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Shifts in Plankton, Nutrient and Light Relationships in Small Tundra Lakes Caused by Localized Permafrost Thaw

MEGAN S. THOMPSON,[1,2] FREDERICK J. WRONA[1,3] and TERRY D. PROWSE[1,3]

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ABSTRACT. Tundra lakes located in the Mackenzie Delta uplands, NWT, Canada, are increasingly being affected by permafrost thaw in the form of shoreline retrogressive thaw slumping. This form of thaw-induced disturbance is used as a surrogate indicator of landscape-related disturbance linked to regional climate warming. We compared 22 lakes, half affected by thaw slumping and half unaffected, to determine whether water column nutrient concentrations, light availability, and plankton biomass differed between these two lake types. Total phosphorus (TP), total dissolved nitrogen (TDN), dissolved organic carbon (DOC), and chlorophyll *a* concentrations were higher in unaffected lakes than in slump-affected lakes. Absorbance related to water colour of both UV and photosynthetically active radiation in the water column was also higher in unaffected lakes, but bacterioplankton abundance was not different between lake types. UV light absorbance was found to be the best predictor of pelagic chlorophyll *a* concentrations in unaffected lakes, whereas TDN (and to a lesser extent TP) were the best predictors of pelagic chlorophyll *a* in slump-affected lakes. These findings indicate that slumping arising from permafrost thaw produces a shift in tundra lake nutrient, light, and phytoplankton relationships. Given the projections of continued warming, this result has significant implications for the future biogeochemical and ecological states of Arctic tundra lakes.

Key words: tundra lakes, permafrost thaw, shoreline retrogressive thaw slump, phosphorus, nitrogen, organic carbon, chlorophyll *a*, bacterioplankton, UV light, photosynthetically active radiation

RÉSUMÉ. Les lacs de toundra situés dans les hautes terres du delta du Mackenzie, dans les Territoires du Nord-Ouest, au Canada, sont de plus en plus touchés par le dégel du pergélisol en ce sens qu'il y a glissement régressif du littoral dû au dégel. Cette forme de perturbation attribuable au dégel sert d'indicateur auxiliaire en matière de perturbation du paysage liée au réchauffement climatique de la région. Nous avons comparé 22 lacs, dont la moitié était touchée par le glissement dû au dégel et l'autre moitié ne l'était pas, afin de déterminer si les concentrations en nutriments des colonnes d'eau, la disponibilité lumineuse et la biomasse du plancton différaient entre ces deux types de lacs. Les concentrations de phosphore total (PT), d'azote dissous total (ADT), de carbone organique dissous (COD) et de chlorophylle *a* étaient plus élevées dans les lacs non touchés quand dans les lacs où il y avait glissement du littoral. L'absorbance liée à la couleur de l'eau du rayonnement actif photosynthétique et du rayonnement actif ultraviolet dans les colonnes d'eau était également plus élevée dans les lacs non touchés, mais l'abondance du bactérioplancton ne différait pas d'un type de lac à l'autre. On a déterminé que l'absorbance de lumière ultraviolette était le meilleur prédicteur de concentrations de chlorophylle *a* pélagique dans les lacs non touchés, tandis que l'ADT (et le PT, dans une moindre mesure) constituaient les meilleurs prédicteurs de chlorophylle *a* pélagique pour ce qui est des lacs faisant l'objet d'un glissement. Ces constatations indiquent que le glissement attribuable au dégel du pergélisol altère les relations qui existent entre les nutriments, la lumière et le phytoplancton des lacs de toundra. Compte tenu des projections à l'égard d'un réchauffement continuel, ce résultat revêt d'importantes incidences sur les états biogéochimiques et écologiques des lacs de la toundra arctique.

Mots clés : lacs de toundra, dégel du pergélisol, glissement régressif du littoral dû au dégel, phosphore, azote, carbone organique, chlorophylle *a*, bactérioplancton, lumière ultraviolette, rayonnement actif photosynthétique

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INTRODUCTION

Permafrost thaw can lead to retrogressive thaw slumps that occur along the shoreline of lakes in areas of ice-rich permafrost such as the Mackenzie Delta uplands in Canada's Northwest Territories (Burn and Lewkowicz, 1990). Such slumps can be relatively large, with headwalls greater than 2 m and areas as large as the adjacent lakes (Kokelj

[1] Department of Geography, University of Victoria, Victoria, British Columbia V8W 3R4, Canada
[2] Corresponding author: Megan.Shera@gmail.com
[3] Water and Climate Impacts Research Centre, Environment Canada, Victoria, British Columbia V8W 3R4, Canada

et al., 2005). A survey of 2880 lakes in a 3739 km^2 upland study region found that 8% of the lakes were affected by shoreline slumping (Lantz and Kokelj, 2008). An observed increase in shoreline retrogressive thaw slumping in this area appears to be related to the observed increase in air temperatures in the western Canadian Arctic (Lantz and Kokelj, 2008).

Across the Arctic, the areal extent of permafrost is expected to decrease by 20–90%, and active layer deepening is projected to increase by approximately 30–100% by the year 2100 (Frey and McClelland, 2009). These changes have implications for all Arctic freshwater systems. The occurrence of highly visible shoreline thaw slumps (STS) on several small, first-order lakes located on continuous permafrost near the Mackenzie Delta in the western Canadian Arctic provides an opportunity to measure the impacts of a readily identifiable form of permafrost thaw across several relatively homogeneous lakes. Since each disturbance was confined to a single lake catchment, the effects of STS were not masked by the homogenization of water chemistry that may occur in a more hydrologically connected landscape.

Thawing permafrost has the potential to deliver large volumes of solutes, sediments, vegetation, and debris to freshwater systems. The possible outcomes of such a process include increased delivery of nutrients from the landscape, an increase in freshwater turbidity, and physical changes to lake and streambeds (Bowden et al., 2008). An increase in phosphorus, nitrogen, or organic carbon supplies, or a combination of these, would affect the biological productivity of freshwater systems. Hobbie et al. (1999) predicted that an increased supply of phosphorus to an Alaskan lake resulting from localized permafrost thaw would generally result in eutrophication through stimulation of algal productivity, which could lead to an increase in the number of food web levels. Permafrost is also estimated to contain more carbon than the current atmospheric pool (Schuur et al., 2008), and permafrost thaw is expected to release this carbon, some of which will be transported to freshwater systems by infiltrating runoff or through thermokarst development (Prowse et al., 2006). The fate of this carbon, particularly if it is released to the atmosphere, may have further climate impacts.

In addition to an increasing nutrient supply, related changes in light availability and quality can affect primary production in STS-affected lakes. A multivariate study of 73 lakes in the Mackenzie Delta uplands (including the 22 lakes sampled in this study) found significantly higher concentrations of major ions in slump-affected lakes and, counterintuitively, that slump-affected lakes have significantly lower water colour (light absorbance) than unaffected lakes (Kokelj et al., 2009). Adsorption of chromophoric dissolved organic matter (CDOM) to basic cations and clay particles in the slump sediments was thought to be responsible for the observed shift from brown water in unaffected lakes to clear water in slump-affected lakes (Thompson et al., 2008). Because brown water (humic) conditions can lead to light limitation of phytoplankton productivity (Jones, 1992; Klug, 2002), lower light levels in lakes unaffected by slumping may limit phytoplankton growth. In a complementary study, Mesquita et al. (2010) found macrophyte biomass to be significantly higher in STS-affected lakes than in unaffected lakes. The higher macrophyte biomass was proposed to be the result of enhanced benthic light regimes produced by the change in water transparency related to thaw-slump activity or enhanced benthic nutrient availability, or both (Mesquita et al., 2010). Moreover, the higher macrophyte biomass might indicate enhanced lake eutrophication that is evident as an ecological shift from pelagic-dominated to benthic-dominated production.

The first objective of this study was to determine whether thaw slump activity leads to an increase in nutrient concentrations and light availability related to the concentration of humic material in the water column of Arctic lakes. A modeling analysis followed to determine whether the nutrient and light conditions in these lakes differed in their relation to pelagic algal and bacterioplankton biomass.

METHODS

Study Area

The study area comprises 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, NWT, Canada (Fig. 1). The lake-rich landscape is the apparent result of a thaw lake formation cycle approximately 11.6 to 8.5 ka BP (Dallimore et al., 2000). The localized thermokarst activity involved in STS may have been ongoing for some time, as indicators of local shifts in water chemistry, possibly caused by deep permafrost thaw, appear in paleolimnological records of the area as early as 3 ka BP (Dallimore et al., 2000).

The study lakes occur across a northward gradient of decreasing annual total precipitation (248 mm at Inuvik to 139 mm at Tuktoyaktuk) and mean annual temperatures (-8.8˚C at Inuvik to -10.2˚C at Tuktoyaktuk) (Environment Canada, 2012). The area includes the transition from brush tundra (alder and willow cover) in the south to open tundra in the north (Lantz et al., 2010). 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). The active layer in this area reaches a maximum thaw of about 1 m, restricting infiltrating runoff to a thin layer of organic-rich soil horizons and allowing for export of terrestrial organic material to lakes and streams (MacLean et al., 1999). However, the deep thaw associated with STS and the export and leaching of undeveloped glacial till underlying the surface soils may contribute to the high conductivity found in STS-affected lakes (Péwé and Sellman, 1973; Kokelj et al., 2005, 2009).

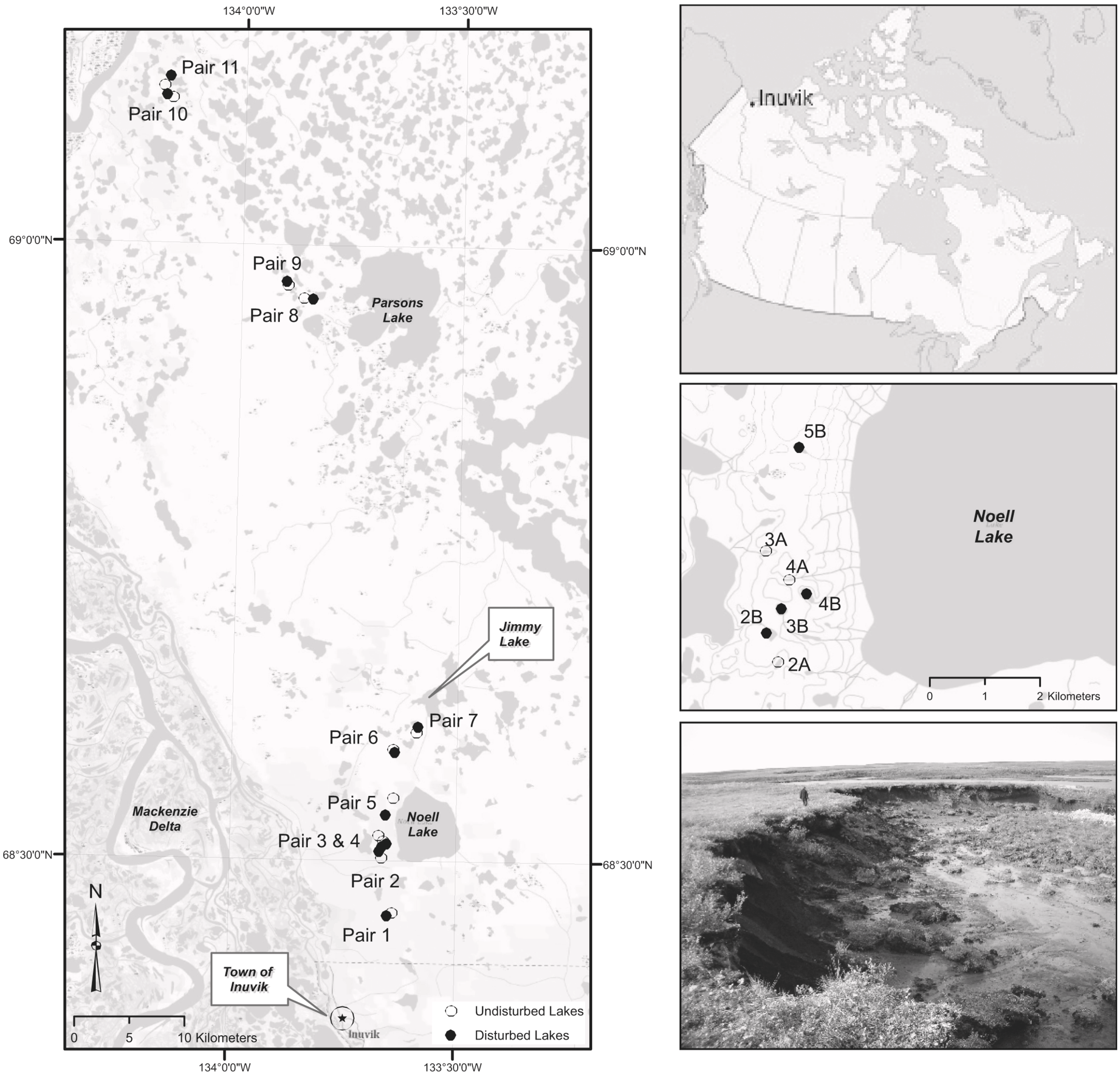

FIG. 1. Map of the study lakes presented as pairs (left), with location within Canada (top right) and an expansion near Noell Lake (middle right). A picture of a shoreline slump at lake 9B is shown with a person walking along the headwall for scale (lower right).

Lake Selection

Twenty-two lakes were selected along a 100 km north-south transect (69˚08′12″ N to 68˚27′27.5″ N) between the town of Inuvik (68˚21′42″ N, 133˚43′50″ W) and the Beaufort Sea coast, east of the Mackenzie River Delta (Fig. 1, Table 1). Kokelj et al. (2005), who selected and sampled these lakes, provide an in-depth site description. The lakes ranged in surface area from approximately 1 to 17 ha (Table 1). Eleven of the study lakes were affected by thaw slumping, while the remaining 11 lakes were unaffected. The area of the STS disturbances in the 11 affected lakes ranged from 0.3 to 7.1 ha, representing 2–26% of the lake catchment area. STS activity has been ongoing at virtually all of the affected lakes since at least the 1970s (S.V. Kokelj, pers. comm. 2011). To control for potential landscape effects (e.g., latitude and catchment vegetation), the study lakes were selected in pairs of STS-affected and unaffected systems less than 5 km apart along the north-south transect. The lakes were also exclusively first-order lakes (drained by first-order headwater streams, Riera et al., 2000). It was anticipated that the small size and hydrologic isolation of

TABLE 1. Study lake characteristics. z_{max} = maximum depth, LA = lake area, CA = catchment area, SA = slump area. Data are also presented in Kokelj et al. (2005) except for z_{max}, which was measured independently.

Unaffected lake	Latitude (°N)	z_{max} (m)	LA (ha)	CA (ha)	Slump-affected lake	Latitude (°N)	z_{max} (m)	LA (ha)	CA (ha)	SA (ha)
1A	68.458	2.8	0.9	8.0	1B	68.455	2.8	17.1	63.8	2.9
2A	68.503	6.1	1.7	14.8	2B	68.507	3.4	4.0	14.3	0.8
3A	68.521	10.3	1.1	16.4	3B	68.511	11.3	3.3	17.9	3.3
4A	68.516	2.5	1.2	11.9	4B	68.514	9.9	4.4	21.5	1.6
5A	68.551	10.9	2.7	23.7	5B	68.538	9.0	2.5	28.9	1.9
6A	68.590	2.3	3.1	37.5	6B	68.588	2.0	0.9	6.1	0.3
7A	68.605	2.7	1.1	37.9	7B	68.609	5.0	2.7	28.8	0.6
8A	68.958	1.5	2.0	15.3	8B	68.957	4.1	5.3	29.9	3.4
9A	68.968	2.7	2.9	28.0	9B	68.971	3.0	3.7	8.8	1.7
10A	69.119	3.4	2.2	15.6	10B	69.121	10.4	8.0	27.5	7.1
11A	69.129	2.5	9.5	44.6	11B	69.137	5.2	9.2	27.4	2.5

the lakes would maximize potential impacts of slumping on nutrient concentrations, making them more detectable. Water-column conditions were then compared between these populations of slump-affected and unaffected lakes.

Sampling

Water-column chlorophyll *a* and nutrient concentrations in the 22 study lakes were sampled during late summer over three years (late August to mid-September 2005–07). The sampling regime was expanded in 2006 to include water colour to better assess the factors limiting plankton growth. Because bacterioplankton are important producers in brown water high-latitude lakes (Jansson et al., 2000), measurements of water-column bacterioplankton cell density were begun in 2006 to monitor for differences in pelagic heterotrophic production.

Sampling was performed from a helicopter fitted with floats. Water was collected near the middle of each lake at 0.5 m below the surface. Additional water samples were collected from pools of standing water within four of the slumped areas in 2007. Within 24 hours of collection, water samples were shipped to Environment Canada (EC) laboratories in Saskatoon and Edmonton for analysis. Total phosphorus (TP), total dissolved nitrogen (TDN), and dissolved organic carbon (DOC) were analyzed following standard methods (APHA et al., 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 determined after acidification and combustion with a carbon analyzer as the difference between total dissolved carbon and dissolved inorganic carbon (DIC).

Water samples for chlorophyll analysis were filtered (glass fibre filter, GFC) at Inuvik, frozen, and shipped to the EC lab in Saskatoon 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 (adapted from Sartory and Grobbelaar, 1984).

Water colour was determined after filtration (GFC) by spectrophotometrically scanning for absorbance from 200 to 900 nm. Absorbance was measured using a spectrophotometer. Representative absorbance measurements at 320 nm (UV-B, a320 nm) and 440 nm (photosynthetically active radiation, PAR, a440 nm) were corrected for turbidity-related light scattering by subtracting absorbance values at 740 nm.

Bacterioplankton enumerations were performed on duplicate lake water samples preserved with formaldehyde. Subsamples of 2 ml were stained for five minutes with 1 ml solution of 10 $\mu g ml^{-1}$ fluorescent DAPI dye (4',6-diamidino-2-phenylindole). 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 for use in analyses (APHA et al., 2005).

Statistical Analyses

TP, TDN, DOC, absorbance at 320 nm and 440 nm, chlorophyll *a* and bacterioplankton were compared between the two lake types using factorial ANOVAs for mixed designs, which tested the effects of slump occurrence (lake type) as a between-subjects effect and sampling year as a within-subject effect. Post-hoc comparisons of significant effect levels were completed using a conventional two-way ANOVA with Tukey's HSD. A further ANOVA analysis was used to determine whether the concentrations of nutrients (TP, TDN, and DOC) in the water sampled from onshore slumps differed from those in the adjacent lakes. All data were log-transformed in the analyses to meet normality assumptions.

Predictor variables that were significantly correlated with chlorophyll *a* (Pearson's correlation, significant at Bonferroni corrected $p < 0.05$) were identified, and data were pooled across all years. The correlation analysis included one calculated interaction term, TDN*TP, which was added to assess the potential for phosphorus and nitrogen co-limitation, a condition which is common in Arctic lakes (O'Brien et al., 1992; Levine and Whalen, 2001). The linear relationships between chlorophyll *a* and the correlated predictor variables in each lake type were subsequently assessed using Akaike's Information Criterion (AIC). AIC is a model selection method that measures

TABLE 2. ANOVA table for parameters measured in 22 survey lakes from 2005 to 2007. Dependent parameters were tested for differences according to lake type (slump-affected or unaffected) and by year of sampling. Significant results ($p < 0.05$) 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.

		Lake type (slump status)			Year			Post Hoc
	n	F	df	*p*	F	df	*p*	(Tukey's)
Abiotic variables:								
Total phosphorus	66	7.202	1	**0.014**	0.929	2	0.347	
Total dissolved nitrogen	66	5.962	1	**0.024**	0.183	2	0.673	
Dissolved organic carbon	66	12.710	1	**0.002**	48.515	2	**0.000**	2005 < 2007
UV Abs (320 nm)	43	45.470	1	**0.000**	51.028	1	**0.000**	2006 > 2007
PAR Abs (440 nm)	43	54.034	1	**0.000**	25.491	1	**0.000**	2006 > 2007
Biotic variables:								
Chlorophyll *a*	66	13	1	**0.002**	0.063	2	0.804	
Bacteria (cells ml^{-1})	44	0.016	1	0.901	18.301	1	**0.000**	2006 > 2007

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 predictor variable selection was chosen over multiple stepwise regression because AIC makes no assumption of independence between the predictor variables considered, many of which were found to be correlated. The availability of an AIC correction for a small sample size was also useful in the following analysis (AIC_c, Burnham and Anderson, 1998).

The AIC for each possible combination of models with one through three predictor variables (seven combinations in all) using the selected factors was calculated separately for slump-affected and unaffected lakes data in order to determine which predictor(s) best determined chlorophyll *a* concentrations in each lake type. The AIC correction for small sample size, AIC_c, was subsequently calculated for all 15 models, and these values were then used to determine the Akaike weight for each model (Johnson and Omland, 2004). These weights in slump-affected and unaffected lake types were compared by inspection. 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).

RESULTS

Comparative Analyses

Pelagic TP, TDN, and DOC concentrations were all significantly higher ($p < 0.05$) in unaffected lakes than in slump-affected lakes (Table 2). Since several values for TP were below detection limits in 2006, we substituted the detection limit value (0.01 mg/L) for six slump-affected and four unaffected lakes in the TP ANOVA and subsequent analyses. Absorbance at both UV and PAR wavelengths was also significantly higher in unaffected lakes, which were consistently brown water lakes. Absorbance data were missing for one unaffected lake (7A) in the year 2006. Phytoplankton biomass was significantly higher in unaffected lakes than in slump-affected lakes, while bacterioplankton density was not significantly different between lake types. Interactions between lake type and sampling year were not significant except for bacterioplankton density. This result supports the pooling of data across sampling years, as presented in Figure 2. TP concentrations and both UV and PAR absorbance measurements were variable across unaffected lakes.

Table 2 and Figure 3 summarize significant among-year differences in mean values for DOC, a320 nm, a440 nm, and bacterioplankton.

Landscape Geochemistry

TP, TDN, and DOC concentrations were all significantly higher in the onshore slump water compared to pelagic water samples taken from the adjacent lakes ($p < 0.05$). In the lakes, DOC, TP, and TDN mean values (± SD) were 16.0 (± 1.6) mg/L, 0.011 (± 0.003) mg/L and 0.405 (± 0.072) mg/L, respectively. In contrast those mean values in the slump pools were 48.0 (± 36.3) mg/L, 0.465 (± 0.421) mg/L and 1.640 (± 1.401) mg/L, respectively. It should be noted that because there was no observed standing water to analyze in catchment areas unaffected by slumping, the relative importance of slump-derived nutrients as part of those delivered from the entire catchment landscape is unknown. In addition, the four slump/lake sites from which these samples were taken were all actively degrading slumps, bare earth and mud with little or no established vegetation. In slump areas with established vegetation that are not actively degrading, these abundant nutrients may be intercepted by terrestrial vegetation before export to the lakes.

Factors Affecting Pelagic Primary Production

Determination of the chemical and physical parameters that could affect phytoplankton biomass (inferred from

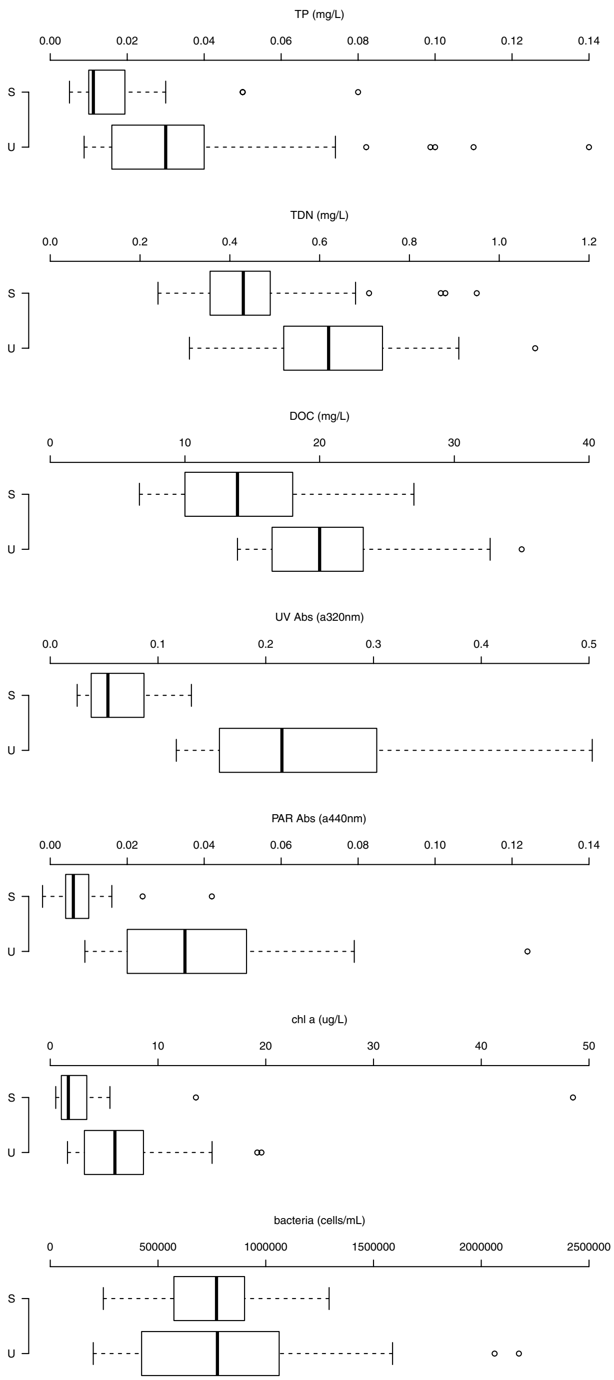

FIG. 2. Boxplots for measured parameters in the 22 lakes (pooled data, 2005 to 2007), presented by lake type (S = slump-affected, U = unaffected). The thick line marks the median value, the box indicates the second and third quartiles, and the open circles indicate values greater than 50% of the interquartile range.

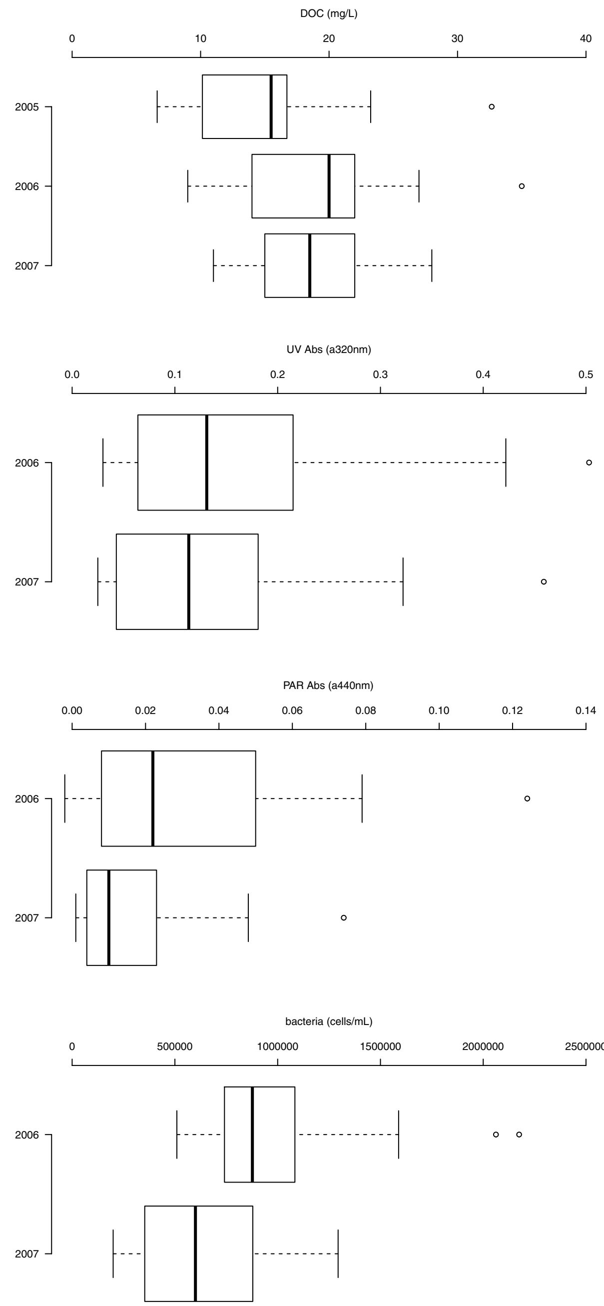

FIG. 3. Boxplots for measured parameters in the 22 lakes pooled across lake type (unaffected and slump-affected lakes) presented by sampling year. The thick line marks the median value, the box indicates the second and third quartiles, and the open circles indicate values greater than 50% of the interquartile range.

chlorophyll *a*) in each of the two lake types was assessed through a series of steps. First, correlations between possible physical-chemical predictor variables were calculated separately for slump-affected and unaffected lakes (Table 3). In slump-affected lakes, chlorophyll *a* was positively correlated with the nutrients TP and TDN. In unaffected lakes, chlorophyll *a* was more positively correlated with UV light absorbance than with TP and was not significantly correlated with TDN. It is noteworthy that in unaffected lakes chlorophyll *a* was positively correlated with light absorbance. Absorbance is higher because less light (both UV and PAR) is available in the water column of the lake. Chlorophyll *a* was not correlated with DOC, PAR absorbance, or the interaction term TDN*TP in either affected or unaffected lakes, so these parameters were not included in subsequent analyses.

TABLE 3. Correlation coefficients (Pearson's r) for five regression factors considered as possible explanatory variables for phytoplankton biomass estimates. Significant correlations (Bonferroni corrected $p < 0.05$) are in bold. For slump-affected lakes: TP, TDN, DOC, Chl *a*, n = 33; UV Abs and PAR Abs, n = 22. For unaffected lakes: TP, TDN, DOC, Chl *a*, n = 33; UV Abs and PAR Abs, n = 21.

	TP	TDN	TDN*TP	DOC	UV Abs	PAR Abs
Slump-affected lakes:						
TDN	**0.798**					
TDN*TP	**-0.550**	-0.011				
DOC	0.488	**0.646**	0.117			
UV Abs	0.325	0.450	0.207	0.612		
PAR Abs	0.336	0.256	-0.054	0.177	**0.778**	
Chlorophyll *a*	**0.666**	**0.607**	-0.360	0.383	0.183	0.007
Unaffected lakes:						
TDN	**0.513**					
TDN*TP	**-0.610**	0.221				
DOC	0.463	**0.681**	0.019			
UV Abs	0.600	0.304	-0.373	**0.671**		
PAR Abs	0.450	0.167	-0.422	0.501	**0.900**	
Chlorophyll *a*	**0.515**	0.238	-0.386	0.429	**0.690**	0.563

The second step in the analysis was to determine which variables would be entered into the predictor variable selection. Since TP, TDN, and UV absorbance were significantly correlated with chlorophyll *a* in either slump-affected lakes, unaffected lakes, or both lake types, these parameters were entered into the AIC model selection analysis. The inclusion of UV absorbance restricted the AIC analysis to 2006 and 2007, the years in which water colour was sampled.

Finally, AIC (AIC_c) weights and weighted average parameter estimates for the predictor variables were calculated (Table 4). AIC weights provide information on which potential model(s) best fits the given data set, with the best predictor(s) having the highest relative AIC weight. The AIC calculations included data from 22 STS-affected and 21 unaffected "lake years" pooled from the 2006 and 2007 surveys and are based on seven possible linear model fits using all combinations of predictor variables for each lake type. In unaffected lakes, UV light absorbance (a320 nm) had a much higher weight than the nutrient parameters. In contrast, in slump-affected lakes, TDN and to a lesser extent TP shared high weights, while that for UV light absorbance was low.

TABLE 4. Akaike weights and AIC_c-weighted average parameter estimates from the seven considered models for the predictor variables used in the chlorophyll *a* model selection analysis. Parameter estimates are calculated for log-transformed data.

	Akaike weight	Weighted average parameter estimate
Slump-affected lakes:		
TDN	0.79	1.27
TP	0.18	0.32
UV Abs	0.02	-0.06
Unaffected lakes:		
UV Abs	0.99	0.17
TP	0.01	0.44
TDN	0.00	1.33

DISCUSSION

Study lakes unaffected by shoreline STS had higher concentrations of the nutrients TP, TDN, and DOC than slump-affected lakes. Unaffected lakes also had higher water colour and UV and PAR light absorbance than slump-affected lakes, even after correcting for possible turbidity effects. The consistent pattern of low nutrient concentrations in slump-affected lakes does not support the hypothesis that thaw slumping causes nutrient enrichment in these lakes. While bacterioplankton are important producers in high-latitude lakes (Jansson et al., 2000), there was no difference in bacterioplankton biomass between lake types at the time of sampling, when much of the bacterioplankton community would likely be dependent on phytoplankton to produce DOC (Crump et al., 2003).

It has been noted that in freshwaters containing moderate to high concentrations of dissolved inorganic carbon (DIC), DOC concentrations can be overestimated if calculated as the difference between total carbon and DIC (Findlay et al., 2010). DIC was present in high concentrations in slump-affected lakes (M. Thompson, unpubl. data), and the temporal pattern of DOC concentrations found in the study lakes was not in agreement with a pattern of relatively dilute ionic conditions in 2005 and 2007 (Kokelj et al., 2008). However, DOC was significantly lower in slump-affected than in unaffected lakes, so that if DOC was overestimated in slump-affected lakes, our general comparative conclusions do not change.

The high water clarity in the slump-affected study lakes was counterintuitive, considering the amount of sediment and debris that can enter a lake with slump activity. However, slump-affected lakes were consistently clear, contrasting with the brown water in the unaffected study lakes. A larger regional synoptic study of lakes in the Mackenzie Delta uplands has confirmed that this pattern is consistent across a large lake population (Kokelj et al., 2009). Humic material, including DOC, is known to limit the penetration of biologically damaging UV light through the water column (Jones, 1992; Klug, 2002). Since phytoplankton biomass in unaffected lakes was positively correlated with UV light absorbance, it is possible that the negative effect of incoming UV radiation could be more significant than the positive effect of PAR radiation for photosynthesis in determining phytoplankton biomass. The increase in pelagic light availability (low light absorbance) in slump-affected lakes could therefore be significant in determining overall system productivity and sensitivity to changing environmental conditions.

The high nutrient concentrations measured in the thaw slump pools indicate that the thawing permafrost could act as a source of nutrients to the adjacent lakes, depending on the pattern and rate of export. The low nutrient concentrations and the subsequent nutrient limitation of phytoplankton in the slump-affected lakes may therefore be explained by within-lake processes. Nutrients are subject to within-lake biological uptake, sedimentation, and degradation and do not appear to behave like other, less labile solutes in these lakes (e.g., major ions, Kokelj et al., 2005). For example, Bowden et al. (2008) 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. The unknown rate of supply of nutrients from slumps compared to unaffected catchment areas as well as the dilution factor of terrestrial nutrients once delivered to the lakes complicates this assessment of terrestrial nutrient supplies. Although no evidence of pelagic nutrient uptake (high phytoplankton or bacterioplankton biomass) is apparent in slump-affected tundra lakes, the necessary assumption in both streams and lakes would be that primary producers were highly resource-limited and capable of rapid nutrient uptake once nutrients were made available through permafrost thaw. Low phytoplankton and bacterioplankton biomass may then be a result of high grazing pressure by consumers that were not measured here, such as zooplankton (Carpenter et al., 1998) or phagotrophic flagellates (Jansson et al., 1996). It is also possible that the significant macrophyte communities found in some slump-affected lakes (Mesquita et al., 2010), as well as benthic algae and other producers, are taking up slump-derived nutrients, representing an important shift from pelagic to benthic production within the affected lakes.

The sedimentation of nutrients in slump-affected lakes is another within-lake process by which slump-derived nutrients may be removed from the water column to the sediments (Prentki et al., 1980). Thompson et al. (2008) found that the addition of slump sediments and meltwater to humic lake water decreased the CDOM concentrations; they hypothesized that CDOM-associated nutrients may also have been removed via the proposed sedimentation process. If thaw slumping is in fact acting as a source of nutrients, the concentration of these nutrients in the receiving lakes may not reflect slump activity because of these removal processes. Further investigation into the within-lake cycling of nutrients, the hydrological regimes and water balances of these lakes, and estimates of primary and overall production will be required to determine whether degrading shoreline permafrost is a significant source of nutrients for these tundra lake ecosystems.

CONCLUSIONS

Nutrient concentrations and plankton biomass in small tundra lakes east of the Mackenzie Delta do not appear to increase as a result of STS. This finding contrasts with the prediction made by Hobbie et al. (1999) that freshwaters influenced by degrading permafrost would be subject to eutrophication. Despite the high concentrations of nitrogen, phosphorus, and organic carbon in runoff pools within the sampled slump sites, these nutrients are not present in high concentrations in the water column of the adjacent lakes. Instead, the shift in pelagic UV and PAR light conditions, probably caused by the lower water colour in slump-affected lakes, is an important influence on pelagic primary producer biomass in these small tundra lakes. The fate of permafrost-derived nutrients in freshwaters is likely determined by complex within-lake nutrient cycles and trophic interactions, and further study is needed to determine the dominant processes involved. Nutrient, light, and producer biomass relationships were changed in the tundra lakes affected by permafrost thaw-induced shoreline slumping. With projected future warming, these changes represent a significant potential impact for freshwater systems in this ice-rich thermokarst region and in similar areas across the Arctic.

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