

Effects of Retrogressive Thaw Slumps on Sediment Chemistry, Submerged Macrophyte Biomass, and Invertebrate Abundance of Upland Tundra Lakes

P.S. Mesquita

Water and Climate Impacts Research Centre, Department of Geography, University of Victoria, Victoria, Canada

F.J. Wrona

Water & Climate Impacts Research Centre, Environment Canada, Department of Geography, University of Victoria, Canada

T.D. Prowse

Water & Climate Impacts Research Centre, Environment Canada, Department of Geography, University of Victoria, Canada

Abstract

Global warming is forecasted to cause significant thawing of the permafrost that surrounds lakes and rivers across the Arctic, with wide-scale effects on the water quality and biotic characteristics of these water bodies. The benthic environment is believed to be especially sensitive to permafrost-induced ecological change, and this has been the focus of recent field-intensive research. Five lakes affected and three lakes not affected by retrogressive thaw slumps were sampled during late summer of 2006 to assess the potential effects of slumping on benthos. Water quality parameters, submerged macrophytes, benthic invertebrates, and sediment were collected. GLM, Kruskal-Wallis, and ANOVA were used to test for differences between both groups, as well as for possible interaction effects from sample depth. A significant difference ($p < 0.05$) between disturbed and undisturbed lakes was found for macrophyte, invertebrates, underwater light attenuation, and some sediment variables. The results suggest that thaw slumps can affect the freshwater food-web through an increase in benthic production.

Keywords: invertebrates; macrophytes; permafrost retrogressive thaw slumping; sediment chemistry; tundra lakes.

Introduction

The arctic region has been predicted to be especially sensitive to the impacts of global warming (ACIA 2005). It is forecasted that warming will cause significant thawing of the permafrost that surrounds the lakes and rivers that dominate much of the arctic landscape.

Permafrost terrains in non-bedrock areas commonly have an ice-rich zone at the top of the permafrost table that are formed from downward moisture movement from the active layer at the end of summers and upward moisture movement from permafrost at winter. The seasonal leaching from thawed soils and ionic movement resultant from thermal induced moisture migration contribute to the solute enrichment encountered at the near-surface permafrost (Kokelj & Burn 2003, 2005).

Deepening of the active layer in a warmer climate can lead to the release of these solutes at near-surface permafrost increasing nutrient input to freshwater bodies, which in conjunction with a raise in solute-rich runoff from the landscape will probably affect primary production (Wrona et al. 2005, Hobbie et al. 1999). It is further predicted these changes will consequentially be reflected in modification of food-web structures and biogeochemical cycles (Wrona et al. 2005).

Considering that benthic production can be an important part of the overall primary and secondary production in arctic lakes (Sierszen et al. 2003, Rautio & Vincent 2007) a more comprehensive understanding of the effects of permafrost slumping on the benthic compartment is warranted. Among the benthic biota, a special focus should be placed on macrophytes as they contribute significantly to primary

production, increase habitat heterogeneity (being beneficial to benthic invertebrates and fishes), and are involved in other important in-lake processes (Vadebouncoeur et al. 2003, Kalff 2001).

Many variables have been considered important for macrophyte production, such as underwater light availability, water nutrient content, lake morphology, littoral slope, sediment composition, and organic matter content. Lake sediment, besides acting as a base for physical attachment, has been recognized as an important source of nutrient supply to submerged macrophytes (Barko et al. 1991).

Some studies have already documented differences in lake water chemistry related to permafrost retrogressive thaw slumps (e.g., Kokelj et al. 2005) in a number of lakes in the area between Inuvik and Richards Island, Northwest Territories, Canada. However, the role of such landscape-related slumping on sediment loading, chemistry, and benthic biota still remains unclear and is predicted to be more frequent in a warmer climate (Wrona et al. 2005). This study focused on investigating the hypothesis that retrogressive slumping can produce significant differences in sediment and water chemistry, submerged macrophyte biomass, and benthic invertebrate abundance between undisturbed (*U*) and disturbed (*D*) lakes in a similar geographical region.

Lake Selection and Sampling Methodology

To test the above hypothesis, a set of lakes were selected between Inuvik and Richards Island (N.W.T). Based on lake/catchment characteristics and water quality data from a 60-lake survey (Thompson, unpubl.) and field logistics, a final subset of 3 lakes not affected by retrogressive slumping

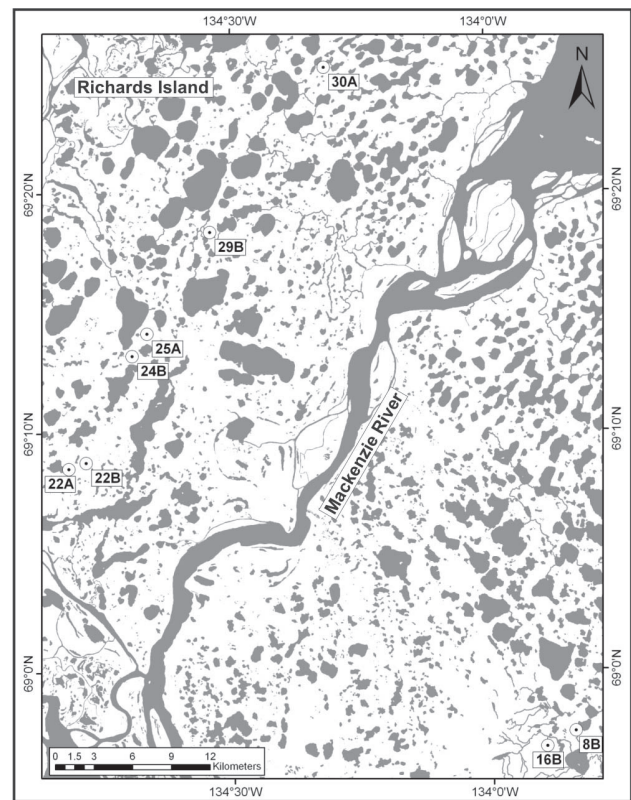
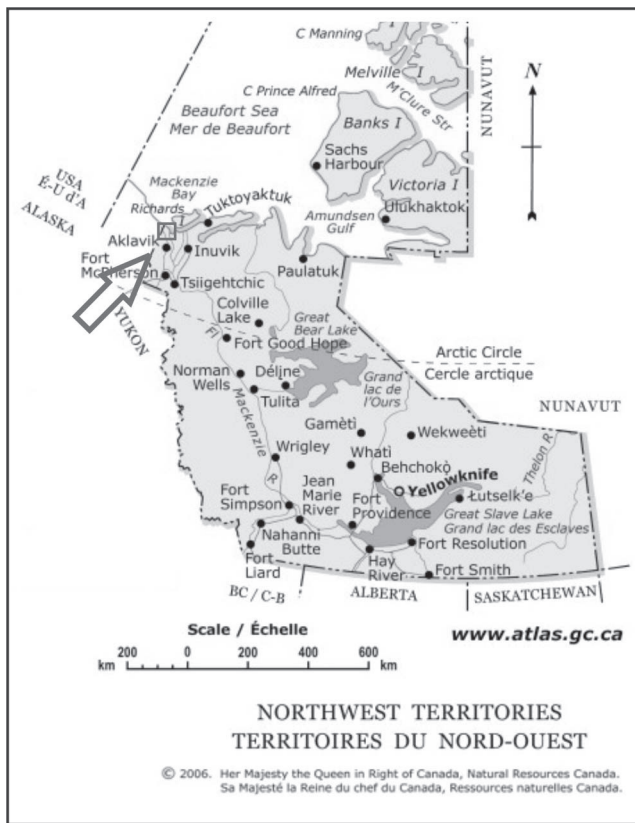


Figure 1. Geographic location of studied lakes. Source: Natural Resources Canada/CanVec (www.geogratis.gc.ca).

(undisturbed or *U* lakes) and 5 lakes affected (disturbed or *D* lakes) were selected for detailed study (Fig 1, Table 1). Disturbed lakes were sampled in two areas: one located at the opposite side (*Do*) of the physical disturbance caused by the slump, and another one in an area adjacent (*Da*) to the slump and thus directly physically affected by the disturbance. This allowed for testing whether undisturbed lakes are similar in their physical, chemical, and biological properties to disturbed systems (particularly with areas in disturbed lakes that are physically removed from the slump (*Do*)).

Stratified radial transects starting from the shoreline towards the center of the lake were used as the main sampling unit (replicate) in the present study, and were distributed in order to encompass the different areas of each lake. Taking into consideration the focus on the littoral benthos, sampling points were randomly placed in 1 m, 2 m, and 3 m deep strata along the transects, yielding a maximum of 9 replicates (3 depths x 3 transects) in undisturbed lakes and a maximum of 18 replicates in disturbed lakes (9 in each disturbance zone - *Do* and *Da*). However, due to logistical constraints in the field, some variables could not always be sampled at all strata depths in all lakes.

Between the end of August and the beginning of September 2006, samples of sediment, submerged macrophytes, benthic invertebrates, and pelagic water were taken from the selected lakes. In addition, interval measurements of underwater photosynthetic active radiation (PAR) (Li-cor LI-192) were taken at each of the transect points from the near surface

to the maximum depth of one meter or before reaching the top of macrophytes. The results were used to calculate the light underwater attenuation coefficient (K_d) at each point in accordance with Kalff (2001).

Submerged macrophytes were collected at 1 m, 2 m, and 3 m deep strata with a telescopic macrophyte sampler (Marshall & Lee 1994) that covered an area of 0.164 m². The macrophytes were subsequently separated, washed, and oven-dried to a constant weight at 60°C for dry weight determination, and then extrapolated to represent a total biomass per m².

Sediment samples were collected with a sediment corer at 1 m and 3 m depths. Samples from the top 15 cm were transported to the laboratory, homogenized, and separated into two fractions. One fraction was frozen, freeze-dried, and sent for analysis of recoverable metals (i.e., environmentally available) and nutrients at the Environment Canada National Laboratory for Environmental Testing (NLET), Burlington, ON (Table 2). The remaining fraction was oven-dried and burned for calculations of loss of ignition (as a measure of organic matter content) in accordance with Hakanson & Jansson (1983).

Sediment samples for estimating invertebrate abundance were collected at 1 m, 2 m, and 3 m depths. Samples from the top 5 cm were washed through a 250 µm sieve, and the invertebrates were subsequently sorted, counted, and extrapolated to 1 m². Water physico-chemical parameters were collected at the deepest point in each lake previously determined from a bathymetric survey. A handheld

Table 1. Lake attributes summary table. Lake area (La), catchment area: lake area (Ca:La) ratio, catchment area: lake volume (Ca:Lv) ratio, maximum depth (Zmax), mean depth (Zmean), lakes (U = undisturbed, D = disturbed), number of lakes (N), mean, standard deviation (S.D), minimum and maximum values (Min and Max).

Lakes		La (m ²)	Ca:La	Ca:Lv	Zmax	Zmean
U lakes	Mean	40100	4.78	1.77	7.30	2.88
	N= 3					
	S.D	19419	0.44	0.14	2.88	0.92
	Min.	18700	4.28	1.61	4.20	1.92
	Max.	56600	5.11	1.88	9.90	3.76
D lakes	Mean	76380	3.99	1.15	9.54	3.48
	N= 5					
	S.D	40514	1.18	0.63	4.33	0.80
	Min.	35500	2.41	0.66	5.30	2.44
	Max.	142900	5.04	2.01	16.80	4.52

multiparameter Y.S.I was used to collect pH, temperature, and conductivity data. In addition, water samples were collected and sent to the NLET lab for analysis of particulate organic carbon (POC), dissolved phosphorus (DP), orthophosphate (OP), total phosphorus (TP), ammonium (NH₃N), nitrite-nitrate (NO₃NO₂), total dissolved nitrogen (TDN), particulate organic nitrogen (PON), and total nitrogen (TN).

Statistical analyses

All the variables were tested for normality using a Kolmogorov-Smirnov (K-S) test ($p < 0.05$) and, when necessary, log₁₀ transformed to fit the assumptions of parametric testing. General Linear Model (GLM) regressions were performed to test for differences in sediment chemistry and invertebrate abundance between undisturbed (U) and disturbed (D) lakes, using depth as a co-variate.

In cases where a significant difference ($p < 0.05$) between disturbed and undisturbed lakes was found, a subsequent GLM with a Bonferroni simultaneous *a posteriori* test between lake/disturbance location (U , Do – opposite to slump, Da – adjacent to slump) and depth was performed. These analyses were used to ascertain whether the differences were related to in-lake processes (Do vs. Da) versus between lake (U vs. Da , U vs. Do) processes and physical proximity to the slump.

Since some sediment variables and macrophyte biomass data were not normally distributed even after transformation, the non-parametric Kruskal-Wallis test was used in these cases. As water nutrient data were only collected at one station per lake system, differences between undisturbed and disturbed lakes were analyzed using one-way Analysis of Variance (ANOVA). All the analyses were performed with MINITAB 13.1 (Minitab Inc. 2000).

Results

ANOVA tests for water nutrient data between undisturbed and disturbed lakes revealed no significant differences ($p > 0.05$) for all measured constituents (POC, DP, OP, TP, NH₃N, NO₃NO₂, TDN, PON, TN). However, pH (mean = 7.6 in U vs. 8.19 in D) and specific conductivity (mean =

Table 2. List of key nutrient, metals and metalloids analyzed from sediment samples.

Carbon (organic/inorganic)	Sodium (Na)	Potassium (K)	Arsenic (As)
Nitrogen (organic)	Zinc (Zn)	Calcium (Ca)	Beryllium (Be)
Phosphorus (inorganic)	Cooper (Cu)	Magnesium (Mg)	Bismuth (Bi)
Phosphorus (P)	Nickel (Ni)	Iron (Fe)	Cadmium (Cd)
Manganese (Mn)	Molybdenum (Mo)	Cobalt (Co)	Gallium (Ga)
Antimony (Sb)	Lanthanum (La)	Chromium (Cr)	Aluminum (Al)
Thallium (Tl)	Lithium (Li)	Strontium (Sr)	Rubidium (Rb)
Uranium (U)	Lead (Pb)	Vanadium (V)	Barium (Ba)

128.6 μ S/cm in U vs. 516.7 μ S/cm in D) were significantly different ($p < 0.05$).

GLM tests revealed significant differences ($p < 0.05$) in only seven sediment variables between U and D lakes. Mg and Ca means showed highly significant differences, ($p < 0.01$) with higher values in D lakes (Ca= 4.85 g/Kg in U vs. 9.44 g/Kg in D , and Mg= 5.74 g/Kg in U vs. 7.35 g/Kg in D (Fig. 2)).

Organic N and C, As, Ni, and Zn were also significantly different between U and D lakes ($p < 0.05$). However, the highest mean values for these variables consistently occurred in undisturbed (U) lakes. The mean values of each of the variables for U and D were 7.29% and 4.90% of organic C, 0.61% and 0.34% of organic N, 0.02 g/Kg and 0.015 g/Kg of As, 0.052 g/Kg and 0.041 g/Kg of Ni, and 0.137 g/Kg and 0.106 g/Kg of Zn, respectively (Fig 2).

Bonferroni *a posteriori* testing revealed no significant differences ($p > 0.05$) between in lake disturbance regions (Da and Do) and between disturbed regions and U lake comparisons for As, Ni, and Zn.

Mg and Ca were not significantly different between Da and Do , but were different between these regions and undisturbed lakes. In contrast, organic N content in Da (0.24%) was significantly different ($p < 0.05$) from Do (0.24% vs. 0.44%), and highly significantly different ($p < 0.01$) to undisturbed lakes (0.61%). Organic C was only significantly different ($p < 0.05$) between Da and U lakes. These indicated that Do , a region within the disturbed systems, was similar to a “control” undisturbed lake for the variables organic N and C.

Kruskal-Wallis tests on Mn, Co, Sr, and ignition loss showed a significant difference ($p < 0.05$) between U and D lakes. Median Mn concentrations varied from 0.83 g/Kg in U versus 0.42 g/Kg in D -lakes; Co ranged from 0.015 g/Kg on U to 0.013 g/Kg on D ; ignition loss varied from 13.26% on U to 9.67% on D ; and Sr, the only of these variables with

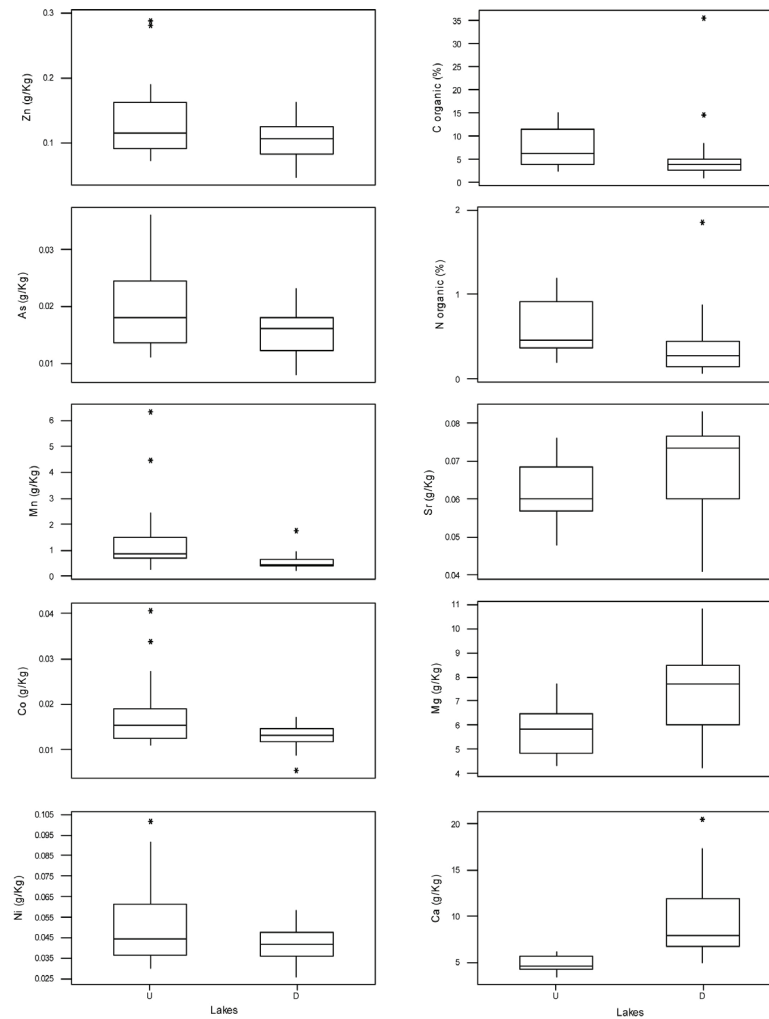


Figure 2. Box plots for sediment chemistry variables that were significantly different between undisturbed (*U*) and disturbed (*D*) lakes. All variables in g/Kg with the exception of C and N in %.

higher values in *D*, varied from 0.06 g/Kg on *U* versus 0.073 g/Kg on *D* (Fig2).

Mn, Co, and Sr were not significantly different between *Do* and *Da* regions ($p > 0.05$) but were different to the undisturbed lakes. Ignition loss results had a similar pattern as found from the Bonferroni test for organic C. The K-W test revealed that only *Da* was significantly different from *U* ($p < 0.05$). Correlation analysis showed a strong positive association between organic C and ignition loss ($r = 0.947$, $p < 0.01$).

Although the median values for macrophyte biomass were the same (zero) at *U* and *D* lakes, the distributions were significantly different ($p < 0.01$) according to Kruskal-Wallis test, with higher values on *D* lakes. This can be explained by the fact that macrophytes were more frequently found in *D* lakes (44%) than in *U* lakes (11%). The biomass present on *Do* was significantly different from *Da* and *U* lakes ($p < 0.01$), while differences between *U* lakes and *Da* were not significant ($p > 0.05$) (Table 3).

The difference in invertebrate abundance between *U* and *D* lakes was highly significant ($p < 0.01$), with higher abundance values in *D* lakes. Differences between *U*, *Do*

and *Da* were also significant, with *Da* having the highest abundance and being different from *U* ($p < 0.01$), and from *Do* ($p < 0.01$). Also, the interaction between *U/D* lakes and depth was significant ($p < 0.05$), indicating a covariation between these two variables (Table 4).

Discussion and Conclusions

Significant differences were found between disturbed and undisturbed lakes for a variety of environmental variables. In general, disturbed lakes exhibited higher mean values of Mg, Ca, and Sr in sediments, and pH and conductivity in the water column. Undisturbed lakes had higher levels of organic C and N, As, Ni, Zn, Mn, Co, and organic matter in the sediment, and higher values of littoral underwater light coefficient of attenuation (K_d). The conductivity pattern is in accordance with previous observation by Kokelj et al. (2005), where lakes with catchments disturbed by thermokarst slumping had higher water ionic content and conductivity than undisturbed lakes in the same geographic area.

Macrophyte biomass and invertebrate abundance were higher in disturbed lakes, being postulated that this difference

Table 3. Macrophyte biomass (g/m^2) summary data from all lake, *U*, *D*, *Do*, and *Da*. Number of sample points (N), number and percentage of cases where macrophytes were present (N_p), minimum and maximum biomass (Min., Max.), median, and first and third quartiles (Q1, Q3).

Lakes/Areas	N	N_p and % presence	Min.	Max.	Median	Q1	Q3
<i>All lakes</i>	90	31 (34%)	0	705.5	0	0	19.21
Undisturbed lakes (<i>U</i>)	27	3 (11%)	0	24.268	0	0	0
Disturbed lakes (<i>D</i>)	63	28 (44%)	0	705.5	0	0	55.9
<i>Opposite region (Do)</i>	33	24 (72%)	0	705.5	28.7	0	104.1
<i>Adjacent region (Da)</i>	30	4 (13%)	0	76.22	0	0	0

is related to higher water transparency and concentrations of key chemical elements originated from the slump and transferred to the sediment. Thus, it is expected that a higher availability of nutrients for the growth and maintenance of macrophyte community produce a structurally more complex benthic habitat, having a positive effect on benthic invertebrates.

Previous studies have suggested that the sediment is the primary source of N, P, Fe, Mn, and other micronutrients necessary for macrophyte metabolism (Barko et al. 1991). However, the present study did not find macrophytes predominant at lakes with higher levels of organic N and Mn (undisturbed lakes). A possible explanation is that higher amounts of organic matter found in the sediment of undisturbed lakes could be affecting nutrient availability and uptake processes (Barko & Smart 1986).

In addition to decreased nutrient availability due to complexation with organic matter in organic sediments, macrophyte growth can be disrupted by the presence of phytotoxic compounds produced during anaerobic decomposition (Barko et al. 1991) For instance, accumulation of large quantities of refractory organic matter in sediments are shown to decrease nutrient availability and the growth of rooted submerged macrophytes, while additions of low quantities of labile organic matter in sediments may benefit macrophytes, especially on coarse textured sediments in oligotrophic systems (Barko et al. 1991).

With the exception of organic N, all the sediment variables and the light attenuation coefficient values were not significantly different within disturbed lakes, leading to the question of what factors might be influencing the absence of macrophytes in areas adjacent to the actual slump (*Da*). Since submerged macrophyte biomass is documented to be related more to underwater substrate slope at depths where irradiance is not the primary limiting factor (Kalff 2001), slope and related substrate stability is postulated to be the major factor influencing the almost complete absence of macrophytes in *Da* areas.

Based on preliminary results of bathymetric surveys and field observations, the underwater substrate slope near the slump disturbance is consistently higher than observed in opposite areas in the same lake or in undisturbed lakes. More detailed field analyses need to be conducted to determine the possible causal physical mechanism for this observation. It is possible that macrophyte colonization in disturbed areas is being constantly subjected to burial by soil and vegetation from the lakeshore slump.

Table 4. Invertebrate abundance (individuals/ m^2) summary table from *U*, *D*, *Do*, and *Da*. Number of samples (N), minimum and maximum abundance (Min., Max.), mean, and standard deviation (S.D).

Lakes/Areas	N	Min.	Max.	Mean	S.D
Undisturbed lakes (<i>U</i>)	26	3215	39460	13232	8786
Disturbed Lakes (<i>D</i>)	68	2037	119549	28630	24482
<i>Opposite region (Do)</i>	35	2037	97334	22247	22818
<i>Adjacent region (Da)</i>	32	4584	119549	35631	25055

The observed water transparency and related light penetration values (PAR) in the littoral zone of disturbed lakes also contradicts what would be expected in a scenario of higher suspended sediments and color (dissolved organic carbon) arising from the input of landscape material into the lake water.

Two possible mechanisms could be operating individually or jointly to produce these observed patterns. First, higher ionic concentrations supplied to the lakes from the enriched slump runoff as those shown in Kokelj et al. (2005) could be adsorbing to organic compounds on the water column, causing them to precipitate and “clearing” the water. Secondly, adsorption of organic substances to the exposed mineral soils could be producing runoff with low concentration of colored material in disturbed catchment, while in undisturbed ones colored runoff would be a result of water flux through the shallow organic soils (Carey 2003, Kokelj et al. 2005). Further process-based research is necessary to elucidate the relative importance of these two possible processes and some preliminary experiments examining possible causal mechanisms can be found in Thompson et al. (2008).

In general, benthic invertebrates were found to be more abundant in disturbed lakes. However, while it was expected that areas with more macrophytes would support higher number of invertebrates, areas adjacent to slumps were found to have the highest mean abundance. Other factors, such as periphyton and bacterial abundance, pH, and oxygen, could be influencing benthic invertebrate communities and this needs to be further explored.

In summary, a warmer climate regime accompanied by enhanced seasonal thawing of the active layer will significantly affect benthic macrophyte and invertebrate communities of upland tundra lakes. The present work shows that in addition to the changes in water column characteristics already documented in previous studies (Kokelj et al. 2005), thermokarst retrogressive slumping also affects sediment chemistry and water transparency

relationships in upland tundra lakes. In addition to influences related to input of enriched runoff, deposition of landscape material (i.e., soil and terrestrial vegetation) at the littoral zone can have an impact in macrophyte colonization rates and littoral complexity, affecting benthic invertebrates and upper level consumers.

Complementing the mentioned processes, other environmental changes need to be taken into consideration when projecting the effects of a warmer climate on upland tundra lakes. Active layer deepening could act synergistically with higher temperatures, higher UV penetration in lakes, changes in biota composition/ metabolism, and changes in runoff input due to alterations of biogeochemical cycles at landscape level which could all ultimately lead to a variety of different balances. Contrary to the expected increase in pelagic productivity and decreased transparency associated with permafrost degradation (Wrona et al. 2005), it is suggested that at an earlier stage, increases in the macrophyte biomass associated with higher transparency could be a possibility, being later followed by greater disturbance of littoral zone and decrease of macrophyte communities.

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