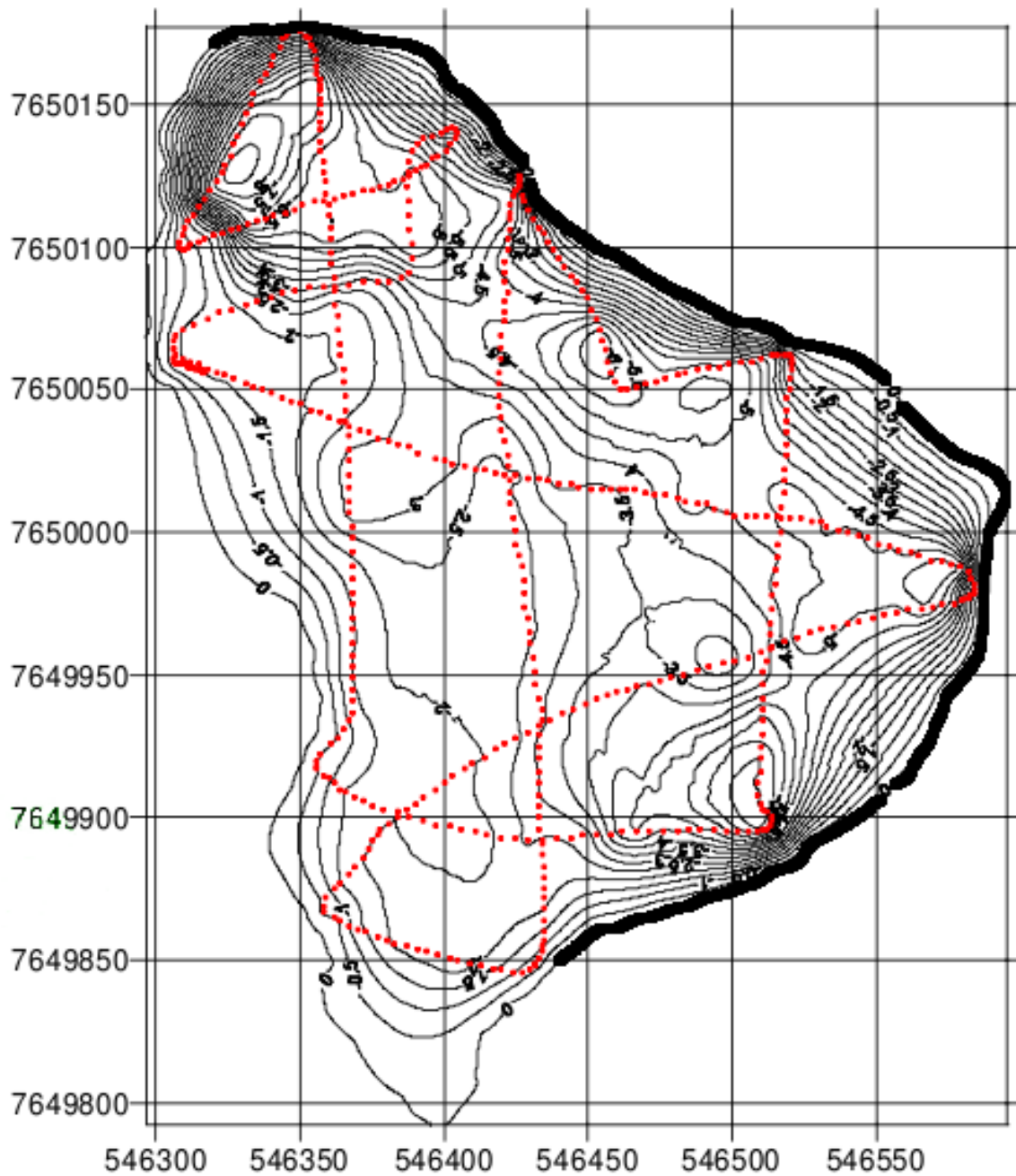


Figure 4-3. Interpolated bathymetry of lake 8B based on depth-soundings at the points indicated by red dots. Isoclines are labeled with water depth in metres. The shoreline affected by SRTS is indicated with a thick black line (several separate SRTS sites occur in the outlined area).

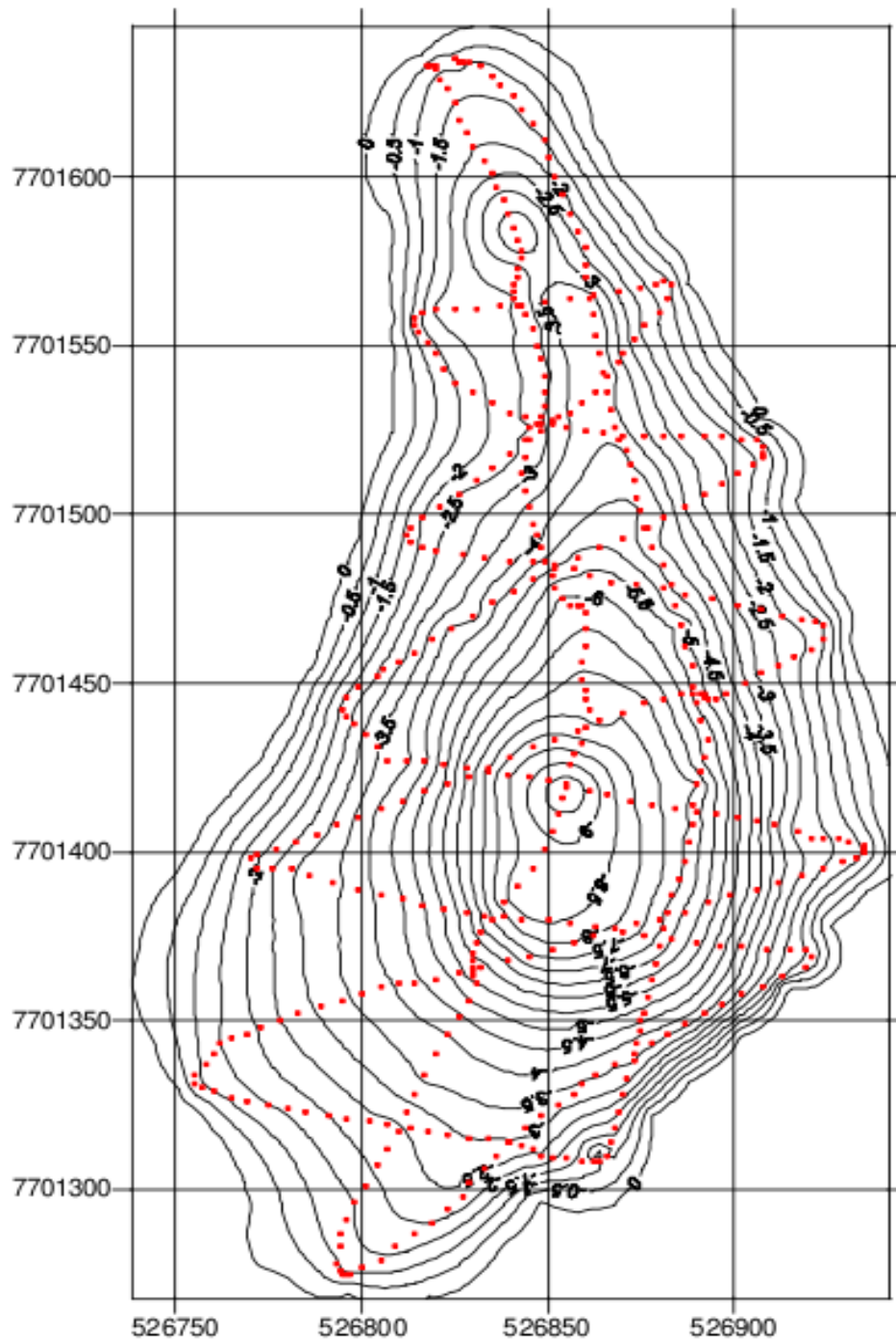


Figure 4-4. Interpolated bathymetry of unaffected lake 30A based on depth-soundings at the points indicated by red dots. Isoclines are labeled with water depth in metres.

Lake-bottom “pits” were most common in active lakes and least common in unaffected lakes. Localized stratification occurred where the thermocline was deeper than the majority of the lake bottom, so that many of the pits were separated by bottom areas that were shallower than the thermocline. This may have implications for hypolimnion mixing regimes and possibly creating more than one hypolimnion unit within a single lake. It may also have an important effect on the suitability of these tundra lakes as fish habitat. Northern pike (*Esox lucius*) have been observed in stable lake 29B (S.V. Kokelj, personal communication) and a Northern pike skull was found on the shore of active lake 8B. Many large fish species require cool deep areas through the warmer open water season and sufficient stores of dissolved oxygen under ice (Hershey et al. 1999), and the deep stratified pits in the SRTS-affected lakes may provide such conditions.

4.4.2 Analytical Variables

4.4.2.1 Water chemistry

Specific conductivity was significantly different between lake types (Table 4-2), and was highest in active lakes and lowest in unaffected lakes (Figure 4-5). It is noteworthy that specific conductivity data were heteroscedastic even after logarithmic transformation, and variation amongst unaffected lakes was much less than amongst active and stable SRTS-affected lakes. The difference according to lake type was confirmed by performing a nonparametric Friedman's test, which also indicated a significant difference ($Q=20.455$, $df=5$, $p=0.00$). Specific

conductivity was also generally higher in the hypolimnion than in the epilimnion of the stratified lakes, although the lack of replicated hypolimnion sampling precluded a statistical analysis of this difference. In spring 2007, conductivity in the hypolimnion was double that of the epilimnion, and in the autumn surveys it was about 1.5 times that of the epilimnion.

Table 4-2. ANOVA table for two-way ANOVAs conducted on water chemistry, phytoplankton, bacterioplankton and zooplankton data in the nine study lakes, tested by lake type (unaffected by slumping (Unaffected), affected by an actively degrading shoreline slump (Active), affected by a stabilized slump (Stable)) and by time of sampling (spring/autumn and 2006/2007). CWML is the mean length of each zooplankton group, which was averaged following weighting by the group abundance.

Parameter	Lake Type (Slump status)			Season (Spring, Autumn)			Post Hoc differences (Tukey's)
	F	df	p	F	df	p	
<i>i) Abiotic variables</i>							
Specific Conductivity	18.658	2	0.000	0.539	1	0.469	Active and Stable vs. Unaffected
Total Phosphorus	5.873	2	0.007	0.070	1	0.794	Stable vs. Active vs. Unaffected
Total Dissolved Nitrogen	2.496	2	0.099	1.551	1	0.223	
Dissolved Organic Carbon	2.131	2	0.136	1.110	1	0.300	
<i>ii) Biotic variables</i>							
Chlorophyll <i>a</i>	12.703	2	0.000	5.775	1	0.023	Stable vs. Active and Unaffected
Chlorophyll <i>a</i> (19B removed)	8.839	2	0.001	9.857	1	0.004	Active vs. Stable and Unaffected
Bacteria abundance	0.435	2	0.653	4.672	1	0.042	
Zooplankton abundance	12.591	2	0.000	0.301	1	0.588	Stable vs. unaffected
Zooplankton CWML	3.090	2	0.065	0.421	1	0.523	
Copepod:Cladoceran abundance (<i>ratio</i>)	0.874	2	0.431	5.143	1	0.034	

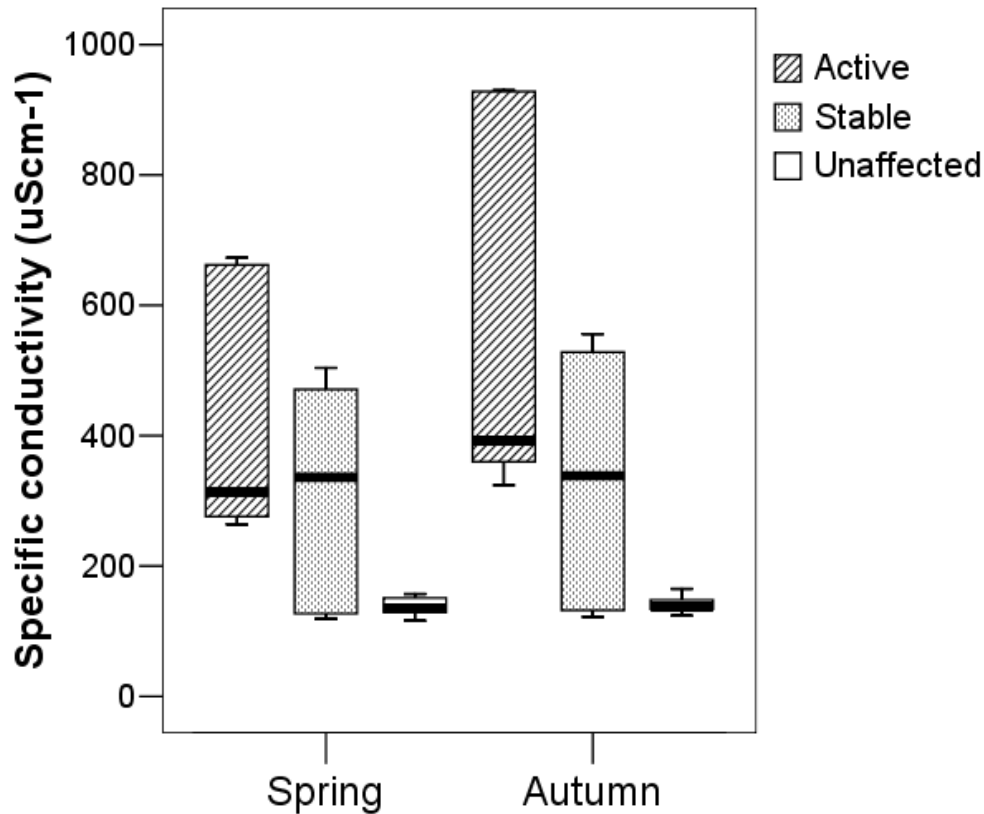


Figure 4-5. Specific conductivity by sampling season for the active (affected by an actively degrading shoreline slump), stable (affected by a stabilized slump) and unaffected (unaffected by slumping) study lakes.

TP was significantly different across lake types, and was highest in stable lakes (Figure 4-6). DOC and TDN were not significantly different across lake types or between sampling seasons (Table 4-2). In the same study area, total and dissolved phosphorus in 59 lakes did not vary with SRTS activity, or with relative catchment size and lake order (Thompson 2009a). Phosphorus concentrations varied with maximum lake depth (Thompson 2009a), which may be explained by the relation between lake depth and thermal stratification determined by wind exposure, since stratification can limit the release of phosphorus from sediments (Zicker et al. 1956). A principal

components analysis using data from 59 lakes showed that TDN and DOC varied with SRTS activity and with LA:CA (Thompson 2009a). TDN and DOC were significantly different between 11 SRTS-affected and unaffected lakes sampled in autumn in the same study area (Thompson 2009b). SRTS-affected lakes also had higher LA:CA than the unaffected lakes, and the difference in TDN and DOC also reflected the same pattern (Thompson 2009b). This was confirmation of the expectation that TDN and DOC would not differ between lake types, since LA:CA was controlled for as much as possible in this study.

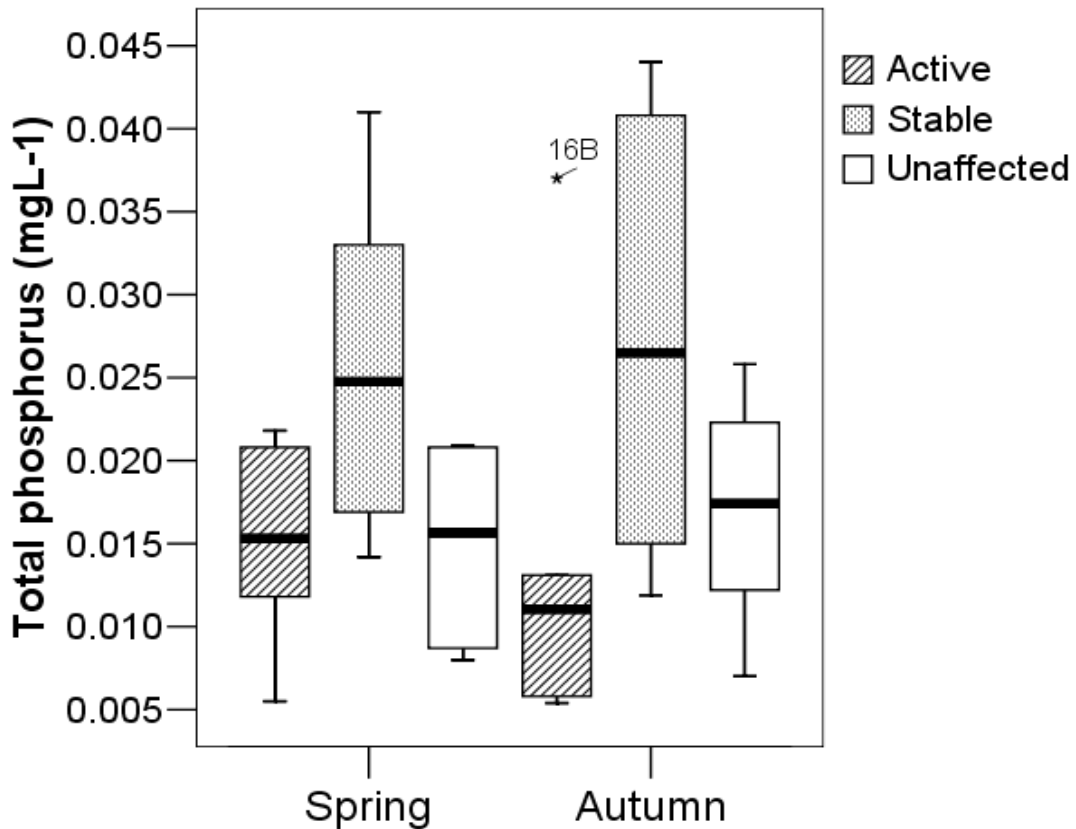


Figure 4-6. Total phosphorus by sampling season for the active (affected by an actively degrading shoreline slump), stable (affected by a stabilized slump) and unaffected (unaffected by slumping) study lakes.

Of the measured water chemistry variables, only specific conductivity reflected the SRTS

activity gradient, and was highest in active lakes and lowest in unaffected lakes. TP was highest in stable lakes, despite the results of a comparative lake survey that found TP was significantly higher in 11 unaffected tundra lakes compared to 11 generally SRTS-affected lakes (Thompson 2009b). The separation between active and stable SRTS-affected lakes is worthwhile in terms of explaining water-column TP concentrations, and as discussed above, may be more influenced by SRTS-related lake bottom “pits” than to the rate of delivery from the SRTS site itself.

4.4.2.2 Phytoplankton

Chlorophyll *a* was significantly higher in stable lakes and lowest in active lakes (Table 4-2) (Figure 4-7), and was significantly higher in autumn than in spring. The range of chlorophyll *a* concentrations in stable lakes is much larger than in the other lake types, and the chlorophyll *a* in lake 19B was consistently an order of magnitude higher than in the other study lakes (Figure 4-7). What has caused lake 19B to contain such high chlorophyll *a* concentrations ($17\text{-}31\ \mu\text{g l}^{-1}$) is unknown; however, it also had relatively high TP concentrations (mean $0.037\ \text{mg L}^{-1}$ in spring and $0.042\ \text{mg L}^{-1}$ in autumn). Although not an order of magnitude higher than TP in the other study lakes, this high TP likely contributed to the high chlorophyll *a* in lake 19B. A re-analysis after the removal of lake 19B produced the same general results as the initial chlorophyll *a* analysis (Table 4-2), however stable lakes were no longer significantly different than unaffected lakes (Figure 4-8).

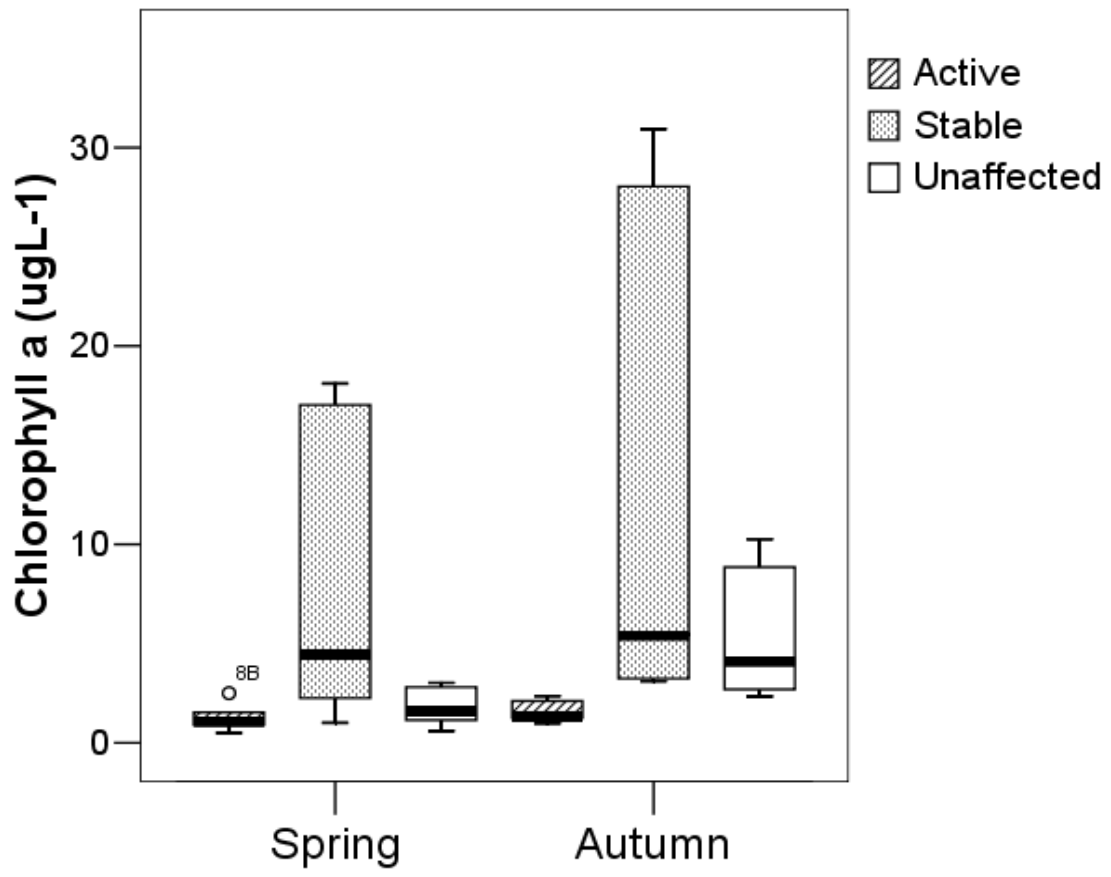


Figure 4-7. Chlorophyll *a* concentration by sampling season for the active (affected by an actively degrading shoreline slump), stable (affected by a stabilized slump) and unaffected (unaffected by slumping) study lakes.

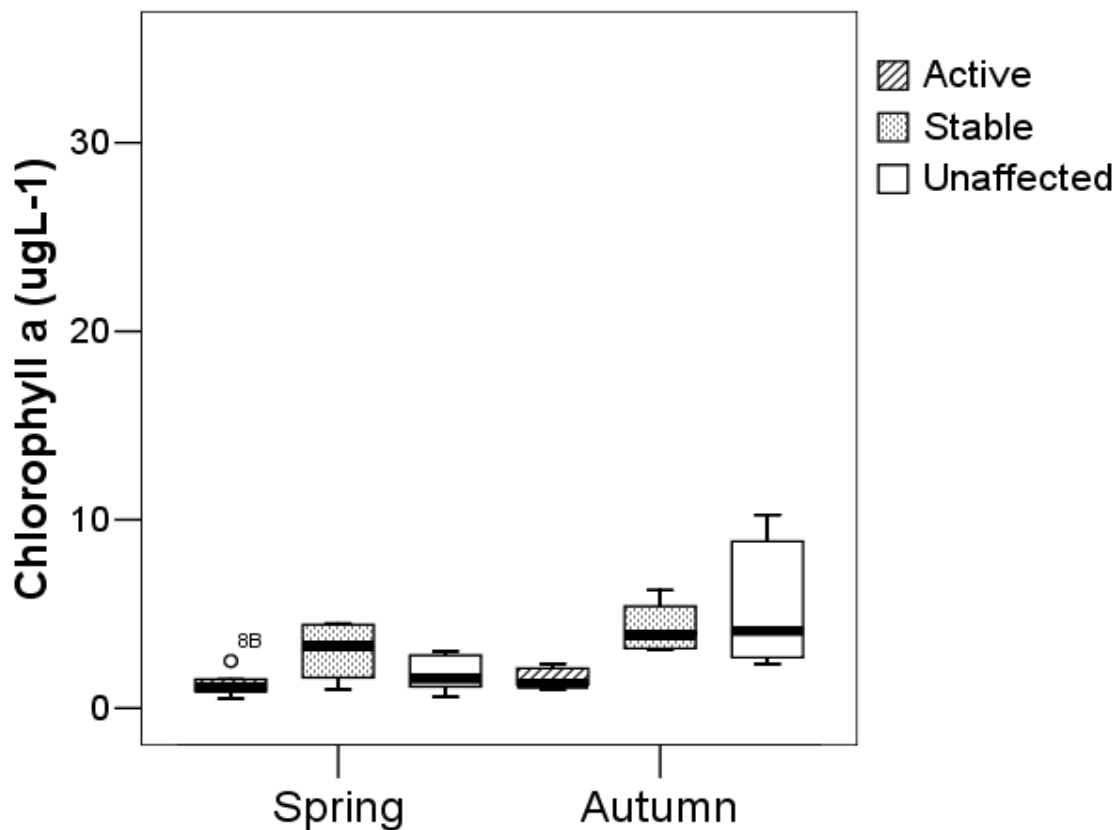


Figure 4-8. Chlorophyll *a* concentrations for all of the study lakes except lake 19B by sampling season for the active (affected by an actively degrading shoreline slump), stable (affected by a stabilized slump) and unaffected (unaffected by slumping) study lakes.

Chlorophyll *a* concentration in unaffected lakes is linked to light limitation of phytoplankton productivity related to high water colour (Thompson 2009b). In contrast, chlorophyll *a* concentration in SRTS-affected lakes is determined by TDN and TP, and to some extent DOC (Thompson 2009b). It is unclear why the lakes affected by stable SRTS would have the same chlorophyll *a* concentrations as the unaffected lakes, since stable lakes had the highest TP concentrations. However, whole-lake primary production in SRTS-affected lakes could have been enriched compared to unaffected lakes, since macrophyte biomass was also significantly

higher in SRTS-affected than unaffected lakes in 8 of the same study lakes (Mesquita et al. 2008). No contrast between the macrophyte data from differing SRTS activities has been completed. The low chlorophyll *a* concentrations in active lakes might be explained if an increase in macrophyte biomass that occurs at the expense of phytoplankton growth in terms of TP availability might be greatest in active SRTS-affected lakes, and less so in stable SRTS lakes.

4.4.2.3. Bacterioplankton and Zooplankton

There was no significant difference in bacterioplankton density between lake types, but it was significantly higher in the autumn surveys than in the spring 2007 survey (Table 4-2) (Figure 4-9). The higher autumn bacterioplankton abundance data for this lake does not reflect the seasonal shift in the copepod:cladoceran ratio, which was low in autumn, inferring that the relative importance of direct grazing by Cladocera on bacteria was greater in the autumn than in the spring (Zollner et al. 2003, Vrede and Vrede 2005, Jansson et al. 2007). However, the ratio remained >1 in autumn, and may not have represented a large enough seasonal shift to significantly negatively impact bacteria abundance.

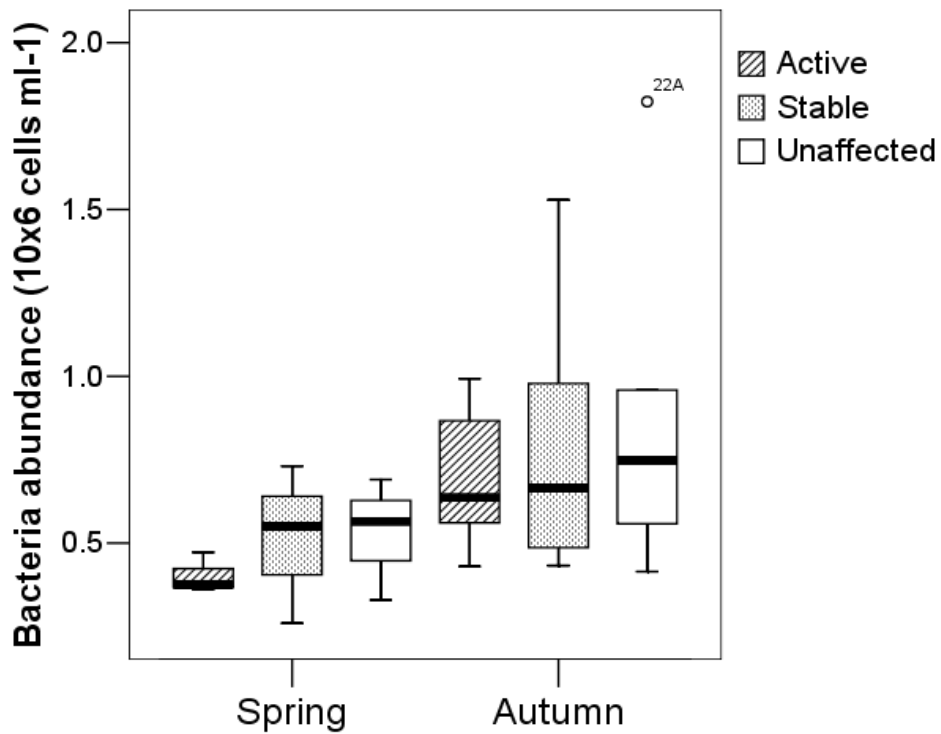


Figure 4-9. Bacterioplankton cell density by sampling season for the active (affected by an actively degrading shoreline slump), stable (affected by a stabilized slump) and unaffected (unaffected by slumping) study lakes.

Zooplankton abundance is presented in terms of community composition for each lake type and for spring and autumn surveys in Figure 4-10. Stable lakes had lower total zooplankton abundance than unaffected lakes, and there was no significant difference in zooplankton abundance across seasons (Table 4-2). In the spring surveys, cyclopoid copepods were the most abundant zooplankton ID group across all lake types, although calanoid copepods were abundant in unaffected lakes. *Daphnia longiremis* and Bosminids made up a larger part of the autumn zooplankton communities in stable and unaffected lakes, and calanoids contributed more to the copepod population in active and unaffected lakes. Cyclopoids remained the most abundant zooplankton group across all study lakes (Figure 4-10). *Holopedium gibberum*, with its large

gelatinous mantle thought to discourage grazing, appeared only in unaffected lakes in the spring. The relatively large *D. middendorffiana* and *D. pulex* made up only a small amount of the overall zooplankton abundance in both seasons (Figure 4-10).

The stable study lakes contained few or no calanoid copepods and relatively large *D. middendorffiana* and *D. pulex*, which were more abundant in unaffected lakes and active lakes in autumn sampling. Top-down influence on aquatic communities can take the form of size-selective predation, in which large-bodied zooplankton are more susceptible to predation by planktivorous fish or invertebrate predators than small-bodied zooplankton (Brooks and Dodson 1965, Hebert and Loaring 1980, O'Brien et al. 1992). Large-bodied zooplankton are more efficient at consuming food particles than smaller zooplankton (Hall et al. 1976), so that in a trophic cascade situation, grazing pressure on phytoplankton would be stronger in a lake lacking planktivorous fish (Mazumder 1994), or containing piscivorous fish (Hershey et al. 1999).

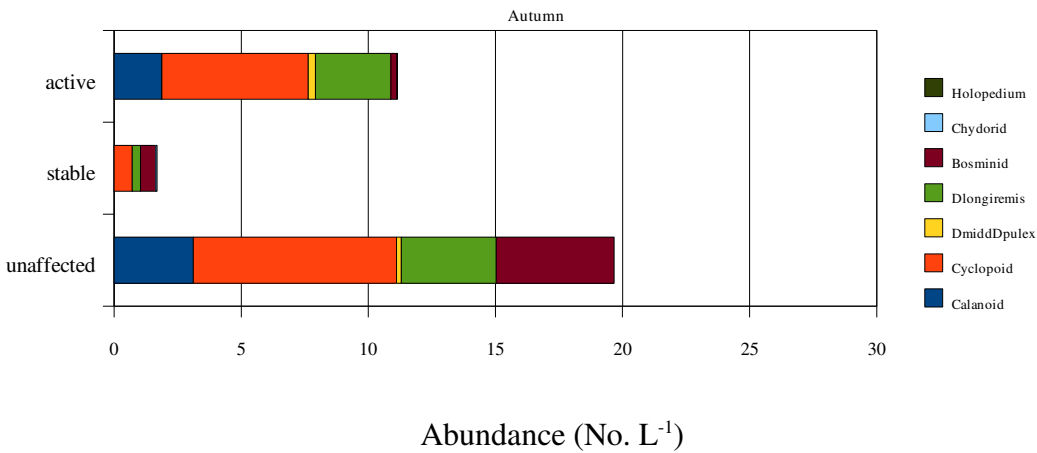
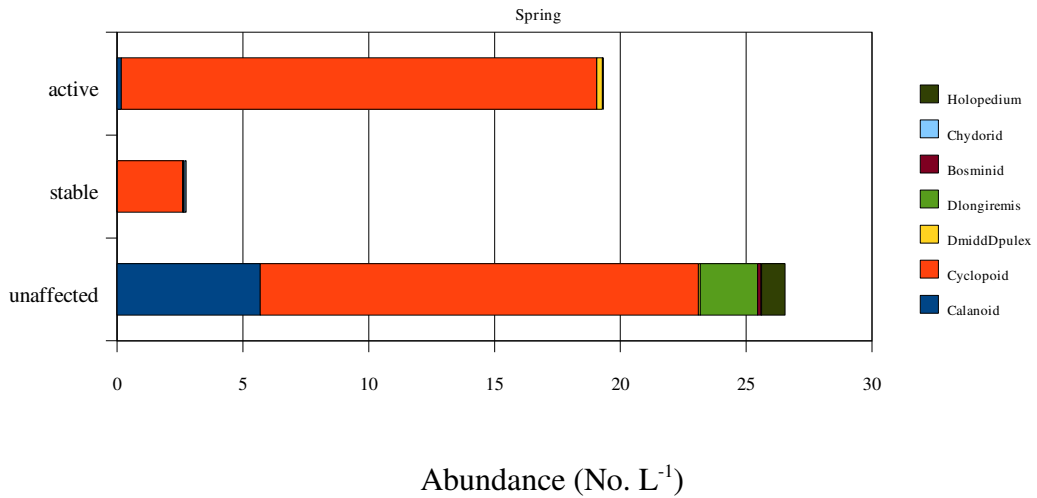


Figure 4-10. Zooplankton composition and abundance for spring and autumn 2006 and 2007 surveys, presented for active (affected by an actively degrading shoreline slump), stable (affected by a stabilized slump) and unaffected (unaffected by slumping) lakes. Zooplankton groups are as indicated in the legend, DmiddyDpulex is the combined abundance for *Daphnia middendorffiana* and *Daphnia pulex*. Data from spring 2006 are partial (one stable and one unaffected lake, 29B and 30A).

Bosminids and *D. longiremis* were most abundant in the autumn zooplankton samples from unaffected lakes, but of the two relatively small cladoceran groups, only *D. longiremis* was abundant in active and stable lakes in autumn. It was also interesting to note that *D. longiremis* were slightly longer in active lakes than in unaffected and stable lakes (Figure 4-11). Stable SRTS lakes had fewer of the large *D. middendorffiana* and *D. pulex* than the other lake types, and more of the relatively small Bosminid Cladocera. *Bosmina longirostris* has been found to be more abundant in lakes with high chloride concentrations (Swadling et al. 2000). However, chloride concentrations in the study lakes were not significantly different across lake type (ANOVA, $F = 2.853$, $df = 2$, $p = 0.075$; M.Thompson, unpublished data), and the highest mean chloride concentration occurred in stable lakes where Bosminids were relatively abundant.

Figure 4-11 summarizes the average zooplankton body length frequency distributions for spring and autumn surveys. In active and unaffected lakes, individuals in each taxonomic group were larger in autumn than in spring. In stable lakes, smaller taxonomic groups were present in autumn, when both the large *D. middendorffiana* and calanoid copepods were absent. Combined weighted mean length (CWML) of all zooplankton were calculated as the mean length of each taxonomic group weighted by the percent abundance of that group, and are presented by lake type and season in Figure 4-12. There was no significant difference in the CWML across lake types and seasons (Table 4-2). In addition, there was no significant difference in the copepod:cladoceran abundance ratio between lake types (Table 4-2) but the ratio was significantly higher in spring (mean 1.3) than in autumn (mean 0.3).

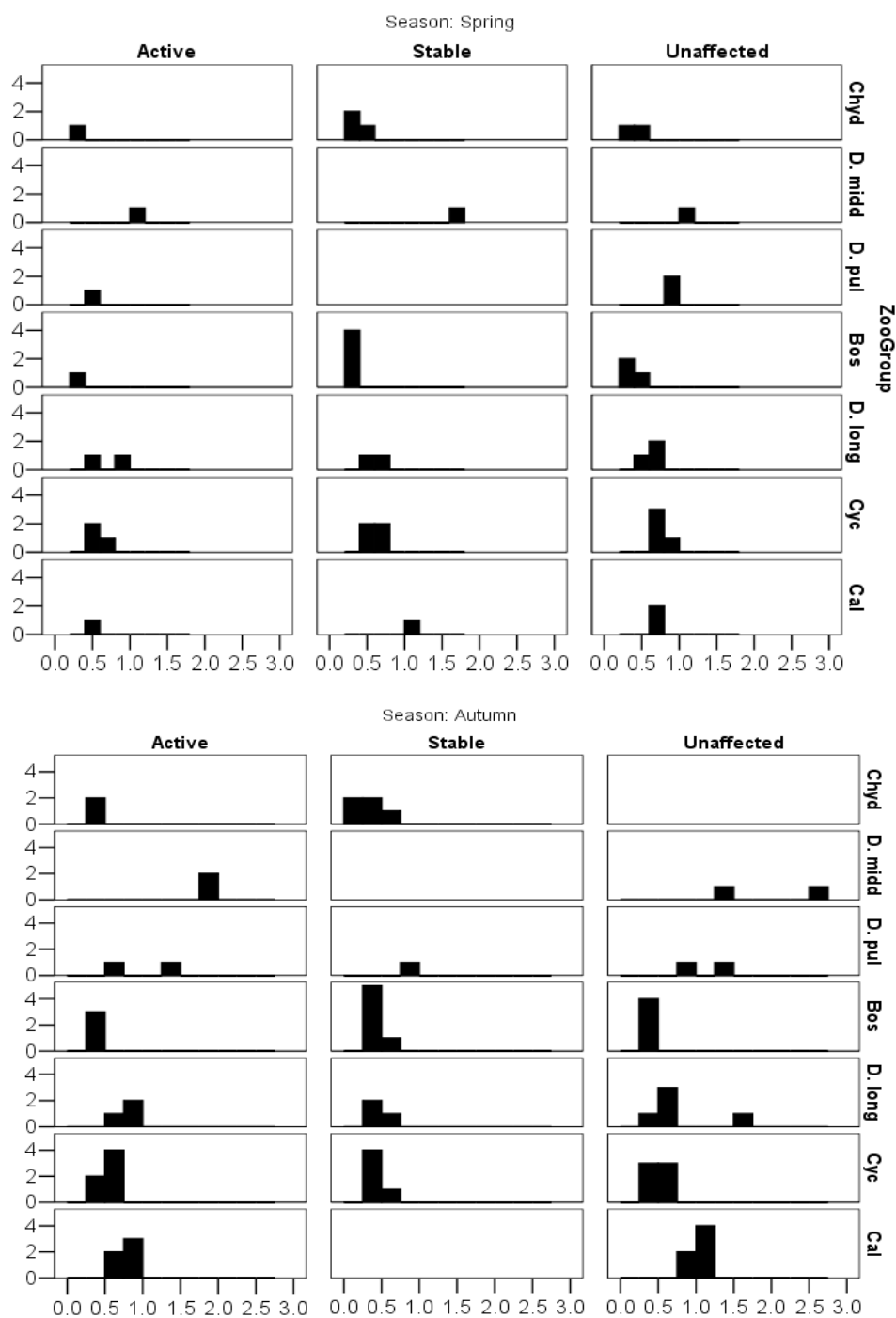


Figure 4-11. Frequency distributions for the mean length (mm) of each of seven zooplankton ID groups from the nine study lakes. Results from the spring and autumn surveys are presented separately. Abbreviations are: Chyd – Chydorid, D. midd – *Daphnia middendorffiana*, D. pul – *Daphnia pulex*, Bos – Bosminid, D. long – *Daphnia longiremis*, Cyc – Cyclopoid, Cal – Calanoid. Data from spring 2006 are partial (one stable and one unaffected lake, 29B and 30A).

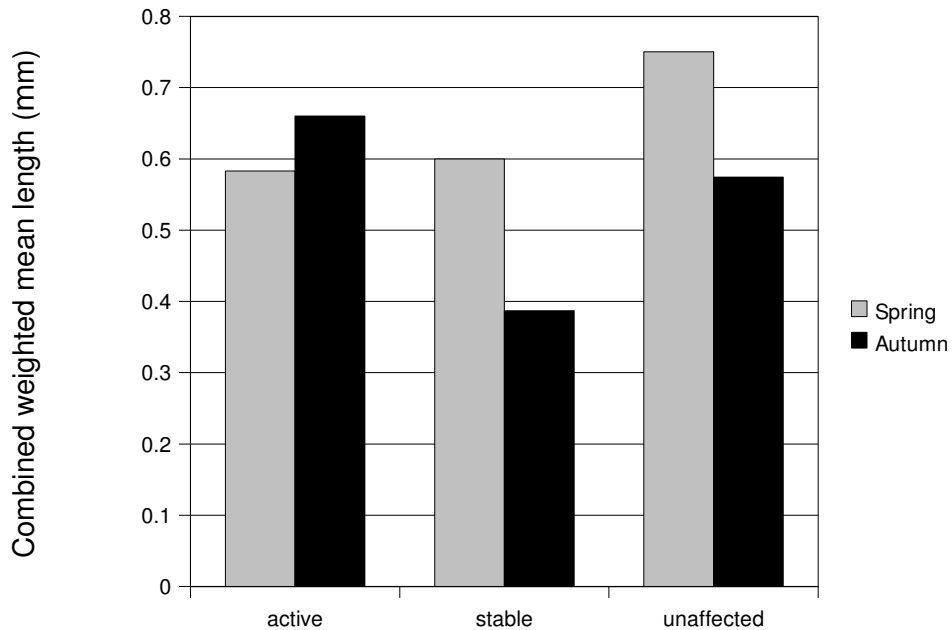


Figure 4-12. Weighted mean length of all zooplankton ID groups from the nine study lakes. Combined weighted mean length is weighted by percentage abundance. Results from the spring and autumn surveys are presented separately.

The mean body length of zooplankton in the study lakes may reflect the reproductive cycles of each group. In particular, Stross et al. (1980) report that *Daphnia* in Alaskan tundra ponds produced a non-overwintering generation while all other zooplankton were monovoltine. Most zooplankton groups hatch in the spring soon after ice-off and begin production of embryonic individuals in autumn (or a larger cyclopoidid in the case of cyclopoid copepods) in preparation for overwintering. Overwintering *Daphnia* hatch a generation of young of year and continue on to produce the next batch of overwintering embryos (Stross et al. 1980). Consequently, *Daphnia* size distributions in autumn may be bimodal, consisting of two generations with potentially differing mean body lengths. While *Daphnia* mean body lengths

appear unimodal in the study lakes in spring, there appear to be two size groups in many of the *Daphnia* groups in autumn, especially in unaffected lakes. This bimodality is not apparent in the non-*Daphnia* zooplankton.

4.5 Conclusions

Lake morphometry, stratification status and specific conductivity varied according to the SRTS activity gradient, from unimpacted in unaffected lakes to intermediate impact in stable lakes and greatest impact in active lakes. However, the hypothesis of a gradient in nutrient concentrations and plankton biomass and abundance that reflects the SRTS activity gradient was not supported by the above results. TP was highest in stable lakes and lowest in active lakes. Chlorophyll *a* also did not reflect the SRTS gradient, somewhat mirroring TP. In addition, while there was no significant difference in bacterioplankton abundance between lake types, zooplankton abundance was lowest in stable lakes, and high in both active and unaffected lakes.

A summary of the findings for each SRTS activity level is presented in Table 4-3. The situation in the stable study lakes, with relatively high nutrient and chlorophyll *a* concentrations but low zooplankton abundance comprised of relatively small taxonomic groups indicates the predation pressure, possibly from planktivorous fish or from macroinvertebrates. The high chlorophyll *a* concentration may be a response to the resulting weak “top-down” grazing pressure from zooplankton or to strong “bottom-up” nutrient enrichment. In active lakes, the low nutrient and chlorophyll *a* concentrations and higher zooplankton abundance indicated a lack of planktivorous fish or invertebrate predators. In the case of a larger food web, the deeper active

lakes may also contain piscivorous fish that consume planktivorous fish and release zooplankton from predation. Phytoplankton biomass, as indicated by chlorophyll *a*, appeared to be nutrient-limited and potentially heavily grazed by large and abundant zooplankton. Finally, in unaffected lakes, TP was intermediate between stable and active lakes, but chlorophyll *a* was not significantly different from stable lakes. Zooplankton were abundant, perhaps exerting grazing pressure and causing the relatively low chlorophyll *a*. However, light limitation due to the higher water colour in these lakes may also negatively affect chlorophyll *a* concentration (Kokelj et al. 2005, Thompson et al. 2009b).

Table 4-3. Comparison chart of measured variables in the study lakes according to SRTS activity status. * indicates the occurrence in that lake type of the conditions listed in the left column.

	Active	Stable	Unaffected
High water colour (from Thompson 2009b)			*
High specific conductivity	*	*	
Deep pits, stratification	*	*	
High phosphorus concentration		*	
High chlorophyll <i>a</i> concentration		*	* (<i>if 19B excluded</i>)
Abundant zooplankton	*		*

Although both SRTS-affected lake types had possible piscivore habitat in the form of lake bottom pits, the inferred predation pressure differs between the two SRTS-affected lake types.

The importance of planktivorous fish vs. macroinvertebrate predators in these lakes is difficult to determine without expanding sampling to include these groups. However, the dependence of arctic fish species on pelagic resources may not be strong. Top consumers (arctic char) in 9 subarctic Swedish lakes receive 62-94% of their energy from littoral carbon, possibly due to higher energy mobilization and larger primary consumers in littoral habitats (Karlsson and Bystrom 2005). The occurrence of phantom midge larvae (Chaoboridae) in some of the study lakes (M. Thompson, unpublished data) indicates the possibility of some macroinvertebrate predation. Rhabdocoel flatworms are also known to structure zooplankton populations in arctic lakes by preying upon certain Cladocera but not larger Calanoid copepods (Schwartz and Hebert 1986). Such a pattern is evident in active and unaffected lakes, but not in stable lakes, but the importance of flatworm predation in these lakes is not known because the zooplankton sampling procedures used in this study would not have detected flatworms.

SRTS appears capable of altering habitat conditions for biota at more than one position in the food web. The physical changes to lake bathymetry related to SRTS activity have the potential to alter “top-down” control of food web structure by creating deep, cool pits and by altering the cycling and availability of phosphorus within lakes. This is in addition to the “bottom-up” impacts of SRTS on water colour and subsequently phytoplankton growth (Thompson et al. 2008, Thompson 2009a). Although the lake-bottom pits occur in both active and stable-SRTS affected lakes, the zooplankton size and abundance in stable lakes suggests the possibility of mortality from greater predation pressure, from either macroinvertebrates or fish, than in active lakes. In addition, the higher TP in stable vs. active SRTS-affected lakes indicates

that the effect of stratification, or perhaps macrophyte growth (Mesquita et al. 2008), on limiting the resuspension of TP is stronger in active than in stable SRTS lakes. At the same time, the higher TP in stable vs. unaffected lakes indicates that stable lakes might be receiving phosphorus subsidies from the SRTS. Further investigation involving repeated measurement of primary production rates, trophic level-specific biomass and the determination of the presence and composition of fish populations would greatly improve the quantification of these impacts and aid in the prediction of SRTS-related impacts to tundra lake food webs.

As a disturbance mechanism, it is difficult to determine when a specific SRTS first appeared, and whether or how often it has re-stabilized and re-activated, particularly in remote arctic regions where monitoring is infrequent or non-existent. For this reason, it is likely inaccurate to infer from present SRTS conditions how long a lake may have been affected by SRTS, and with what intensity over that period. However, the current state of the SRTS (e.g., actively degrading or stabilized and revegetated) can be used to explore the degree of abiotic and biotic impacts in a lake ecosystem, as was done in this study. The potential for future work in determining the history of slump development and activity history as it has affected lake ecosystems will pose both a challenge and a significant opportunity to further characterize disturbance regimes in these lakes.

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**Summary: The limnological characteristics of the Mackenzie Delta uplands
with special consideration of localized permafrost thaw slumping**

The goal of the research described in this dissertation was to characterize the effects of permafrost thaw on the pelagic communities of tundra lakes. The specific form of permafrost thaw considered in this research was intense and localized retrogressive thaw slumping that occurred on the shores of the study lakes. The focus of the sampling regime was nutrient chemistry, primary and secondary producers and primary consumers, because the anticipated effect of the permafrost thaw was soluble nutrient release to the adjacent lakes. Any biotic impact should have therefore be detectable at primary producer and consumer trophic levels. As has been reported, the impact of permafrost thaw was more complicated than a straightforward release of solutes, and particularly nutrients, to the receiving lakes. The impacts also included changes to the pelagic light regime and to the bathymetry of the lakes, with implication for multiple trophic levels.

Previous attempts to quantify the impact of permafrost thaw in freshwater systems have been in part anecdotal (Hobbie et al. 1999), or have considered only water chemistry impacts (Kokelj et al. 2005 , Bowden et al. 2008). This project is the first to investigate the biotic impacts of permafrost thaw on pelagic ecosystems in a systematic way.

5.1 Research Summary

Table 5-1 summarises the dissertation objectives and the conclusions arrived at following the investigations described in the preceding chapters.

Table 5-1. Summary table of dissertation objectives, the methods used in their analysis, the variables measured and the corresponding conclusions.

Question	Method and Sample Size	Special Focus	Answer
Relative to other landscape-scale influences, how strongly does shoreline thaw slumping affect the water-column chemistry of tundra lakes?	Multivariate lake survey, 59 lakes	Water chemistry, especially nutrients (C, N, P)	Significant impacts on inorganic chemistry, but not on nutrient concentrations where relative catchment size and lake depth were more important.
Is there a significant difference in nutrient concentrations and plankton biomass between slump-affected and unaffected tundra lakes?	Comparison between SRTS-affected and unaffected lakes, 22 lakes, half affected by SRTS	Nutrient concentrations and primary and secondary producer biomass	Only [DOC] was significantly different between lake types. Water colour predicted chlorophyll <i>a</i> in unaffected lakes, but TP and TDN predicted chlorophyll <i>a</i> in SRTS-affected lakes.
How do the impacts of SRTS on pelagic nutrients and biota relate to the state of SRTS (actively degrading or stabilized and revegetated SRTS)?	ANOVA design, 9 lakes with three replicates of each slump status	Nutrient concentrations, primary and secondary producer biomass, zooplankton abundance and body size	Complex patterns in most examined variables, and no straightforward response to SRTS gradient. Unexpected bathymetry effects with implications for thermal regime. Highest chlorophyll <i>a</i> and TP but lowest zooplankton abundance in stable -SRTS lakes.

SRTS was the dominant influence over conductivity, Fe, DOC and TDN concentrations in the study lakes. The concentrations of carbon and nitrogen were negatively influenced by SRTS, as was phosphorus to some extent. Contrary to the predicted increase in nutrient concentrations as a result of increased supply from SRTS to the study lakes, the concentrations of these nutrients were lower in lakes affected by SRTS than in unaffected lakes. Phosphorus concentrations varied

most with maximum lake depth. In addition, the variation in phosphorus concentrations was separated according to lake order.

The correlation between LA:CA and DOC and TDN in the study lakes supports the idea that within-lake carbon and nitrogen concentrations are also significantly influenced by catchment-related processes. Relative LA:CA and catchment size may account for variability in concentrations between slump-affected (on average higher LA:CA) and unaffected (on average lower LA:CA) lakes. However, the negative relationship between LA:CA and organic carbon and nitrogen can be related to a catchment source, validating the relationship beyond a correlation with slump status.

The lack of correlations between SRTS activity and TP, and the additional influence of LA:CA on TDN and DOC raised the question as to whether SRTS was a potential source of nutrients to lakes in the study area. Nitrogen, phosphorus and organic carbon concentrations in standing waters within SRTS sites were orders of magnitude higher than in the surface water of the adjacent lakes. Nonetheless, TDN, DOC and TP were significantly lower in 11 slump-affected lakes than in 11 unaffected lakes in 2005, 2006 and 2007. This suggests that degrading shoreline permafrost does not serve as a source of these nutrients to the adjacent lakes. However, further investigation into the cycling of these nutrients and into primary production in the study lakes is required to determine this conclusively.

Tundra lakes that were affected by SRTS had lower autumn chlorophyll *a* concentrations than similar lakes that were unaffected by slumping. In addition, the TP-chlorophyll *a* relationship was stronger in SRTS-affected than unaffected lakes. Finally, chlorophyll *a* was most

strongly influenced by TDN and TP in SRTS-affected lakes, and by water colour ($a_{320\text{nm}}$) in unaffected lakes. A possible explanation for the differing influencing factors between lake types is that high water colour in undisturbed lakes inhibits the phytoplankton response, while in the relatively clear lakes that are affected by shoreline slumps, phytoplankton response is released from inhibition by light availability and more limited by TDN and its correlate TP. The low nutrient concentrations in SRTS-affected lakes would account for the low chlorophyll *a* concentrations in lakes where light is more available, compared to unaffected lakes.

SRTS significantly altered the pelagic habitat of affected lakes. The changes in water chemistry and colour concentrations in the SRTS-affected lakes were expected to be greatest in lakes affected by an actively degrading SRTS (active), and less extensive in lakes affected by stabilized and revegetated SRTS (stable). The chlorophyll *a* concentrations in SRTS-affected lakes were also expected to be lower in active vs. stable lakes, since SRTS-affected lakes were affected by a shift in the limiting factors governing chlorophyll *a* concentration. This expectation was based on the assumption that the water chemistry conditions in SRTS-affected lakes are directly impacted by the SRTS activity, that producer and primary consumer trophic levels would be the most impacted by such a shift in water chemistry and that there were no indirect effects on other lake characteristics.

Contrary to the formulated hypothesis, the response of nutrient concentrations and chlorophyll *a* did not directly reflect the SRTS activity gradient. TP was highest in stable lakes and lowest in active lakes, and chlorophyll *a* did not reflect the SRTS gradient, somewhat mirroring TP. In addition, there was no difference in bacterioplankton abundance between lake

types, but zooplankton abundance was lowest in stable lakes, and high in both active and unaffected lakes.

The bathymetry of the study lakes was also unexpectedly influenced by SRTS. Deep, localized pits were mapped at the bottom of SRTS-affected lakes, and they generally occurred adjacent to the SRTS sites. These pits were most apparent in active lakes, less apparent in stable lakes and not apparent in unaffected lakes. The impacts of the pits on the lake food webs may be significant, since, thermoclines that would not otherwise have occurred in some of lakes were present in these deeper areas. The hypolimnion in these lakes could provide cool summer fish habitat, and may add the required volume and depth for dissolved oxygen conditions required by overwintering fish (Hershey et al. 1999). At the same time, the occurrence of a thermocline in the SRTS-affected lakes may increase the retention of sediment phosphorus since whole-lake mixing would be restricted during summer. This retention of phosphorus in the sediments might have been responsible for the relatively low phosphorus concentrations in the water column of active lakes.

The results of the gradient study lead to the following preliminary system characterizations. Active lakes had low phosphorus and chlorophyll *a* concentrations and high zooplankton abundance, the latter indicating a lack of grazing pressure from secondary consumers, whether macroinvertebrate or fish. Phosphorus, though in high concentration in pooled water within SRTS sites, was possibly removed from the water column via sedimentation and was retained there during thermal stratification. Alternatively, phosphorus may have been taken up by phytoplankton or by benthic producers (Mesquita et al. 2008), while abundant

zooplankton could drive phytoplankton biomass down. The latter possibility is supported by the observation in SRTS-affected lakes that sediment P concentrations are not higher in areas opposite the SRTS vs. in the SRTS-adjacent pits, and that high inputs of SO_4^{2-} from the SRTS could be releasing sediment P for macrophyte uptake. Since phytoplankton in SRTS-affected lakes were nutrient-limited, the low phosphorus availability would lead to low phytoplankton biomass.

In contrast, unaffected lakes had higher phosphorus and chlorophyll *a* concentrations, but had similarly high zooplankton abundance. Phytoplankton in unaffected lakes was light-limited, a condition related to the high water colour in the lakes. Despite the resulting weaker relationship between phosphorus and chlorophyll *a*, the high phosphorus concentrations lead to relatively high chlorophyll *a*. The high zooplankton abundance in these lakes could be related to a lack of predation pressure, which may be explained by a lack of predators or by the negative effects of water colour on any anvisual predators present.

Stable lakes exhibited conditions that were a mix of those found in active and unaffected lakes. Like unaffected lakes, stable lakes had high phosphorus and chlorophyll *a* concentrations, but unlike unaffected lakes where chlorophyll *a* was light limited, chlorophyll *a* in these SRTS-affected lakes was nutrient limited. Stable lakes also had lake-bottom pits similar to those found in active lakes, but stable lakes were not stratified as often during the sampling surveys as were active lakes. This weaker stratification pattern could have led to more frequent resuspension of sediment phosphorus to the water column, and to poorer habitat conditions for some fish species. Since chlorophyll *a* was related most to nutrient concentrations in SRTS-affected lakes, the high

phosphorus and chlorophyll *a* concentrations in these lakes indicate a straightforward resource-producer relationship. At the same time, the uniquely low zooplankton abundance probably resulted in low grazing pressure on phytoplankton while indicating high predation pressure.

Because of the complex dynamics governing the uptake of nutrients and the eutrophication of the study lakes, it is not surprising that the whole-lake response to the SRTS gradient was not a straightforward matter of degree. Instead, many of the nutrient and trophic level conditions in stable lakes do appear to be intermediate to conditions in active and unaffected lakes, while the overall food web response appears distinct in each lake type.

5.2 Links to Theory

SRTS activity acts as a mechanism of disturbance in the study lakes, but as stated above, the resulting impacts do not take the form of a direct cause and effect process. In terms of disturbance, lakes have been described as “climatically buffered, fairly homogeneous and self-contained systems” - in other words, they are relatively benign and do not foster resilience (Holling 1973), while arctic systems, situated in a climatically extreme environment, might be more resilient than previously believed (Holling 1973). However, probable exceptions to this theory of arctic resilience are frozen soils and self-contained arctic lakes (Holling 1973), because these systems are either thought to have a “point of no return” or because they are not accessible to the colonizers that are required to replenish disturbed ecosystems. The study lakes appear to be able to “bounce back” from some degree of permafrost thaw, and the SRTS-affected systems as a whole do not appear to suffer from a lack of colonizing biota. It is acknowledged, however, that in the case of complete thawing of the surrounding permafrost, many of the study lakes would

immediately drain downstream and would cease to exist (Mackay 1992).

Alternative stable states may play a role in arctic lentic systems. The dualities between autochthonous and allochthonous energy sources and benthic and pelagic-dominated production, along with the exceptional changes in lake morphometry and stratification regimes lend themselves to interpretations as alternatively stable equilibria. If there is more than one stable state in these tundra lakes, historical “accidents” such as SRTS activity can be very significant in determining the ultimate form of the system (May 1977). However, significant research and long-term records are required to firmly characterize alternative stable states in an ecosystem, and the general lack of such research and records in arctic lakes makes it almost impossible at this time. Certainly, the rapid climatic change currently being experienced across the Arctic compared to general global conditions could cause a shift in the functioning of these lakes. However, true alternative stable states include positive feedback mechanisms for each alternative equilibria. It is not yet clear how the impacts identified in this project might provide positive feedback for the measured pelagic habitat conditions.

5.3 The Research Process and Future Work

The research process employed in this project was a challenging step-by-step process of data accumulation, with each new finding spurring a new line of investigation. Because the initial plan for the investigation of the impacts of permafrost thaw in these lakes was both comprehensive and ambitious, it was necessary to maintain a focused line of inquiry in order to produce a preliminary characterization of the processes at work. There were challenges in

determining the effects of permafrost thaw on nutrient concentrations, particularly because of the complex cycling of nutrients both in the lake catchments and within the lakes. Because of these unexamined nutrient dynamics, it was particularly difficult to estimate the amount of nutrients released by SRTS activity and in what form the nutrients reached the lakes. Working from the 59-lake synoptic survey to the 22-lake comparative summary was helpful in determining the major differences between SRTS-affected and unaffected lakes. Ultimately, the 9-lake ANOVA design was necessary to separate some of the catchment influences from the processes affecting nutrient concentrations within the study lakes.

Measuring primary production rates instead of biomass indicators would have avoided some of the quantification problems related to nutrient uptake and to grazing pressure-related difficulties encountered while attempting to quantify both the amount of nutrients released from SRTS and the subsequent degree of eutrophication. The measurement of trophic levels adjacent to primary producers compensated for some of this uncertainty, since, according to cascading food web theory, if enrichment is not detectable at the primary or secondary producer level, it should be detectable at the primary consumer level. However, measuring production rates would be the most complete way to assess the impacts of permafrost thaw in lake systems. The sampling and assessment of fish populations in the study lakes would also provide valuable information about food web interactions that are most likely influencing primary producers and the fate of SRTS-derived nutrients. At the other end of the food web, the identification of phytoplankton and picoplankton would be useful in determining possible alternate energy pathways involving bacterioplankton in each lake type (Jansson et al. 2007).

The conclusions outlined in this manuscript will be improved by forthcoming research into the hydrology of the study lakes and catchments. The variation in total nitrogen and organic carbon between the study lakes was related to the lake area:catchment area ratio, a proxy measure of the runoff and associated solute input from the catchment to the lake. Since the slump sites are likely somewhat different from the surrounding hummocky tundra in terms of the ability to collect and deliver precipitation in the form of runoff, they could potentially alter the water budget of the lake. Runoff with origins in the thawing ice was also probably contributing to the water budget of SRTS-affected lakes (Kokelj et al. 2008).

Since very little information is available for the study lakes, more frequent sampling of lakes in the area would also be useful in assessing seasonal variation. In particular, it will be necessary to confirm that late summer sampling captured peak whole-lake productivity conditions and whether the spring sampling period occurred during a phytoplankton bloom. The lack of such basic information for the study area presented both a serious challenge and an exciting opportunity to contribute to the basic knowledge of the factors controlling pelagic ecosystems in these tundra lakes.

5.4 References

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Appendices

Appendix A. Physical and chemical data for 59 lakes in the uplands east of the Mackenzie Delta, NWT. The Survey category indicates which of the lakes from the largest survey (Chapter 2) are used for analyses in Chapter 3 and 4. Below detection limit values are indicated as < x. Fire history divisions are 1 – formerly burned area (1968), 2 – unburned area, 3 – formerly burned area (unknown). Data which were unavailable are indicated by “.” Mean, minimum, maximum and standard deviation values are also presented.

a) Unaffected Lakes

Lake Name	Survey		Burn Unit	Lake Order	Lake Area ha	Catchment		Maximum Depth m	Water Temperature C	Specific Conductivity μScm^{-1}
	Ch 3	Ch 4				Area ha	LA:CA			
1A	*		1	1	1.14	10.87	0.11	2.8	11.0	147.4
2A	*		1	1	2.00	17.23	0.12	6.1	11.3	118.1
3A	*		1	1	1.28	13.15	0.10	10.3	11.4	160.7
4A	*		1	1	1.23	15.52	0.08	1.6	11.1	76.2
5A	*		2	1	2.85	20.95	0.14	10.9	11.3	59.0
6A	*		2	1	3.59	19.71	0.18	2.3	11.1	54.8
7A	*		2	1	1.42	18.11	0.08	2.7	11.3	42.8
8A	*		2	1	2.13	24.41	0.09	1.5	11.1	105.1
9A	*		2	2	3.13	29.30	0.11	2.7	10.6	46.7
10A	*		2	1	2.29	26.31	0.09	3.4	9.0	68.3
11A	*		2	1	9.78	70.09	0.14	6.8	8.0	72.3
14A			1	1	3.42	33.52	0.10	7.5	11.5	572.0
15A			2	1	3.08	38.34	0.08	2.2	7.6	30.9
16A			2	1	8.63	22.25	0.39	1.6	9.5	90.2
17A			2	1	2.17	23.03	0.09	5.9	9.9	108.6
18A			2	1	2.11	18.36	0.11	5.0	9.8	98.2
19A			2	1	2.79	24.64	0.11	3.3	9.2	47.8
21A			2	1	10.93	108.18	0.10	11.2	9.9	90.9
22A		*	2	1	1.87	8.31	0.23	3.7	9.2	150.7
23A			2	1	2.09	18.21	0.11	4.4	8.5	80.0
24A			2	2	12.09	30.04	0.40	15.3	10.0	146.3
25A		*	2	2	4.88	28.48	0.17	5.6	9.6	168.5
26A			2	1	6.47	58.19	0.11	2.4	9.2	100.7
27A			2	1	2.11	16.13	0.13	3.9	9.1	78.0
28A			2	1	22.37	111.73	0.20	2.4	8.5	134.0
29A			2	1	3.03	14.45	0.21	1.6	8.3	93.0
30A		*	2	1	4.36	23.00	0.19	8.4	9.2	130.0
34A			2	1	32.53	150.23	0.22	1.6	9.3	83.0
36A			1	1	0.76	6.55	0.12	9.5	10.7	133.4
Mean					5.40	34.46	0.15	5.1	9.9	113.4
Max					32.53	150.23	0.40	15.3	11.5	572.0
Min					0.76	6.55	0.08	1.5	7.6	30.9
Std. Dev.					6.93	34.05	0.08	3.6	1.1	95.9

a) Unaffected Lakes (cont'd)

Lake name	Fe mgL ⁻¹	DOC mgL ⁻¹	NH ₃ mgL ⁻¹	NO ₃ NO ₂ mgL ⁻¹	SRP mgL ⁻¹	TDN mgL ⁻¹	DP mgL ⁻¹	TP mgL ⁻¹
1A	0.197	15.9	0.040	0.0030	<0.001	0.820	0.0100	0.0200
2A	0.337	15.6	0.020	<0.002	< 0.001	0.520	0.0100	0.0200
3A	0.194	16.5	0.020	<0.002	< 0.001	0.620	0.0100	0.0100
4A	1.240	16.3	0.050	0.0550	0.0030	0.740	0.0200	0.0300
5A	0.287	13.9	0.020	0.0030	< 0.001	0.390	0.0000	0.0100
6A	1.490	17	0.020	0.0020	0.0040	0.520	0.0200	0.0300
7A	2.850	17.5	0.040	0.0060	0.0070	0.610	0.0300	0.0500
8A	0.551	32.7	0.040	0.0060	< 0.001	1.080	0.0100	0.0300
9A	0.945	15.3	0.020	<0.002	0.0010	0.480	0.0100	0.0300
10A	2.390	16.2	0.020	0.0556	0.0048	0.770	0.0400	0.0700
11A	1.410	23.2	0.010	0.0079	0.0034	0.640	0.0300	0.0800
14A	0.152	11.7	0.010	0.0424	0.0003	0.430	0.0000	0.0100
15A	1.940	13.6	0.010	0.0177	0.0026	0.590	0.0300	0.1400
16A	.	6.7	0.010	0.0729	0.0002	0.330	0.0000	0.0100
17A	0.407	23.1	0.060	0.0120	< 0.001	0.880	0.0100	0.0200
18A	.	25.4	0.050	0.0110	0.0020	1.040	0.0100	0.0500
19A	1.480	14.8	0.100	0.0559	0.0042	0.780	0.0400	0.0700
21A	0.631	17	0.010	0.0203	0.0005	0.630	0.0100	0.0200
22A	0.238	11.1	0.020	0.0020	< 0.001	0.430	0.0100	0.0100
23A	1.810	17.3
24A	0.202	11.5	0.020	0.0024	0.0004	0.400	0.0000	0.0100
25A	0.242	10.9	0.010	<0.002	0.0003	0.400	0.0000	0.0100
26A	0.419	14.4	0.010	<0.002	0.0008	0.440	0.0100	0.0100
27A	1.850	11.6	0.010	<0.002	0.0031	0.480	0.0400	0.0700
28A	0.263	10.9	0.010	0.0025	0.0003	0.500	0.0100	0.0300
29A	0.692	15.5	0.020	0.0242	0.0008	0.670	0.0100	0.0400
30A	0.163	8.9	0.020	0.0091	0.0002	0.390	0.0100	0.0200
34A	0.339	11.4	0.080	0.0160	0.0007	0.810	0.0100	0.0400
36A	2.520	13.3	0.010	<0.002	0.0005	0.450	0.0100	0.0200
Mean	0.935	15.5	0.027	0.0203	0.0019	0.601	0.0143	0.0343
Max	2.850	32.7	0.100	0.0729	0.0070	1.080	0.0400	0.1400
Min	0.152	6.7	0.010	<0.002	0.0002	0.330	0.0000	0.0100
Std. Dev.	0.834	5.3	0.023	0.0221	0.0019	0.200	0.0123	0.0296

b) SRTS-affected Lakes

Lake Name	Survey		Burn Unit	Lake Order	Lake Area ha	Catchment		Maximum Depth m	Water Temperature C	Specific Conductivity μScm^{-1}
	Ch 3	Ch 4				Area ha	LA:CA			
1B	*		1	1	18.00	91.55	0.20	2.8	11.3	262.0
2B	*		1	1	4.90	15.87	0.31	3.4	11.1	461.0
3B	*		1	1	3.95	15.34	0.26	15.0	11.4	660.0
4B	*		1	1	5.04	17.80	0.28	9.9	11.4	897.0
5B	*		2	1	2.77	27.70	0.10	9.0	10.9	628.0
6B	*		2	1	1.19	7.54	0.16	2.0	11.3	316.0
7B	*		2	2	3.11	34.75	0.09	4.1	11.5	286.0
8B	*	*	2	1	6.49	32.71	0.20	2.8	10.7	367.0
9B	*		2	1	3.63	7.23	0.50	3.0	10.4	448.0
10B	*		2	1	11.39	23.30	0.49	10.4	9.7	1569.0
11B	*		2	1	10.45	39.37	0.27	6.5	9.3	419.0
13B			1	2	1.43	5.80	0.25	1.7	10.4	408.0
14B			1	3	9.19	45.10	0.20	10.5	11.4	199.6
15B			2	1	10.37	229.90	0.05	7.0	7.3	144.2
16B		*	2	1	14.10	62.97	0.22	6.6	10.9	421.0
17B			2	1	1.86	15.58	0.12	2.6	10.6	206.0
18B			2	1	2.73	4.68	0.58	5.2	11.2	357.0
19B		*	2	1	6.11	28.11	0.22	7.0	10.3	130.6
21B			2	1	18.60	57.07	0.33	4.7	9.9	307.0
22B		*	2	1	3.52	11.70	0.30	6.9	10.1	967.0
23B			2	2	17.68	74.28	0.24	5.9	9.8	187.6
24B		*	2	1	7.56	40.26	0.19	2.9	9.3	280.0
25B			2	3	6.31	76.84	0.08	2.0	8.0	165.4
26B			2	1	116.48	254.39	0.46	3.5	9.5	299.8
27B			2	1	3.81	23.76	0.16	14.2	9.9	125.0
29B		*	2	1	5.72	14.26	0.40	6.7	9.7	537.0
30B			2	1	21.43	69.05	0.31	1.9	8.3	343.0
34B			2	2	77.27	215.76	0.36	1.9	9.2	312.0
35B			3	1	1.44	17.13	0.08	2.9	9.8	153.3
36B			1	1	3.88	24.38	0.16	7.4	11.3	942.0
Mean					13.35	52.81	0.25	5.7	10.2	426.6
Max					116.48	254.39	0.58	15.0	11.5	1569.0
Min					1.19	4.68	0.05	1.7	7.3	125.0
Std. Dev.					23.95	65.61	0.13	3.6	1.1	315.8

b) SRTS-affected Lakes (cont'd)

Lake name	Fe mgL ⁻¹	DOC mgL ⁻¹	NH ₃ mgL ⁻¹	NO ₃ NO ₂ mgL ⁻¹	SRP mgL ⁻¹	TDN mgL ⁻¹	DP mgL ⁻¹	TP mgL ⁻¹
1B	0.129	10.1	0.030	<0.002	< 0.001	0.470	0.0000	0.0100
2B	0.160	.	0.020	<0.002	< 0.001	0.710	0.0100	0.0800
3B	0.125	9	0.010	0.0030	< 0.001	0.330	0.0000	0.0100
4B	0.110	9.1	0.010	0.0030	< 0.001	0.370	0.0000	0.0100
5B	0.142	15.3	0.010	0.0040	< 0.001	0.380	0.0000	0.0100
6B	0.122	19.5	0.040	0.0060	0.0030	0.870	0.0100	0.0300
7B	0.123	16.7	0.020	<0.002	< 0.001	0.450	0.0100	0.0100
8B	0.093	9.4	0.010	0.0030	< 0.001	0.330	0.0000	0.0100
9B	0.102	6.6	0.010	0.0020	< 0.001	0.330	0.0000	0.0100
10B	0.106	8.2	0.010	0.0326	0.0007	0.360	0.0100	0.0100
11B	0.115	10.3	0.010	0.0449	0.0004	0.440	0.0100	0.0100
13B	0.214	19.4	0.020	<0.002	0.0020	0.820	0.0200	0.2300
14B	0.116	15	0.010	0.0247	0.0003	0.690	0.0100	0.0200
15B	0.838	12.2	0.010	0.0880	0.0023	0.450	0.0100	0.0300
16B	0.105	8.3	0.010	0.0598	0.0003	0.340	0.0000	0.0100
17B	0.292	17	0.020	0.0030	< 0.001	0.670	0.0100	0.0200
18B	0.161	8	<0.005	0.0020	< 0.001	0.340	0.0000	0.0100
19B	0.192	11	0.010	<0.002	0.0005	0.430	0.0100	0.0400
21B	0.132	8.6	0.010	<0.002	0.0003	0.360	0.0100	0.0300
22B	0.155	9.2	0.010	0.0095	0.0005	0.390	0.0100	0.0100
23B	0.152	11.7	0.010	<0.002	0.0003	0.410	0.0100	0.0100
24B	0.162	7.9	0.010	<0.002	0.0004	0.320	0.0100	0.0100
25B	0.506	14.9	0.010	<0.002	0.0008	0.470	0.0100	0.0300
26B	0.050	5.5	.	0.0038	0.0005	0.230	0.0000	0.0100
27B	0.255	14.9	0.010	0.0025	0.0002	0.500	0.0100	0.0100
29B	0.135	7.1	0.020	0.1476	0.0005	0.690	0.0100	0.0300
30B	0.155	8.5	0.130	0.0098	0.0005	0.430	0.0100	0.0200
34B	0.128	6.2	0.050	0.0054	0.0003	0.250	0.0000	0.0100
35B	0.855	.	0.020	0.0136	0.0008	0.730	0.0100	0.0400
36B	0.096	14	0.010	<0.002	0.0004	0.420	0.0100	0.0100
Mean	0.201	11.2	0.020	0.0234	0.0008	0.466	0.0070	0.0260
Max	0.855	19.5	0.130	0.1476	0.0030	0.870	0.0200	0.2300
Min	0.050	5.5	0.010	<0.002	0.0002	0.230	0.0000	0.0100
Std. Dev.	0.194	4.0	0.024	0.0372	0.0008	0.169	0.0053	0.0414