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Permafrost thaw and intense thermokarst activity decreases abundance of stream benthic macroinvertebrates

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Abstract

Intensification of permafrost thaw has increased the frequency and magnitude of large permafrost slope disturbances (mega slumps) in glaciated terrain of northwestern Canada. Individual thermokarst disturbances up to 40 ha in area have made large volumes of previously frozen sediments available for leaching and transport to adjacent streams, significantly increasing sediment and solute loads in these systems. To test the effects of this climate-sensitive disturbance regime on the ecology of Arctic streams, we explored the relationship between physical and chemical variables and benthic macroinvertebrate communities in disturbed and undisturbed stream reaches in the Peel Plateau, Northwest Territories, Canada. Highly disturbed and undisturbed stream reaches differed with respect to taxonomic composition and invertebrate abundance. Minimally disturbed reaches were not differentiated by these variables but rather were distributed along a disturbance gradient between highly disturbed and undisturbed sites. In particular, there was evidence of a strong negative relationship between macroinvertebrate abundance and total suspended solids, and a positive relationship between abundance and the distance from the disturbance. Increases in both sediments and nutrients appear to be the proximate cause of community differences in highly disturbed streams. Declines in macroinvertebrate abundance in response to slump activity have implications for the food webs of these systems, potentially leading to negative impacts on higher trophic levels, such as fish. Furthermore, the disturbance impacts on stream health can be expected to intensify as climate change increases the frequency and magnitude of thermokarst.

Keywords: arctic streams, benthic macroinvertebrate, permafrost degradation, sedimentation, thaw slump, thermokarst, total suspended solids

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Introduction

Over the next century, continued increases in air temperature and precipitation at high latitudes are expected to dramatically alter Arctic environments (Prowse *et al*., 2009). Freshwater aquatic ecosystems have the potential to undergo dramatic changes because thaw of ice-rich permafrost can rapidly modify terrain morphology, hydrological flowpaths, sediment loads and geochemistry of streams, lakes, and wetlands (Callaghan *et al*., 2011; Kokelj *et al*., 2013; Thienpont *et al*., 2013). On sloping terrain, the degradation of ice-rich permafrost can cause instability and development of retrogressive thaw slumps (Fig. 1) (Kokelj & Jorgenson, 2013). These thermokarst disturbances are common in ice-rich landscapes across the western Canadian Arctic (St-Onge & McMartin, 1999; Lantz & Kokelj, 2008; Lacelle *et al*., 2010; Brooker *et al*., 2014), the high Canadian Arctic (Pollard, 2000), the Alaskan and Brooks Ranges and their glaciated foothills (Jorgenson *et al*., 2008; Balser *et al*., 2009), and across similar landscapes in northwestern Siberia (Astakhov *et al*., 1996; Alexanderson *et al*., 2002). Individual disturbances can be up to 40 ha in area and may transport hundreds of thousands of cubic meters of sediments from slopes to the valley bottom (Kokelj *et al*., 2015; Lacelle *et al*., 2015). Thaw slumps grow due to ablation of ice-rich permafrost that is exposed in a headwall and disturbances may remain active for decades (Lacelle

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et al., 2015). In recent years, the frequency and magnitude of thaw slumps has increased with climate warming and intensification of precipitation regimes (Kokelj & Jorgenson, 2013; Kokelj *et al.*, 2015).

The growth of thaw slumps can rapidly modify landscapes (Kokelj & Jorgenson, 2013) and contribute immense volumes of sediments and soluble materials to adjacent lakes (Kokelj *et al.*, 2009), streams (Kokelj *et al.*, 2013, 2015; Malone *et al.*, 2013), or coastal zones (Lantuit & Pollard, 2008). In northwestern Canada, hundreds of small- to medium-sized stream catchments are now impacted by large, long-lived retrogressive thaw slumps (Figs 1 and 2) (Kokelj *et al.*, 2013; Lacelle *et al.*, 2015; Rudy *et al.*, 2015). These disturbances have significantly increased stream sediment and solute loads, affecting water quality across a range of watershed scales (Kokelj *et al.*, 2013; Malone *et al.*, 2013). Climate warming will likely increase thermokarst impacts on drainage and stream networks in areas of ice-rich permafrost; however, the influence of these disturbances on stream ecology remains a significant knowledge gap, limiting our capacity to anticipate the nature and magnitude of aquatic ecosystem change in a warming Arctic.

Freshwater invertebrate communities are particularly sensitive to stream sediment and water quality conditions (Larsen & Ormerod, 2009; Wagenhoff *et al.*, 2011; Benoy *et al.*, 2012) and can act as indicators to assess impacts of disturbance on stream ecosystems. Benthic invertebrates can withstand short-term increases in suspended sediment concentrations and bed deposition; however, chronic input of fine sediments into the water column can significantly affect faunal assemblages by changing macroinvertebrate population density, relative abundance and taxonomic richness (see review in Jones *et al.*, 2011). It is also well-established that substantial increases in stream nutrient concentrations can shift benthic communities toward lower diversity and a greater tolerance to disturbance (Hilsenhoff, 1988; Donahue *et al.*, 2009; Medeiros *et al.*, 2011). However, there have been no studies documenting the combined impacts of sediment and nutrient inputs from intensive thaw slumping on stream invertebrates. Investigating the response of stream benthic communities to increasing thermokarst activity is critical for understanding how aquatic ecosystems and fisheries resources will respond to emerging stressors in a warming circumpolar Arctic.

A recent intensification of thaw slump activity on the Peel Plateau and the well-documented stream sedimentary and geochemical impacts provides context for this study, which investigates the influence of this disturbance regime on benthic communities in Arctic gravel-cobble bed streams. We hypothesized that thaw slump activity can cause a shift in stream benthic macroinvertebrate abundance and community composition due to increased inputs of sediment and nutrients. To test this hypothesis, we compared the benthic communities and environmental variables associated with 24 stream reaches affected by thaw slumps of varying disturbance

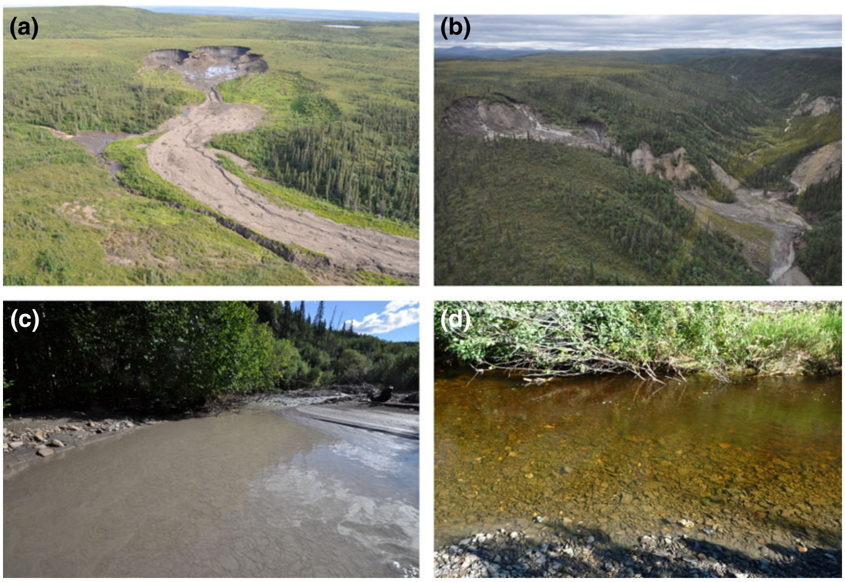

Fig. 1 (a) Retrogressive thaw slump in the Peel Plateau, showing a headwall of exposed ground ice about 10 m in height, a saturated scar zone and a downslope debris tongue and rill system which extends into the stream, with incision of stream through the debris tongue visible in the foreground; (b) Thaw slump showing the direct debris input into a stream; (c) Image of an impacted stream located ~5 km downstream from a mega slump; and (d) Image of an unimpacted stream.

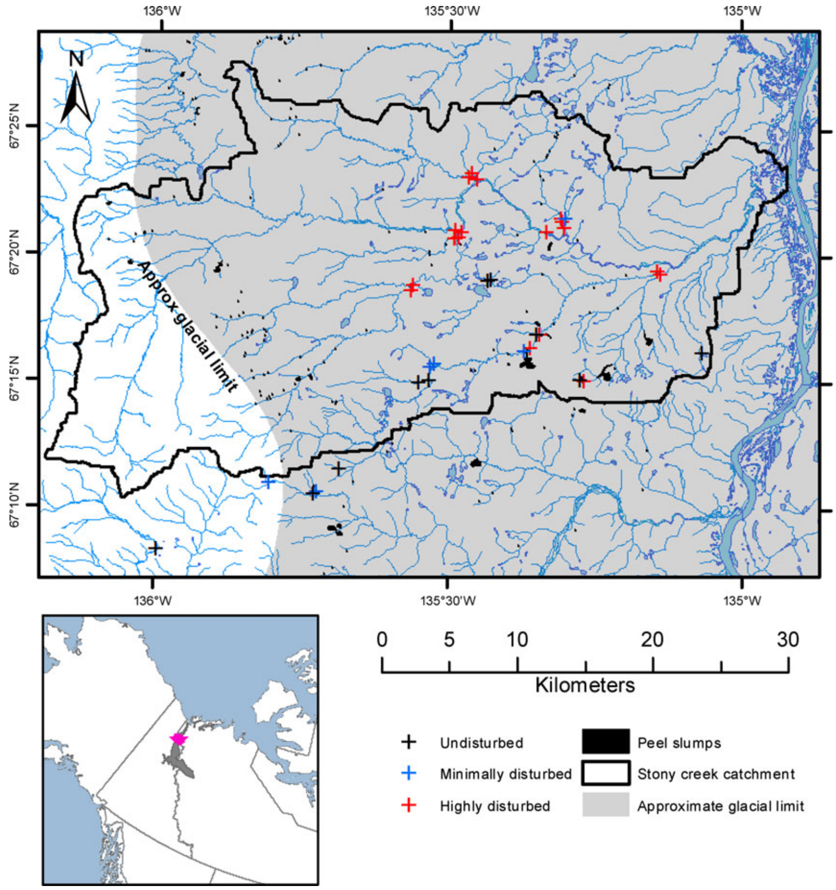

Fig. 2 Map showing the Stony Creek watershed and study sites. Inset shows the location of the study area and the Peel Plateau within Canada.

intensity, and 10 undisturbed stream reaches to determine whether they could be differentiated on the basis of their benthic macroinvertebrate communities. We predicted that slump-impacted systems would have decreased abundance and diversity of invertebrates relative to undisturbed streams. We further explored the relationships between physical and chemical variables and benthic macroinvertebrate taxonomic composition to evaluate the mechanisms by which thaw slumps impact stream communities. This study provides empirical data which illustrate how intensification of thermokarst can transform the ecology of Arctic and subarctic streams.

Materials and methods

Study system

This research was conducted in the ~1100 km^2 watershed of Stony Creek, one of several medium-sized tributaries of the Peel River which drain eastward from the Richardson Mountains through the Peel Plateau (Fig. 2) (Kokelj *et al*., 2013). The Plateau is a fluvially incised, ice-rich moraine landscape approximately 24 000 km^2 that extends along the eastern margins of the Richardson Mountains and northeastern Mackenzie Mountains. Stony Creek watershed contains several small gravel-cobble bed streams that are typical of hundreds of Plateau streams. The upper portions of many streams originate in unglaciated mountainous terrain and are largely free of significant thermokarst disturbances, but thaw slumping is widespread throughout the Plateau below elevations of about 700 m asl (Lacelle *et al*., 2015). The entire region is underlain by continuous permafrost and the sediments are ice-rich (Lacelle *et al*., 2004). The mean annual ground temperatures are relatively warm (<−2.5 °C) due to atmospheric temperature inversions in winter (O'Neill *et al*., 2015). Sloping terrain and the high ice content of the permafrost favor the development of large retrogressive thaw slumps which are common throughout much of the Stony Creek watershed and other Peel Plateau drainages (Kokelj *et al*., 2013; Brooker *et al*., 2014). Boreal forest occupies the lower watershed and valley bottoms, sedge and cottongrass tussock tundra occur at higher elevations, and shrub tundra is found in the transition zone between the lower and upper portions of the watershed (Ecosystem Classification Group, 2009). The geomorphology, permafrost, and stream conditions are characteristic of hundreds of watersheds that incise a broad band of ice-rich morainal deposits on the western slopes of the Mackenzie and Richardson Mountains (Lacelle *et al.*, 2010, 2015) of Northwestern Canada.

Site selection

Sites were selected for accessibility (the area is extremely remote, the terrain difficult to navigate and most sites were only accessible by helicopter), number of upstream disturbances (though sites impacted by multiple disturbances were common, sites impacted by 0–2 disturbances were more rare), as well as their proximity to thermokarst disturbances including shallow active-layer detachment slides, small retrogressive thaw slumps (≤5 ha in area), and mega slumps (>5 ha in area). The latter are extremely large retrogressive thaw slumps typically exceeding 5 ha in area and with debris tongues extending from the slump floor to the valley bottom (Fig. 1a and b) (Kokelj *et al.*, 2015). Sites were classified according to the relative intensity of upstream disturbance. The disturbance intensity was assessed using SPOT imagery and confirmed by aerial reconnaissance. Site classification 1 (n = 10) described stream reaches with catchments containing no visible or known retrogressive thaw slumps. Disturbed sites were grouped into two classes based on the number and size of disturbances found in the upstream catchment. Site classification 2 (n = 6) described sites with watersheds that were affected by few (1–2) small slumps (<5 ha) and/or landslides and were referred to as sites with minimal disturbance. Site classification 3 (n = 18) described sites with watersheds affected by numerous slumps, some of which were very large, and/or abundant landslides and were referred to as highly disturbed (Table 1).

Data collection

Water samples were collected for analysis of major ions (SM4110:B), nitrogen [total nitrogen (TN) (ISO/TR 11905:1997 (E)), nitrate (SM4110:B), and ammonia (SM4500-NH3:G)], phosphorus [ortho-phosphate (SM4500-P:D) and total phosphorus (TP) (SM4500-P:D)], dissolved organic carbon (DOC) (SM5310:B), and total suspended solids (TSS) (SM2540:D) by Taiga Environmental Laboratory, which is certified and accredited by the Canadian Association for Laboratory Accreditation Inc. using ISO or standard methods (International Organization for Standardization, 1997; Eaton *et al.*, 2005). The suspended sediment load in many samples was sufficiently large to preclude filtering of samples, and analysis of TP was therefore conducted on unfiltered samples for all sites. Water temperature, pH, specific conductance, dissolved oxygen, and turbidity measurements were collected on site using calibrated Oakton pHTestr30, Hach Conductivity and LDO probes, and Hanna turbidity meters. Benthic macroinvertebrate samples were collected using Environment Canada's Canadian Aquatic Biomonitoring Network (CABIN) protocol (Environment Canada, 2012). A 400-μm, triangle-framed kick net was used to collect samples along stream bottoms using a 3-min traveling kick method. The sample operator moved in a zigzag fashion upstream, disturbing (i.e., kicking) the substrate at a depth of ~5–10 cm and holding the net downstream of the disturbed area to collect any dislodged organisms and material carried by the current. Boulders/large rocks were brushed by hand as the net was held downstream. Samples were sorted and identified to the lowest practical taxonomic level (generally family or genus for insects) following standard CABIN protocols (Environment Canada, 2010).

Substrate composition was characterized by randomly selecting 100 stones within the sampling reach, measuring the intermediate axis of each stone, then calculating the median Wolman diameter (Wolman, 1954). Substrate embeddedness (i.e., how deep the sampled rock was buried in the surrounding material) was measured for 10% of the stones that were sampled. Measured channel characteristics included bankfull width, wetted width and bankfull-wetted depth. Habitat descriptors, such as periphyton, riparian vegetation, macrophyte and canopy coverage, and microhabitat classification were recorded using visual observations.

Valley morphometry was described for the sites to provide supplementary data describing the geomorphic nature of the stream. The classifications were as follows: (i) gentle slope with little stream incision, (ii) braided channel and moderate incision to highly incised valley with a broad valley floor, or (iii) deep incision or v-shaped valley form. Valley morphometry was assessed using topographic maps (1 : 250 000; National Topographic Data Base), SPOT imagery and field verification. Distance (m) to the nearest slump or landslide was measured using SPOT imagery.

Table 1 Summary and description of the number and size of slump/landslide disturbances that defines the site classification of stream in the Peel Plateau, Northwest Territories, Canada

Site description	Site classification	n	No. of slumps/ landslides	Maximum slump size
Undisturbed	1	10	0	n/a
Minimally disturbed	2	6	1–2	<5 ha
Highly disturbed	3	18	>2	~40 ha

Statistical analysis

Data preparation. Taxonomic community structure was summarized by 35 biological metrics that included measures of richness, diversity, and composition at multiple taxonomic levels (e.g., order, family, and chironomid subfamily; metrics were not calculated at the level of genus because many individuals were too small to identify past the level of family or subfamily) to test the prediction that permafrost thaw slump activity would cause declines in abundance and diversity of stream invertebrates. The full suite included metrics that have been shown to respond to perturbation in North American streams (Barbour *et al.*, 1999) and to distinguish among eastern Canadian low Arctic streams (Lento *et al.*, 2013). These biological metrics were thus expected to differentiate among and reflect perturbation in western Canadian Arctic streams. Metric values were $\log_{10}(x + 1)$ or arcsin $(\sqrt{x})$ transformed, and Pearson correlation coefficients were used to remove redundant metrics ($|r| > 0.7$). This resulted in a subset of 14 biological metrics to be used in further analysis to summarize differences in abundance and diversity of invertebrate assemblages. Measures of richness and diversity (with abbreviations used in figures) included: family richness (Rich), Simpson's reciprocal index (SimpR), Fisher's alpha (Fisher), taxonomic distinctness (Distinct), and the number of Ephemeroptera families (Num_Eph), Plecoptera families (Num_Ple), and Chironomidae subfamilies (Num_Chid). Measures of abundance and composition (with abbreviations used in figures) included: abundance (Abund), and the relative abundance of Ephemeroptera (RA_Eph), Plecoptera (RA_Ple), Trichoptera (RA_Tri), noninsects (RA_NonI), and the Chironomidae subfamilies Chironominae (RA_Chin), and Orthocladiinae (RA_Orth).

Environmental variables were classified as habitat- or water quality-related for the subsequent statistical analysis. Habitat variables described the physical habitat of the stream site or its catchment, and were derived from geospatial analysis or on-site observations. Water quality variables described the chemical habitat of the stream site, and relied on sample collection and laboratory analysis. Water quality variables were directly correlated with slump intensity, although most habitat variables were also related to slumping through direct or indirect mechanistic associations. Environmental variables were $\log_{10}(x)$ or arcsin $(\sqrt{x})$ transformed as appropriate. In order to reduce the number of variables for the analysis, Pearson correlations were used to remove highly redundant variables from within the water quality and habitat classifications. When strong correlations were detected [$|r| > 0.7$ for water quality variables; $|r| > 0.4$ for habitat variables due to the large number (24) of potential variables], the variable that was deemed to be most ecologically important or that had fewer strong correlations with other variables was retained for analysis, resulting in a subset of four water quality variables and seven habitat variables. To further reduce the number of environmental variables to avoid over-fitting, Pearson correlations were tested between water quality and habitat variables, and valley morphometry was removed from analysis due to a strong correlation with TSS ($r = 0.85$), resulting in final subsets of four water quality variables and six habitat variables. Water quality variables (with abbreviations used in figures) included: TSS, DOC, nitrate (NO_3), and ammonia (NH_3). Habitat variables (with abbreviations used in figures) included: % silt/clay (%SiltClay), % periphyton cover (Periphyton), presence/absence of coniferous trees (Coniferous), presence/absence of grasses/ferns (Grass/Fern), % embeddedness (Embed), and maximum catchment slope in % (MaxSlope).

Analytical approach. To confirm the impacts of thaw slumps on stream water quality and to describe conditions among our study sites, we compared water quality parameters, including TSS, magnesium, TN, and TP, across disturbance levels. One-way ANOVA and Tukey's honestly significant difference (HSD) test for pairwise comparisons were conducted in SYSTAT (Version 12.02.00) to compare mean values of each parameter among the three levels of site classification. Because TP samples were unfiltered and therefore measured both biologically available phosphorus and phosphorus bound to sediment particles, the analysis of TP was conducted on rank data to focus on differences in the relative ranking of samples rather than in the absolute magnitude of measured phosphorus. A nonparametric Tukey-Kramer multiple comparisons test was used to determine differences in rank TP among site classes (nonparametric Tukey–Kramer test conducted in R 3.0.3 using the Rfit package; Kloke & McKean, 2012). We also used one-way ANOVA and Tukey's HSD to compare mean invertebrate abundance and taxonomic richness among the three levels of site classification to characterize the benthic community. Assumptions of the one-way ANOVA test were met for all variables except $\log_{10}$ TSS and $\log_{10}$ richness, both of which failed the test for normality. However, nonparametric analysis of rank data for both variables provided results consistent with those of the parametric test, which confirmed that the ANOVA was not affected by deviations from normality. Results from the more powerful parametric analysis are therefore presented for $\log_{10}$ TSS and $\log_{10}$ richness.

Indirect gradient multivariate analysis was used to examine the spatial separation of sites based solely on biological metrics. Detrended correspondence analysis (DCA) was used to determine the proper response model for the data. The gradient length within our study sites was low for biological metrics (gradient length = 0.877 standard deviations), which suggested that a linear response model would be most appropriate (ter Braak & Prentice, 1988; Legendre & Legendre, 1998). We used principal components analysis (PCA) to examine the separation of stream sites based on biological metrics. Because metrics were measured on different scales, metric scores were divided by their standard deviation to standardize them and downweight the effect of any metrics that had a large variance (though standard deviations were low, ranging from 0.07 to 0.69). The resultant ordination diagram presented standardized metric scores and expressed the relationship among metrics as correlations rather than covariances (ter Braak, 1994). To determine whether community structure differed significantly across disturbance levels, we conducted analysis of similarity (ANOSIM; performed in Primer 6) on the Euclidean distance matrix (calculated from biological metrics) for all samples.

Direct gradient analysis tested the association between biological metrics and environmental variables, to examine the ability of the environmental drivers to differentiate among undisturbed and impacted sites. Redundancy Analysis (RDA) was used to evaluate biotic-abiotic associations because biological metric data were best described by a linear response model. Undisturbed sites were more common at higher elevations (in the unglaciated headwaters above the westward margin of the Laurentide Ice Sheet) (Lacelle *et al.*, 2015); therefore, elevation was used as a covariable in the analysis to ensure that differences among site classification levels were not due to the geographic location of sites. Metric scores were divided by their standard deviation to standardize them and downweight the effect of any metrics that had a large variance, resulting in an ordination diagram that expressed the relationship among metrics as correlations rather than covariance (ter Braak, 1994). RDA axis eigenvalues were compared with PCA eigenvalues to determine the proportion of unconstrained community variance explained by each RDA axis. Most multivariate analyses (DCA, PCA, RDA) were conducted in Canoco for Windows (Version 4.5), and ANOSIM was conducted in Primer (Version 6.1.13).

The impacts of slumping on macroinvertebrate assemblages was further explored through regression analysis to determine whether measures of abundance or diversity could be predicted based on disturbance-related variables. This analysis used biological metric(s) responsible for separating undisturbed from disturbed sites as the response variable. TSS and TP were used as measures of sediment and nutrient inputs related to slumping. The sediment analysis using TSS was an ordinary least squares (OLS) simple linear regression. Because the unfiltered TP results included biologically active phosphorus and phosphorus bound to sediments, rank regression was conducted to focus on changes in abundance in response to changes in rank TP (though the OLS regression line was included in the plot for comparison). In addition, the relationship between the chosen biological metric(s) and stream distance to the closest disturbance was investigated for disturbed sites (classifications 2 and 3) using OLS simple linear regression analysis.

Community resilience to slump impacts was evaluated by using regression-tree analysis to estimate the change-point in the relationship of the selected biological metric(s) with log TSS. Culp *et al.* (2013) used regression-tree analysis to estimate ecological reference conditions for TSS using biological metrics. Following from Culp *et al.* (2013), regression-tree analysis was conducted using a least-squares loss function to determine the change-point in each of the independent variables at which there was the greatest change in the biotic metric, as measured by the goodness-of-fit term and the Proportional Reduction in Error (PRE; equivalent to an R^2 in a regression). Because the regression-tree analysis is based on maximizing change in the dependent variable (rather than the independent variable), a change-point was also determined for the relationship between the biological metric and rank TP. Although this change-point does not indicate the actual value of TP at which there was the greatest change in the biotic metric, it can be used to evaluate whether undisturbed, minimally disturbed, and highly disturbed sites fall above or below the threshold of maximum change in that metric. Linear regression and regression-tree analyses were completed in SYSTAT (Version 12.02.00) and rank regression was completed in R 3.0.3 using the Rfit package (Kloke & McKean, 2012).

Results

Water chemistry

Our results confirm that thaw slumping had a major effect on variation in stream water quality conditions. Mean TSS differed significantly among the three site classifications ($F_{2,31} = 33.62$, $P < 0.001$; Table 2), increasing with intensity of watershed disturbance (Fig. 3a). The mean TSS was 16.60 mg L^{-1} in streams with undisturbed catchments, 872.67 mg L^{-1} in watersheds with minimal disturbances and 2856.33 mg L^{-1} at sites in highly disturbed watersheds. There were significant differences in concentrations of magnesium and TN among site classes (magnesium $F_{2,31} = 11.30$, $P < 0.001$; TN $F_{2,31} = 4.93$, $P = 0.014$), with greater concentrations in highly disturbed sites than in undisturbed sites (Table 2; Fig. 3b and c). Rank TP also differed significantly among site classifications ($F_{2,31} = 18.15$, $P < 0.001$). Rank total phosphorous was significantly greater (indicating higher TP values) at highly disturbed watersheds than at undisturbed or minimally disturbed sites (Table 2; Fig. 3d).

Benthic macroinvertebrate community structure

There were strong differences in total macroinvertebrate abundance among sites in watersheds impacted by thaw slumping and those in undisturbed watersheds ($F_{2,31} = 27.649$, $P < 0.001$; Table 3). Undisturbed sites had a significantly higher mean abundance of macroinvertebrates than minimally disturbed or highly disturbed sites (Tables 2 and 3). Mean abundance did not differ significantly among site classifications 2 or 3; although, the average, minimum, and maximum abundances all declined with increasing intensity of disturbance (Tables 2 and 3). There were no significant differences in taxonomic richness among disturbed and undisturbed sites ($F_{2,31} = 1.47$, $P = 0.246$). However, the undisturbed stations did have a slightly higher richness on average, and a higher minimum and maximum richness than the disturbed sites (Table 3).

Undisturbed sites were clearly separated from highly disturbed sites along the first axis of the biological metric PCA, which explained 55.1% of the total community variance (Fig. 4a). High macroinvertebrate abundance was most strongly associated with undisturbed sites (site classification 1). Undisturbed sites were also associated with high abundance and richness of the dipteran family Chironomidae and its subfamilies, and with high overall taxonomic richness (Fig. 4a). The Orthocladiinae and Chironominae subfamilies of chironomids were found at high relative abundances at undisturbed sites compared to highly disturbed sites (28.4% and 20.3% at undisturbed sites and 8.7% and 0.7% at highly disturbed sites respectively). Although taxonomic richness was greater in undisturbed sites, assemblages were often dominated by a small number of taxa, resulting in lower evenness. In contrast, highly disturbed sites (site classification 3) were positively

Table 2 The upper and lower 95% confidence intervals from Tukey's HSD for the difference in total suspended solids (TSS), magnesium (Mg), total nitrogen (TN), and invertebrate abundance and from the Tukey–Kramer test for the difference in rank total phosphorus (TP) from the comparison of stream site classifications 1 (undisturbed), 2 (minimally disturbed), and 3 (highly disturbed). Confidence intervals in bold indicate a significant difference between site classifications for the parameter of interest; results are presented only for those parameters that were found to differ significantly ($P < 0.05$) among site classifications in a one-way ANOVA

	Log_{10} TSS		Log_{10} Mg		Log_{10} TN		Rank TP		Abundance	
Classification	Lower	Upper	Lower	Upper	Lower	Upper	Lower	Upper	Lower	Upper
1 vs. 2	**−1.90**	**−0.38**	−0.58	0.07	−0.41	0.14	−0.19	1.45	**0.26**	**1.35**
1 vs. 3	**−2.52**	**−1.35**	**−0.72**	**−0.23**	**−0.48**	**−0.06**	**−1.56**	**−0.07**	**0.84**	**1.67**
2 vs. 3	**−1.49**	**−0.10**	−0.52	0.07	−0.39	0.12	**0.82**	**2.07**	−0.04	0.95

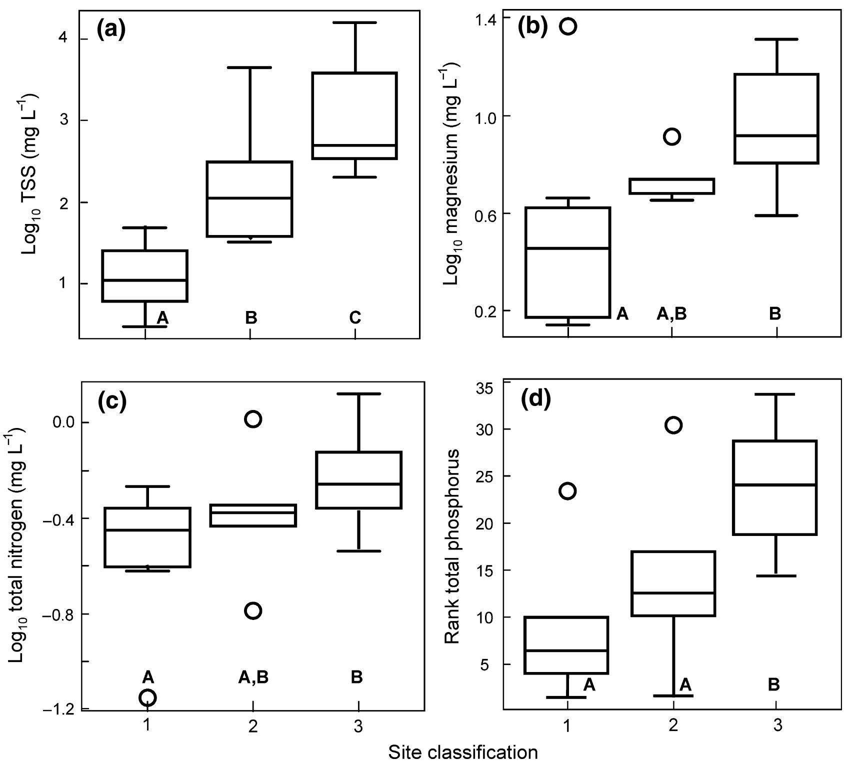

Fig. 3 Boxplots of log_{10}-transformed (a) total suspended solids (TSS; mg L^{-1}), (b) magnesium (mg L^{-1}), (c) total nitrogen (mg L^{-1}), and (d) rank total phosphorus (mg L^{-1}) for sites in each of three site classes. Sites classified in group 1 are undisturbed, group 2 are minimally disturbed with 1–2 small landslides and/or thaw slumps (<5 ha) and group 3 are highly disturbed with >2 thaw slumps and/or landslides, potentially including mega slumps (>5 ha). Statistical significance [Tukey HSD for (a)–(c) and nonparametric Tukey–Kramer for (d)] at $\alpha = 0.05$ is indicated by lettering in each plot.

Table 3 Summary statistics describing the abundance and richness of benthic macroinvertebrates in Peel Plateau sites classified by disturbance status

Site classification	Avg abundance ± SE	Range	Avg richness ± SE	Range
1: Undisturbed	1811 ± 524	295–6033	12 ± 1	8–17
2: Minimally impacted (few disturbances)	457 ± 276	57–1800	11 ± 2	3–13
3: Highly impacted (many disturbances)	93 ± 15	9–280	10 ± 1	7–14

associated along the first PCA axis with high taxonomic distinctness (a measure of taxonomic relatedness, with high distinctness indicating that insect families/subfamilies that were present came from many different insect orders and were not all from, for example, the order Diptera) and high diversity (reflecting more even taxonomic composition among families/subfamilies than in undisturbed sites). Highly disturbed sites were further separated along the second PCA axis, primarily due to the abundance and richness of nondipteran orders such as Ephemeroptera and Plecoptera (Fig. 4a). Of taxa that were found in disturbed sites, Baetidae and Heptageniidae (Ephemeroptera) were found at high relative abundances (23.7% and 23.2%, respectively) compared to undisturbed sites (1.4% and 0.1%, respectively) and were present at most of the highly disturbed sites (16 and 14 of 18 sites respectively).

Minimally disturbed sites (site classification 2) were distributed across the disturbance gradient of the first PCA axis and could not be visually distinguished from undisturbed and highly disturbed sites on the basis of biological metrics. However, the results of the ANOSIM indicated that community structure differed significantly among all disturbance levels (global $R = 0.571$, $P < 0.001$). Undisturbed and highly disturbed sites were clearly distinct in pairwise comparisons, with a high R statistic ($R = 0.748$, $P < 0.001$), but although the distinction was weaker, minimally disturbed sites were also found to be significantly different from undisturbed and highly disturbed sites in pairwise comparisons ($R = 0.342$ and 0.378, respectively; $P = 0.009$ and 0.007 respectively).

Macroinvertebrate responses to thaw slumping

The first and second axes of the RDA explained 45% and 11.1% of the unconstrained variance in the biological metrics respectively. The first axis, which primarily separated undisturbed from highly disturbed sites, was dominated by TSS (which was strongly positively correlated with valley morphometry; not shown), and showed a strong negative association between TSS and macroinvertebrate abundance (Fig. 4b). Although most undisturbed sites were negatively associated with TSS, three undisturbed sites were uncorrelated with TSS and were more strongly associated with physical habitat descriptors including the proportion of silt/clay comprising the stream bed, embeddedness, and the maximum catchment slope (Fig. 4b). The separation of heavily disturbed sites from undisturbed sites was also driven by a gradient that reflected a negative association of NO_3 and taxonomic distinctness and richness with DOC and the relative abundance of the chironomid subfamilies Orthocladiinae and Chironominae, though this gradient was not as strong as that seen for TSS (Fig. 4b). As in the PCA, minimally disturbed sites were found along the entire disturbance gradient of the

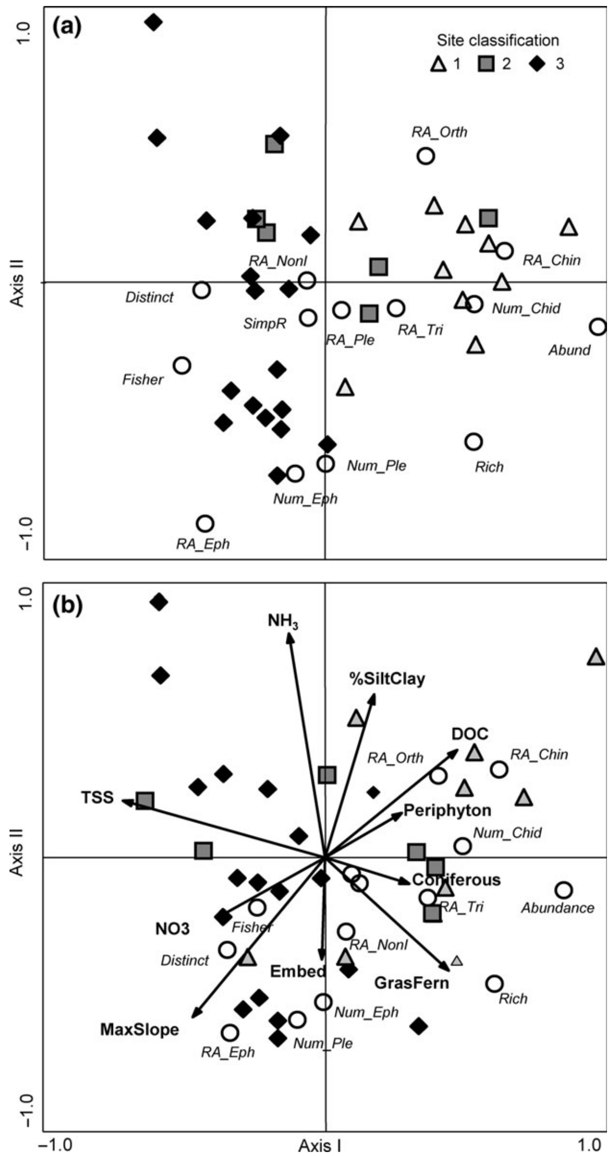

Fig. 4 Multivariate analysis for sites in each of three site classes, including the (a) PCA biplot that displays variation in sites based on biological metrics, and (b) RDA biplot that constrains the biologic metric-site relationship to maximize associations with environmental variables. Sites classified in group 1 are undisturbed, group 2 are minimally disturbed with 1–2 small thaw slumps and/or landslides (<5 ha) and group 3 are highly disturbed with >2 thaw slumps and/or landslides, potentially including mega slumps (>5 ha); site classifications are presented for interpretive purposes only. Biological metric and environmental variable abbreviations are listed in the Methods section. Biological metrics that were only weakly correlated with axes I and II were not labeled to improve readability of the plot.

first RDA axis. Two of the sites were positively associated with TSS, whereas the three minimally disturbed sites that were more reflective of undisturbed conditions clustered together with a positive association with the presence of coniferous vegetation and a negative association with TSS (Fig. 4b).

The gradient in TSS was responsible for the primary separation of most undisturbed sites from heavily disturbed sites along the first axis of the RDA, but differences among sites within disturbance classifications were primarily evident along the second axis. The second axis was dominated by a negative association between NH_3 and the family richness of Ephemeroptera and Plecoptera that appeared to separate among a number of heavily disturbed sites (Fig. 4b). The second axis was also described by a negative association of embeddedness and maximum catchment slope with the proportion of silt/clay, which was responsible for some separation among undisturbed sites and further separation among heavily disturbed sites.

Total abundance was selected for direct analysis of the response of macroinvertebrates to slumping because of the dominance of this metric in the PCA ordination. There was a strong negative linear relationship between abundance and TSS ($P < 0.001$; $R^2 = 0.759$; Fig. 5a, Table 4). Undisturbed and highly disturbed sites were clearly separated in the regression along the gradient in TSS, but sites with minimal disturbances could not be distinguished from the undisturbed or highly disturbed classes (Fig. 5a). Regression-tree analysis identified a change-point of 295.8 mg L^{-1} TSS, which primarily separated undisturbed and highly disturbed sites and indicated a large decline in mean abundance from 1495 to 80 individuals (Fig. 5a, Table 5).

Macroinvertebrate abundance also showed a significant ($P < 0.001$) decline with increasing rank TP, but it was a weaker relationship than that of abundance and TSS, with more variability in abundance with increasing rank TP ($R^2 = 0.419$; Table 4; Fig. 5b). OLS and rank regression yielded significant results, indicating that the relationship between abundance and TP was evident whether or not the magnitude of TP was considered. Regression-tree analysis of the relationship between abundance and rank TP indicated a decline in mean abundance from 1420 to 195 individuals after the change-point (Fig. 5b, Table 5). Although mean abundances below and above the rank TP change-point were similar to those for TSS, the relationship was weakened by high variability below the change-point and one undisturbed site above the change-point that had high abundance (change-point PRE = 0.517, compared to 0.726 for TSS; Table 5, Fig. 5b).

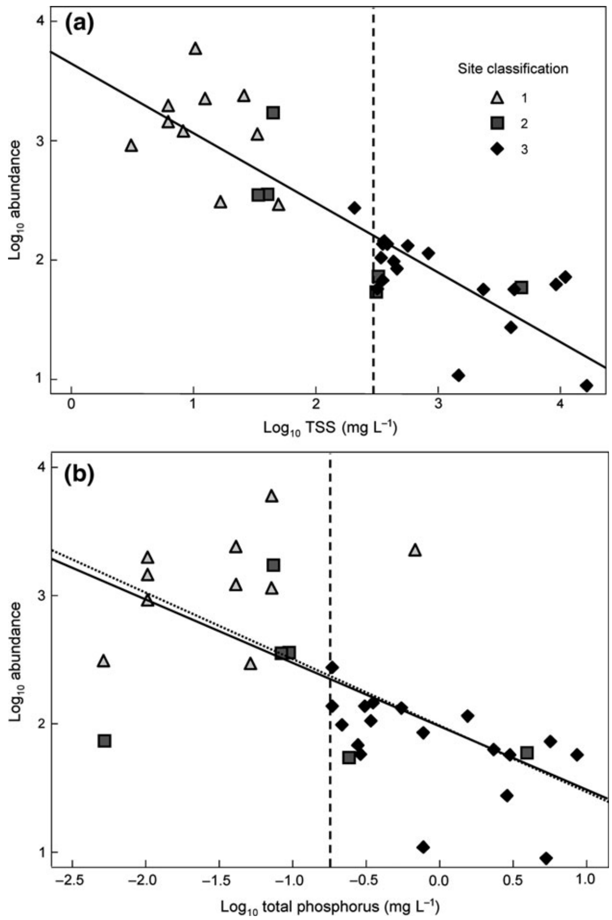

Fig. 5 $\log_{10}$ abundance as a function of (a) $\log_{10}$ total suspended solids (mg L^{-1}) and (b) $\log_{10}$ total phosphorus for all undisturbed and disturbed sites ($n = 34$). The solid line in each plot is an ordinary least squares regression line and the dotted line in (b) is a rank regression line. The vertical dashed line on each plot indicates the change-point at which there was the greatest response of $\log_{10}$ abundance to $\log_{10}$ total suspended solids or rank total phosphorus, as identified through regression-tree analysis.

Table 4 Ordinary least squares linear regression analysis of $\log_{10}$ macroinvertebrate abundance as a function of $\log_{10}$ TSS (mg L^{-1}) and $\log_{10}$ distance to nearest slump or landslide (km), and rank regression of TP (mg L^{-1}) showing the intercept, slope, sample size (N), residual mean square (RMS), R^2, and P-value for each regression. The regressions of TSS and TP used all sample sites, whereas the regression of distance only used sites affected by disturbance

Variable	Intercept	Slope	N	RMS	R^2	P
$\log_{10}$ TSS	3.639	−0.579	34	0.117	0.759	<0.001
Rank TP	1.987	−0.521	34	N/A	0.419	<0.001
$\log_{10}$ Distance	2.023	0.298	24	0.117	0.482	<0.001

Table 5 Regression-tree analysis of the relationship of $\log_{10}$ invertebrate abundance with $\log_{10}$ total suspended solids (TSS) and rank total phosphorus (TP), showing the change point in each of the two variables that represents the point at which there is the greatest change in macroinvertebrate abundance. The mean (±SE) invertebrate abundance below and above the change-point and the Proportional Reduction in Error (PRE) for the change-point are presented

Variable	Change-point	Mean abundance below change-point	Mean abundance above change-point	Proportional reduction in error (PRE)
$\log_{10}$ TSS	295.80 mg L^{-1}	1495.1 ± 404.5	79.8 ± 9.2	0.726
Rank TP	14.5 (rank)	1419.7 ± 435.7	194.6 ± 105.3	0.517

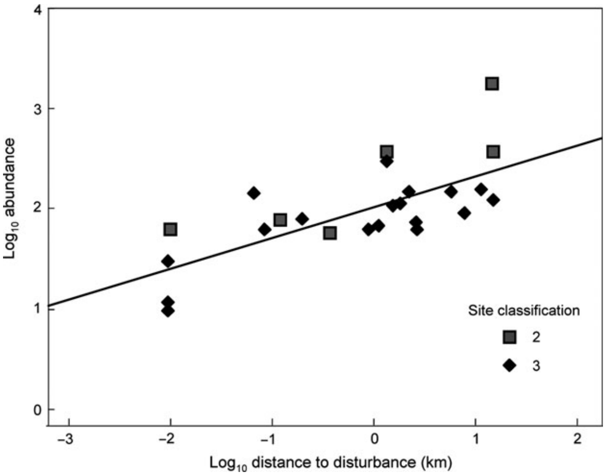

Fig. 6 $\log_{10}$ abundance as a function of the $\log_{10}$ distance to the closest slump or landslide (km) for all disturbed sites (n = 24). The solid line is an ordinary least squares regression line for the relationship.

Among sites with watersheds affected by slumping, macroinvertebrate abundance decreased with proximity to the closest slump or landslide (distance ranged from <0.01 to 15.72 km; Fig. 6). This relationship was statistically significant (P < 0.001) with an R^2 of 0.482 (Table 3). The three minimally impacted sites that grouped with more intensely disturbed sites in the PCA and the regression of abundance and TSS were all located less than 0.4 kilometers from the nearest thaw slump or landslide. In contrast, each of the three minimally disturbed sites that grouped with the undisturbed sites were located more than one kilometer downstream, and up to 14.8 km away from a disturbance.

Discussion

Impacts of thaw slumping

Retrogressive thaw slumps have had a significant impact on the physical and chemical environment of numerous stream systems in northwestern Canada through dramatic increases in sediment and nutrient inputs (Kokelj *et al.*, 2013; 2015; Malone *et al.*, 2013), but the effect of these disturbances on stream invertebrate communities has not been investigated. In this study, we confirmed that intensive thaw slumping has caused significantly elevated sediment, solute and nutrient loads in disturbed streams. The physical and chemical impacts of slumping were associated most strongly with significant declines in abundance in the benthic macroinvertebrate community. Additionally, differences in compositional indices contributed to the sharp contrast between undisturbed and highly disturbed streams. Though both sediment and nutrient inputs from slumping appeared to influence community shifts, the strong negative relationship between invertebrate abundance and TSS indicated that the increase in sediments was the dominant driver of biotic change.

To anticipate the effects of thermokarst disturbance on Arctic stream biota, it is necessary to have a clear understanding of the point at which community resilience is compromised and community structure begins to shift to reflect disturbance. However, this point may be difficult to detect if the initial impacts on the community are subtle (Dodds *et al.*, 2010). There was a gradient response of biota to thaw slumping within our study sites, with an intermediary response of systems impacted by minimal disturbance that was generally indistinguishable from that of either high disturbance or the absence of disturbance. This suggested that the macroinvertebrate resilience threshold may lie along the gradient of minimally disturbed sites; however, this initial point of change may be difficult to detect given the strong overlap with undisturbed sites. The change-point at which macroinvertebrate abundance showed the greatest response to TSS was high compared to those determined for agricultural regions of Canada (e.g., Culp *et al.*, 2013 determined that ecological change-points for TSS ranged from 3.5 to 11.1 mg L^{-1}, compared with the change-point of 295.8 mg L^{-1} identified in our study), which suggested that macroinvertebrates were resilient to change in these northern systems. However, lack of data at the intermediate levels of TSS where the change-point was identified suggests that they may not have been an accurate reflection of the point at which ecological condition began to change in response to TSS. Additional sampling of minimally disturbed streams is necessary to more accurately determine the point along the gradient of increasing disturbance intensity where community resilience is compromised.

Though water quality variables related to sediment and nutrient inputs from slumping appeared to be the most dominant drivers of community shifts, the distance to disturbance was also related to invertebrate abundance and could have the potential to be used as a measure of disturbance intensity. If distance to disturbance were developed as a measure of disturbance intensity, it may be best described by a metric incorporating additional factors such as the size and number of disturbances (*sensu* the glacial index described by Jacobsen & Dangles, 2012) or valley morphometry (which was highly correlated with TSS), as several highly impacted sites were located far from the nearest disturbance. However, when only one or two small slumps or landslides were located within a catchment, the proximity to disturbance appeared to be an important determinant of the level of impact on the invertebrate community in streams. This is in contrast with the patterns observed in lakes, where the input of solutes from thaw slumps is the dominant driver and slump-impacted systems, following stabilization of the disturbance, have higher water clarity (Kokelj *et al*., 2009). Moquin *et al.* (2014) found lake macroinvertebrate abundance to be higher in closer proximity to disturbance, which reflected a biotic response to increased solute levels (including calcium, nitrogen, and organic carbon) and an absence of sediment-driven impacts. It is likely that this difference stems from contrasts in the intensity of disturbance between these environments and the settling of sediment inputs in lentic systems, compared with the continued transport and suspension of sediment inputs from large thaw slumps to rivers that is caused by slope sediment delivery by mud flow, directly to the stream channel and subsequent erosion by turbulent streamflow in these systems. The sharp difference in community response to slump impact in lake systems highlights the extreme dominance of sediment impacts on stream systems.

Community shifts in response to nutrient and sediment inputs

The effects of increased nutrients and TSS on stream benthic macroinvertebrates are generally reflected through shifts in community structure and/or abundance (Dodds & Welch, 2000; Bilotta & Brazier, 2008; Jones *et al*., 2011). In nutrient-poor aquatic systems, such as those generally found in the Arctic, nutrient inputs can increase primary production (Peterson *et al*., 1993), which can initially increase invertebrate species richness, diversity, biomass, or abundance (Mesquita *et al*., 2008). There was evidence of a positive relationship between levels of nitrates and taxonomic richness and distinctness, which could reflect indirect effects of increases to primary production. However, high levels of nutrients were also associated with low total abundance of invertebrates and with low relative abundance of chironomid subfamilies. Moreover, relationships between invertebrate metrics and nutrients were weaker than those observed for TSS. Despite elevated nutrient concentrations in highly impacted streams relative to undisturbed streams, this study indicates that sediment input due to intensive thermokarst is the primary driver of change in the macroinvertebrate assemblages of these systems.

Within the Stony Creek watershed, high concentrations of TSS suppressed the abundance of all taxa. Because these large thaw slumps grow over time, the biological response noted within our systems may reflect both an increase in the magnitude of sediment inputs and the continued exposure to these inputs over time. Reductions in benthic invertebrate density in response to increased suspended sediments have been noted in several studies of temperate streams, with as much as a 77% decrease in population size noted with prolonged exposure (see reviews in Bilotta & Brazier, 2008; and Jones *et al*., 2011). High turbidity and TSS can decrease taxa survival by smothering macroinvertebrate eggs, clogging filtering apparati (Wood & Armitage, 1997; Jones *et al*., 2011), causing physical injury to eye and gill membranes (Bilotta & Brazier, 2008; Jones *et al*., 2011), and increasing invertebrate drift (Culp *et al*., 1986). At low to moderate levels of sediment inputs to streams, sedimentation may benefit some benthic taxa through the creation of additional habitat types (e.g., Lenat *et al*., 1981). However, at the extreme levels of sediment inputs observed in slump-impacted systems, the accumulation of fine sediment homogenizes the benthic floor and fills interstitial space, decreasing habitat availability and suitability for taxa (Hynes, 1960; Bilotta & Brazier, 2008; Jones *et al*., 2011), an effect clearly observed at intensively disturbed sites (Fig. 1).

The apparent tolerance of Ephemeroptera taxa to slump impacts is consistent with previous studies that have documented high tolerance of some genera to sedimentation and nutrient enrichment (Angradi, 1999; Harrington & Born, 2000). For example, following the release of suspended sediments from a reservoir, Gray & Ward (1982) found no evidence of negative impacts on Baetidae, noting increased densities after the silt pulse. Furthermore, baetids are strong swimmers and are often among the first organisms to recolonize a disturbed area (Boyero & Bosch, 2004) or colonize a new one (Rutherford, 1995). In contrast, Heptageniidae have been shown to decrease in abundance in response to an increase in fine sediments in other studies (Culp *et al.*, 1986; Richards & Bacon, 1994; Angradi, 1999), which is inconsistent with the high relative abundance of this family in slump-impacted streams in our study. However, Relyea *et al.*(2012) examined benthic invertebrate tolerance to fine sediment across 1139 streams and found that Heptageniidae varied widely in their tolerance to fine sediments. Moreover, the heptageniid genus *Cinygmula*, which was found within our study sites, was identified by Relyea *et al.* (2012) as being only slightly sensitive to fine sediments.

Diptera taxa appeared to be most sensitive to the impacts of slumping, and the chironomid subfamilies Orthocladiinae and Chironominae were abundant at undisturbed sites. Abundances of Orthocladiinae and Chironominae have been documented to be negatively associated with high levels of suspended sediments (Gray & Ward, 1982) and fine sediment deposition (Angradi, 1999; Logan, 2007). High levels of suspended sediments may hinder feeding or respiration in chironomids, particularly in taxa that inhabit silk tubes (Gray & Ward, 1982) such as some genera of Orthocladiinae and Chironominae. In addition, some Chironominae are burrowers, staying within the top 8 cm of the sediment (Cole, 1953; Charbonneau & Hare, 1998). High sedimentation rates at the highly disturbed sites could potentially exceed the tolerance threshold for Chironominae.

In addition to direct impacts on benthic macroinvertebrates, increased suspended sediment concentrations from slumping are expected to have direct and indirect impacts throughout the stream food web. Suspended sediments decrease light penetration through the water column, thereby suppressing the growth of primary producers, and consequently the populations of benthic macroinvertebrates and fish that utilize/feed on them (Hynes, 1960; Davies-Colley *et al.*, 1992; Bilotta & Brazier, 2008; Jones *et al.*, 2011). Suspended sediments may also have a scouring effect on benthic algal assemblages (Bilotta & Brazier, 2008). Lastly, salmonid fish may be affected by increased sediment inputs through clogging and abrasion to gills and smothering of eggs (Bilotta & Brazier, 2008; Jones *et al.*, 2011). Moreover, benthic macroinvertebrates represent an important food source for fish, and the dramatic declines in macroinvertebrate abundance observed in our study indicate that thaw slumping may have significant indirect impacts on fish communities through the loss of food resources.

Regional and global implications of continued climate warming

There has been a recent acceleration in thaw slump activity across various landscapes in the North American western Arctic (Lantz & Kokelj, 2008; Kokelj *et al.*, 2015). Increases in permafrost temperatures and active layer depths have been recorded in this area over the last three decades (Burn & Kokelj, 2009), and are expected to persist as climate warming continues to drive rising temperatures and precipitation (Prowse *et al.*, 2009). In the Peel Plateau, increasing rainfall intensity has played a significant role in the acceleration of thaw slump activity and development of large, persistent disturbances (Kokelj *et al.*, 2015). The increase in magnitude of geomorphic disturbance can impact the slope-stream sediment cascade, intensifying impacts to downstream aquatic and riparian ecosystems. The progressive growth and longevity of thaw slumps can chronically impact stream systems for at least decades and likely centuries, and as this study shows, can significantly alter the physical, chemical, and biological aspects of the stream ecosystem.

Thaw slump disturbances impact a broad range of landscapes in northwestern Canada and across the circumpolar Arctic (Kokelj & Jorgenson, 2013). Permafrost in ice-rich glaciated terrain in northern Canada (Pollard, 2000; Lantuit & Pollard, 2008; Lantz & Kokelj, 2008; Lacelle *et al.*, 2010), Alaska (Balser *et al.*, 2009), and Siberia (Alexanderson *et al.*, 2002) are particularly susceptible to retrogressive thaw slumping, and stream and lake ecosystems in these environments are therefore prone to the potential physical and biological impacts that we report here. The increased delivery of solutes, sediments and debris into stream systems will influence stream ecosystem patterns and processes, including food web structures, species richness, abundance, diversity, range and distribution of taxa at multiple spatial and temporal scales (Berkman & Rabeni, 1987; and see review in Bilotta & Brazier, 2008). Our study indicates that thaw slumping may have a particularly strong impact on macroinvertebrate assemblages, with a significant negative relationship evident between suspended solids and invertebrate abundance. As predicted climate warming is expected to increase the abundance and magnitude of thaw slumping (Kokelj & Jorgenson, 2013; Kokelj *et al.*, 2015), it is probable that the biological impacts will also increase, not just for benthic macroinvertebrates, but for all taxa that interact with them. If more accurate disturbance thresholds can be determined for the relationship of macroinvertebrate abundance with TSS concentrations and distance to and intensity of thermokarst disturbance, then these parameters could be used in combination to predict macroinvertebrate community response, and by extension, stream food web response to thermokarst disturbance in other regions.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Metric scores (adjusted for metric variance) and eigenvalues for the first three axes of the PCA of undisturbed, minimally disturbed, and highly disturbed streams from the Peel Plateau, NWT.

Table S2. Results of redundancy analysis of Peel Plateau streams using chemistry and habitat variables, including eigenvalues and percent constrained and unconstrained variance in biological metrics explained by the first three axes.