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1 **Bacterial production in subarctic peatland lakes enriched by thawing permafrost**

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Abstract. Peatlands extend over vast areas of the northern landscape. Within some of these areas, lakes and ponds are changing in size as a result of permafrost thawing and erosion, resulting in mobilisation of the carbon-rich peatland soils. Our aims in the present study were to characterize the particle, carbon and nutrient regime of a set of thermokarst (thaw) lakes and their adjacent peatland permafrost soils in a rapidly degrading landscape in subarctic Québec, Canada, and by way of fluorescence microscopy, flow cytometry, production measurements and an in situ enrichment experiment, determine the bacterial characteristics of these waters relative to other thaw lakes and rock-basin lakes in the region. The soil active layer in a degrading palsa (peatland permafrost mound) adjacent to one of the lakes contained an elevated carbon content (51% of dry weight), low C:N ratios (17:1 by mass), and large stocks of other elements including N (3% of dry weight), Fe (0.6%), S (0.5%), Ca (0.5%) and P (0.05%). Two permafrost cores were obtained to a depth of 2.77 m in the palsa, and CT scans of the cores confirmed that they contained high concentrations (>80%) of ice. Upon thawing, the cores released nitrate and dissolved organic carbon (from all core depths sampled), and soluble reactive phosphorus (from bottom depths), at concentrations well above those in the adjacent lake waters. The active layer soil showed a range of particle sizes with a peak at 229 µm, and this was similar to the distribution of particles in the upper permafrost cores. The particle spectrum for the lake water overlapped with those for the soil, but extended to larger (surface water) or finer (bottom water) particles. On average, more than 50% of the bacterial cells and bacterial production was associated with particles >3 µm. This relatively low contribution of free-living cells (operationally defined as the <1 µm fraction) to bacterial production was a general feature of all of the northern lakes sampled, including other thaw lakes and shallow rock-basin lakes (average ± SE of 25 ± 6%). However, a distinguishing feature of the peatland thaw lakes was significantly higher bacterial specific growth rates, which

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averaged 4 to 7 times higher values than in the other lake types. The in situ enrichment experiment showed no no difference between organic carbon or phosphorus enrichment treatments at day 5 relative to the control, however there was a significant, >100% increase in bacterial growth rates between days 1 and 5 in the soil and the carbon plus phosphorus enrichments. Collectively these results indicate that particles, nutrients and carbon are released by degrading permafrost peatland soils into their associated thermokarst lakes, creating favorable conditions for production by particle-based as well as free-living aquatic bacterial communities. The reduced bacterial concentrations despite high cellular growth rates imply that there is strong control of their population size by loss-related factors such as grazing and viral lysis.

Keywords: bacteria, climate change, northern lakes, peatlands, permafrost, thermokarst

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1 Introduction

Aquatic environments in permafrost landscapes are biogeochemical hotspots that provide microbial communities with access to substrates that have been previously locked in frozen soils for centuries to millennia (Kling et al., 1991; Vonk et al., 2015). The highest soil organic carbon contents of the permafrost environment are found in areas of sporadic or isolated permafrost peatland, which span more than 5×10^5 km^2 of land in the circumpolar North (Tarnocai et al., 2009). The availability of organic substrates from these vast permafrost peatland environments to bacterial communities in aquatic ecosystems is likely to be influenced by a variety of factors, including the soil biogeochemical composition, particle and molecular size, and potentially other environmental factors, such as nutrient concentrations and temperature. Lakes in the boreal zone with flat catchments dominated by forest and peatland areas are strongly heterotrophic systems that have high rates of bacterial production (e.g., Kankaala et al., 2006), but less is known about the bacterial characteristics of peatland lakes further northwards, in permafrost regions.

Decomposition processes in aquatic ecosystems are mediated by bacterial communities that can be separated into two ecological groups: (1) free-living bacteria, in which solitary cells are suspended in the medium and break down dissolved organic matter, and (2) particle-attached bacteria, in which the communities are associated with various size-fractions of particles and break down this particulate organic material, as well as accessing dissolved materials (Kirchman and Mitchell, 1982). In both cases, these activities result in consumption of oxygen, production of carbon dioxide, and the mineralization of organic materials.

In most lake and ocean environments, free-living bacteria dominate the total bacterial community in terms of numerical abundance (Unanue et al., 1992; Kirchman and Mitchell, 1982; Simon et al., 1990; Lami et al., 2009). However, there are many environments in which particle-

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based bacteria play a major role. Several studies from estuarine- and marine-waters show that particle-attached populations can account for 10 to 100 times more bacterial cells and activity than free-living bacteria, depending on particle concentrations (Crump et al., 1999; Ghiglione et al., 2007; Acinas et al., 1999; Lami et al., 2009). A study of seven freshwater ecosystems including two marsh-systems showed that a small proportion of particle-attached bacteria (<10%) was associated with >40% of the bacterial community activity, and it was hypothesized that lake size may influence the presence of particulate matter for colonization via interactions between sediments and the water column (Kirchman and Mitchell, 1982). In the turbid waters of the Mackenzie River, which are strongly influenced by permafrost as well as fluvial erosion, more than 90% of the total bacterial production was associated with particles >3 µm (Vallières et al., 2008). Similarly, in the coastal waters of the Beaufort Sea, the >3 µm size-fraction often accounted for >50% of total bacterial production (Garneau et al., 2006; Galand et al., 2008). Other research has identified that a dominant portion (>50%) of bacterial cells were attached to particles (Masin et al., 2012), especially in turbid systems with high concentrations of particulate organic matter (Fletcher 1990; Lami et al., 2009).

Particle localisation of microbial processes has wide-ranging implications for trophic processes in the water column and material fluxes to the sediments. In the oceanographic literature, large particles are referred to as “marine snow”, and many studies that have shown the importance of these aggregates for food-web dynamics (Michaels and Silver, 1988; Alldredge and Silver, 1988; Kiørboe, 2001). Similarly, there has been attention given to “lake snow”; Grossart and Simon (1993) found lake particle aggregates to be densely colonized by bacteria, with approximately 10^8 bacterial cells per mL, 100 times higher than concentrations in the bulk water. The presence of particle-attached bacteria may also result in greater community diversity,

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as has been demonstrated in studies of estuarine mixing zones (Crump et al., 1998; Waidner and Kirchman, 2007). A study by Ploug and Grossart (2000) identified a positive correlation between bacterial production, particulate organic carbon and aggregate size. Size also affects sinking velocities through Stokes' Law, and therefore the flux rates for transfer of materials from the pelagic zone to the sediments (Ploug and Grossart, 2000).

Permafrost thaw lakes are rich in suspended particulate material as a result of permafrost erosion (Breton et al., 2009; Watanabe et al., 2011). They are also continuously supplied with organic as well as inorganic inputs from the thermokarst processes in their surrounding catchments (Vonk et al., 2015), and there is increasing attention to the bacterial responses to such inputs. In the Mackenzie River Delta region, a mesocosm assay showed decreased planktonic bacterial production rates in response to permafrost soil enrichment, but a strong increase in benthic bacterial production rates (Moquin and Wrona, 2014). In a set of subarctic thermokarst ponds, late winter bacterial production was low and dominated by free-living bacterioplankton, while much higher production rates in summer were dominated by particle-attached bacteria, correlated with terrestrial carbon concentrations (Roiha et al., 2015). Permafrost peatland lakes are known to be strong emitters of greenhouse gases with diverse microbiota (Liebner et al., 2015), but little is known about the controls on their bacterial populations and productivity.

Our aims in the present study were to determine the distribution of bacterial production between the suspended and free-living size fractions in subarctic peatland lakes, and their responses to permafrost soil inputs. Two hypotheses were evaluated: firstly, that particle-attached bacteria account for the dominant (>50%) fraction of the total microbial activity, and secondly that organic carbon and nutrients originating from the erosion of permafrost soils promote bacterial metabolic activity and cellular growth. We focused this research on a set of peatland

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lakes in subarctic Québec and first determined the chemical composition of the soil active layer and underlying permafrost in a palsa (organic permafrost mound) that was adjacent to and eroding into a one of the peatland thaw lakes. We examined the distribution of soil particle sizes and compared these with particle distributions in lakes, with comparisons of particle size spectra, nutrients and organic carbon with other types of lakes in the region. We then measured bacterial abundance (BA) and production rates (BP) associated with different size fractions in the peatland and other lakes, and tested the effects of phosphorus, carbon and soil enrichment on bacterial concentrations and activity by way of an in situ incubation experiment.

2 Materials and methods

2.1 Study sites

The primary sampling sites were near Kuujjuarapik-Whapmagoostui (K-W, 55° 17' N, 77° 47' W) in thermokarst lakes and their surrounding soils in the peatland palsa valley of the Sasapimakwananistikw River (SAS; Fig. 1). Additional sampling for comparison took place in thermokarst lakes in the mineral lithalsa (mineral permafrost mounds) valley of the Kwakwatanikapistikw River (KWK) near K-W; glaciated rock-basin lakes, also near K-W, but not influenced by permafrost (RBL); and lithalsa lakes up to 200 km further to the North (SEC, BGR, NAS). This coastal region of northern Québec has experienced rapid climate change, including an increase in mean annual temperatures from –4.2 °C for 1932–1960 to –2.6 ± 1.2°C for 2001-2010, accompanied by changes in the permafrost landscapes, including expansion of the tree line, changes to snow conditions, and various changes in thermokarst lakes frequency and extent (Bhiry et al., 2011). A total of 15 lakes were sampled at the five sites (Fig. 1; detailed location and depth information is given in Table S1 in the Supplement).

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136 The SAS valley is an area of sporadic permafrost (<2% frozen ground) mainly colonized
137 by *Sphagnum* and *Carex*, with dark brown and black colored thermokarst lakes (Arlen-Pouliot
138 and Bhiry, 2005; Fillion et al., 2014). This peat bog contains more than 50 isolated permafrost
139 mounds (palsas; Fig. 2) covered by a 60 cm soil active layer (Arlen-Pouliot and Bhiry, 2005;
140 Fillion et al., 2014). Two sets of lakes were sampled in the SAS valley: SAS1 to the south and
141 SAS2 located to the north of the river. The SAS lakes are stratified, heterotrophic lakes with
142 anoxic zones throughout the majority of the water column, and surface waters that are under-
143 saturated in oxygen (Deshpande et al., 2015). These lakes have abundant and active
144 methanotrophic bacterial communities indicating their high methane supply rates (Crevecoeur et
145 al., 2015), and they , emit greenhouse gases to the atmosphere at flux rates up to 10 mmol CH_4 m^{-2} d^{-1} and >200 mmol CO_2 m^{-2} d^{-1} (A. Matveev et al., unpublished).

147 The valley of the Kwakwatanikapistikw River (KWK) is also in an area of sporadic
148 permafrost, located only 8 km from SAS. It is colonized by lichen-moss, shrub-tundra vegetation,
149 and forest patches in wind-sheltered areas (Arlen-Pouliot and Bhiry, 2005), and contains
150 numerous thermokarst lakes that vary in color from blue-green to brown. The SEC site (55°
151 42.067' N, 76° 38.604' W) was located 86.0 km north-east of K-W and the BGR site was located
152 near the Hudson Bay and the village of Umijuaq (56° 36.63' N, 76° 12.85' W), both in areas of
153 discontinuous permafrost. BGR1 appears to be a rapidly expanding lake, with a maximum depth
154 of 3.2 in 2006 (Breton et al., 2009) that had increased to 4.0 m in 2013 (Deshpande et al., 2015),
155 and 4.2 m in the present study. The Nastapoka River valley (NAS) contains thermokarst lakes
156 that were formed by thawing lithalsa mounds in this region of continuous permafrost. The non-
157 permafrost-affected, rock-basin lakes (RBL) in the K-W region are of similar area and shallow

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158 depth (0.8 – 2.1 m) to the thermokarst systems, but with rock substrate catchments rather than
159 permafrost soils.

160 **2.2 Lake sampling and profiling**

161 Sampling took place during three consecutive summers from 2012 to 2014. At each visit, surface
162 water was sampled using sterile plastic containers. A Van Dorn sampler was used to retrieve
163 samples from the oxycline or the bottom waters, 0.2 above the bottom sediments. Water samples
164 were analysed for soluble reactive phosphorus (SRP), total nitrogen (TN), dissolved organic
165 carbon (DOC), Chlorophyll *a* (Chl *a*), and total suspended solids (TSS) according to methods in
166 Laurion et al., (2010). Ammonium and nitrate (including nitrite) concentrations were measured in
167 water from the SAS valley only using a Lachat autoanalyzer (detection limit of 10 µg N). Soil
168 was sampled from the active layer directly next to a lake at each site and stored in sterile plastic
169 bags. Frozen samples of both water and soils were returned to Université Laval (Laboratoire de
170 géomorphologie et de sédimentologie, FFGG) to determine particle size distribution via Laser
171 Particle Size Analyzer (LA-950V2, Horiba Ltd., Japan).

172 For CDOM analysis, water samples from the surface waters of the SAS lakes were filtered
173 through sample-rinsed 0.47 mm, 0.2 µm pore size cellulose acetate membrane filters and the
174 filtrate was analyzed with the Varian Cary 100 UV-VIS spectrophotometer. The absorbance
175 scans were obtained from the spectrophotometer over the wavelength range of 200-850 nm at
176 natural pH using a 1-cm acid-cleaned quartz cuvette on dual beam mode, at a speed of 240 nm
177 min^{-1} with a slit width of 1 nm. The absorbance was measured against ultra-pure water and
178 corrected against the blanks prepared on site. Absorption coefficients were calculated as $a(\lambda) =$
179 $2.303 \times A(\lambda)/L$, where $a(\lambda)$ is the absorption coefficient at a wavelength λ, $A(\lambda)$ is the optical
180 density (absorbance) for wavelength λ, and L is the path length of the cuvette (m). Spectral slope

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parameters were also determined from absorbance at 275nm (a_{275}) and 295 nm (a_{295}) using the formula $a_{295} = a_{275}e^{-S(295-275)}$, where S (nm^{-1}) is the spectral slope parameter (Fichot and Benner, 2012).

2.3 Active layer and permafrost core sampling

Triplicate soil samples were retrieved from the surface active layer of a palsa adjacent to lake SAS1B on 3 August 2013; the soil was sampled from half way up the face of the palsa (approximately 1 m above the lake surface) that was eroding and collapsing into the lake (Fig. 2). Subsamples were frozen and transported to Quebec City for CHN (LECO analyzer, CEN, Québec) and other geochemical analyses (ICP-AES; INRS-ETE, Québec). Enrichment Factors (EF) for the soil samples were determined as per Gorham and Janssens (2005):

$$EF_{soil} = \frac{[x]_{sample}/[Al]_{sample}}{[x]_{soil}/[Al]_{soil}}$$

where $[x]_{sample}$ is the concentration of a given element, x, in the study sample, $[Al]_{sample}$ is the concentration of the element Al in the study sample, $[x]_{soil}$ is the world median concentration of element x, and $[Al]_{soil}$ is the world median concentration of the element Al. Global average values were taken from Bowen (1979).

Permafrost cores were sampled from two sites 15 m apart on large an organic-rich palsa mound at the SAS2 site (Fig. 1) on 5 August 2013 using a portable drill system (Calmels et al., 2005). The recovered cores were 10-cm in diameter, with lengths of 2.8 and 3.0 m. Samples were returned to the Centre for Northern Studies (Université Laval, Québec) and maintained frozen. The frozen core was characterized by CT scanning (Calmels and Allard, 2004) and later subsampled. Subsamples were 1.5-cm thick and centered at depths of 1.25, 1.75, and 2.77 m from each of the two permafrost cores. Each sub-sample was placed in a sterilized container filled with

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ultrapure Milli-Q water and thawed for a period of 48-hours. Samples were then lightly shaken and then filtered through 0.47-mm, 0.2-µm pore size cellulose acetate membrane filter. The filtrate and a blank (Milli-Q water) were analysed for DOC, NO_3^- (including NO_2^-) and SRP (INRS-ETE, Québec). DOC was analyzed using a Shimadzu 5000A TOC Analyzer (detection limits of 0.05 mg C L^{-1}). SRP and NO_3^- were analyzed using a Lachat autoanalyzer (detection limit of 1 µg N and P L^{-1}). CDOM was analyzed as described above. Unfiltered diluted samples were analyzed for particle-size distribution as described above. Additional subsamples from throughout the core were analysed for total CHN content (LECO analyzer, CEN).

2.4 Size-fractionation

Surface water was sampled from the pelagic zones of lakes BGR1, SEC, KWK12, SAS2A, NAS1A and RBL4K for size fractionation. Phytoplankton and particle-attached bacterial communities were filtered through a 35-µm Nitex screen. The bacteria were then further separated into two size fractions: either by passing through a glass fibre filter (Pall Canada Ltd.) with a nominal pore size of 3.0 µm, or by further filtration through a Whatman GF/B glass fibre filter with a nominal pore size of 1.0 µm. Approximately 2.0 L was filtered for each size fraction, and an unfiltered total community sample was also preserved for concurrent analysis.

2.5 Bacterial community counts

The bacterial communities in the size-fractionated samples were counted after staining with 4',6-diamidino-2-phenylindole (DAPI). Samples were preserved with formaldehyde (3.7% final concentration) in pre-washed plastic bottles, pre-rinsed with the sample and stored at 4°C for up to 6 months. Samples were later shaken to break up larger particles and then filtered onto Nuclepore black polycarbonate membranes (0.22 µm, 25 mm) placed on cellulose acetate

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backing filters (0.7 µm, 25 mm) under low pressure. DAPI was added to 1.5 mL of sample (4 µg mL^{-1} final concentration) and left to stain for 10 min before filtering until dry. Filters were mounted on slides with coverslips and non-fluorescent immersion oil, and stored at -20°C until counting on a Zeiss Axioskip 2 epifluorescence microscope, under UV light and 1000× magnification with immersion oil. A minimum of 15 fields or 400 cells were counted of each sample triplicate.

All other bacterial samples were counted via flow cytometer (FACSCalibur, BD Biosciences Inc., USA) following the procedure described in Rossi et al. (2013). Samples were fixed with glutaraldehyde (1% final concentration) and stored at -80°C until analysis. Bacterial samples were then shaken and stained with the nucleic acid dye SYBR Green I (40 µL mL^{-1} final concentration) for 10 min in the dark, and processed at a low flow rate (12 µL min^{-1}) using 1 µm yellow-green microspheres (Polysciences) solution as an internal standard. Bacterial cells were enumerated based on fluorescence (FL1) and side-scatter characteristics, with data analyzed using the CellQuest Pro software.

2.6 Bacterial production

Bacterial production rates were measured via protein synthesis using radio-labelled leucine incorporation (Kirchman, 2001). Triplicate microfuge tubes plus a killed control each containing 1.5 mL of sample and 40 nM of [4,5-^{3}H]leucine (60 Ci $mmol^{-1}$, PerkinElmer Inc.) were incubated for 1 h at 15°C. After one hour, biomass production was halted by the addition of 100 µL of trichloroacetic acid (100%) and stored at 4°C. Later, the samples were returned to the Takuvik radio-isotope laboratory at Université Laval. Samples were processed using the centrifugation method of Smith and Azam (1992) and then radio-assayed in a scintillation counter to measure the ^{3}H-leucine uptake. Net bacterial C production was estimated using a conversion factor of 3.1

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247 kg C per mole of leucine (Kirchman et al., 1993; Iriberri et al., 1990). Bacterial community
248 specific growth rates were determined using an average cellular carbon content of 18 fg C $cell^{-1}$,
249 as measured in the nearby KWK lakes (Roiha et al., 2015).

250 **2.7 Enrichment experiment**

251 At lake SAS1B, the following treatments were added to triplicate 20 L containers of lake water:
252 43 µmol L^{-1} of glucose (G; to achieve an estimated 20% increase of ambient DOC based on
253 previous measurements), 1.8 µg L^{-1} of phosphorus (P; 10% enrichment of total P), glucose and
254 phosphorus together (G+P), and 6.2 mg L^{-1} of an aqueous suspension of the soil from the SAS1B
255 palsa face, sampled and analyzed as described above (S; equivalent to 20% increase in total
256 carbon relative to ambient DOC). A sample control was also prepared (C). Samples were taken
257 immediately after enrichment (t_0), and from each container after 5 days (t_5) of incubation in situ
258 in the near-surface waters of SAS1B. Chl *a*, bacterial concentrations and bacterial production
259 rates were measured in each treatment.

260 **2.8 Statistical analysis**

261 Environmental and bacterial variables for the comparison of lake waters were analysed by 1-way
262 ANOVA. A 2-way ANOVA was used to compare environmental and biological differences
263 between surface and bottom waters of the various lake types. For the size-fractionation data, a 2-
264 way ANOVA was performed on pre-standardized variables, with the factors of lake and size-
265 fraction following the Shapiro normality test. The enrichment experiment was analyzed via 2-
266 factor repeated measures ANOVA, with each replicate individually tracked. Variables before and
267 after enrichment were also compared via Holm-Sidak pairwise comparisons. Bacterial
268 community growth rates were normalized by square route transformation, and bacterial

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269 abundance was log transformed. Analyses were done using GraphPad Prism (v. 6.0f, GraphPad
270 Software Inc., USA) and SigmaPlot (v. 12, Systat Software Inc., USA).

271 **3 Results**

272 **3.1 Active layer soil analyses**

273 The SAS active layer extended to 60 cm depth and contained 509 g kg^{-1} of carbon, or 50.9% of
274 the soil by mass, and 30 g kg^{-1} of nitrogen (Table 1). Several elements were present in substantial
275 concentrations, including phosphorus at a mean value (±SD) of 545 (19) mg kg^{-1}, iron at 6.0 (1.6)
276 g kg^{-1}, and calcium at 5.2 (3.4) mg kg^{-1}. The soil enrichment factors (EF) were used to compare
277 concentrations of soil elements with world medians (Bowen, 1979) to determine whether the
278 elements were derived uniquely from wind-blown mineral soil (EF ≤1), or were more likely to
279 accumulate due to multiple sources (EF >>1) (Gorham and Janssens, 2005). Several elements had
280 EF values <1, including K, Na, and Mg. For Al, Mn, Pb, Cr, Zn, and Ba, the EF values were
281 between 1 and 2. Phosphorus had an EF of 16, and S had the highest EF value of 132.

282 **3.2 Permafrost core analysis and comparison with lakewater**

283 The frozen permafrost cores were composed mainly of organic matter intercalated with ice
284 (>80%) in the two upper levels, with high concentrations of sediment only in the deepest level at
285 ~2.77 m (Table 2). The soils throughout the core released water containing nitrate and high
286 concentrations of DOC, and the sediment-containing matter near the bottom of the cores
287 additionally released SRP at concentrations up to 30 times those measured in the SAS lakes.

288 The $a_{CDOM}(\lambda)$ spectra for the DOC from the upper two permafrost core samples were
289 almost identical, but differed greatly from those for the bottom-core samples (Fig. 4). Values of
290 $a_{CDOM}(440)$ ranged from 9.96 to 16.2 m^{-1} in all permafrost core samples except the bottom of core

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A, which was 51.5 m^{-1}. The spectral slope parameter ($S_{275\text{-}295}$) ranged from 0.0087 to 0.014 nm^{-1} in the permafrost cores. For SAS lake water samples, $a_{CDOM}(\lambda)$ spectra were similar to those observed from the permafrost core samples (Fig. 4). $a_{CDOM}(440)$ ranged from 8.63 to 18.1 m^{-1}, and was consistently higher in bottom waters than in surface. Spectral slope parameters ($S_{275\text{-}295}$) for the SAS water were within a notably smaller range than for the permafrost cores, and ranged from 0.011 to 0.012 nm^{-1}.

3.3 Particle size distribution in soils and lakes

The particle-size distributions from the SAS permafrost cores followed a bimodal distribution as observed in the SAS active layer soil and the SAS lake water (Fig. 5). The maximum frequency of particle size (PSmax) ranged from 152 to 200 µm for the permafrost layers at 1.25 and 1.75 m for both duplicates. The bottom layer of core A had a distribution maximum of 67 µm while the maximum for core B was 51 µm. The active layer soil was similar to the distribution of particles in the upper permafrost cores, but with a maximum frequency at a slightly higher size (229 µm), and an even distribution of particles from 80 to 300 µm. The particle spectrum for the SAS lake water overlapped with those for the soil, but the surface water spectrum extended to higher sizes and peaked at 394 µm, while the bottom water spectrum peaked at 200 µm and extended to finer particles (Fig 5).

As a further analysis of particle size distribution, difference spectra were calculated relative to the SAS2A surface waters for the active layer soil, upper permafrost soil and bottom waters. These curves emphasize the strong overlap in size spectra, with differences ranging from only -3 to +6%, depending on size class (Fig. 6). These curves also illustrate how the surface water was slightly enriched in larger particles, while the bottom waters were enriched in finer particles.

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314 Within-lake particle sizes showed highly variable distributions across the other lakes
315 studied, with modes that ranged from 4 to 1337 µm (Table 3; Fig. 5). The smallest particles were
316 identified in RBL4K, a rock-basin lake unaffected by permafrost, with a mode particle size of 4
317 µm. Of the thaw lakes, the lakes from areas of sporadic, degrading permafrost had larger particles
318 than the continuous- and discontinuous-permafrost lakes. For example, the mode particle sizes in
319 NAS1A, BGR1, and SEC were 102, 59, and 153 µm, respectively. In contrast, the particle-size
320 modes in SAS2A and KWK12 were 300 µm and 592 µm, respectively.

321 The concordance of particle distributions between the lake waters and their adjacent soils
322 varied among the other sample sites (Fig. 5). For example, the distribution of particles in KWK12
323 was strikingly similar to that of KWK active layer soil, while other lake samples tended to have
324 modes than were higher than the mode observed in the soil, as in SAS. For example, the mode for
325 BGR lake water was 59 µm, but 10 µm for the adjacent mineral soil. As at SAS, the distribution
326 of soil and lake water particles at SEC was bimodal, and the particles encompassed a much wider
327 range in soil than in the lakes.

328 **3.4 Lake properties**

329 The SAS lake surface waters differed significantly in their limnological properties from those of
330 other thaw lakes and also from the rock-basin lakes (Table 3; 1-way ANOVA). The SAS lakes
331 had a mean surface DOC value of 11.5 mg L^{-1}, that was significantly higher than the two other
332 lake categories (Mann-Whitney test, $p = 0.004$). The average surface Chl *a* concentration of 2.29
333 µg L^{-1} was also significantly higher for the SAS lakes relative to the other categories ($p = 0.03$),
334 as was surface TN, which averaged 0.58 mg L^{-1} ($p = 0.004$). TSS and maximum particle size
335 (PSmax) values were variable within each lake type (Table 3), with no significant differences; the
336 surface PSmax values were strikingly variable in rock-basin lakes, ranging over three orders of

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337 magnitude, but much more homogeneous among the SAS waters (mean of 384 µm with a CV of
338 37%).

339 The SAS lakes were well stratified and despite their shallow depths showed substantial
340 differences between the top and bottom of the water column, which was also a feature of the
341 other thaw lakes (Table 3). A two-way ANOVA for depth and the two thaw lake types (SAS
342 versus the other thaw lakes) showed that overall there were significant increases at depth in SRP
343 ($F = 23$; $p = 0.03$); TN ($F = 18$; $p = 0.02$) 2and Chl *a* ($F = 28$; $p = 0.03$), with no significant ($p >$
344 0.05) top-bottom differences in DOC, TSS or PSmax. Consistent with the 1-way analysis for all
345 three lake types, this 2-way analysis (both depths) showed that SAS lakes had significantly
346 higher concentrations of DOC ($F = 65$; $p < 0.0001$) and TN ($F = 32$; $p = 0.004$) relative to other
347 thaw lakes. However, the SAS lakes had significantly lower concentrations of TSS ($F = 23$; $p =$
348 0.05), which were especially high in NAS1A and BGR2, and there were no significant
349 differences ($p > 0.05$) between the two groups of thaw lakes in terms of SRP, Chl *a* or PSmax.

350 Ammonium and nitrate were not analyzed routinely, but the surface waters of the SAS
351 lakes sampled during late June 2014 contained undetectable concentrations of nitrate (<10 µg N
352 L^{-1}) and substantial concentrations of ammonium: 64 (SAS1A), 58 (SAS1B), 49 (SAS2A), 60
353 (SAS2B) and 74 (SAS2C) µg NH_4^+-N L^{-1}. Much higher values were recorded in the anoxic
354 bottom waters of two of the lakes: 1021 (SAS1A) and 178 (SAS1B) µg NH_4^+-N L^{-1}, but values
355 were similar to surface waters in SAS2A (48 µg NH_4^+-N L^{-1}).

356 **3.5 Bacterial abundance and productivity**

357 Bacterial abundance in the surface waters varied over an order of magnitude among SAS lakes,
358 from 2.0×10^5 to 3.1×10^6 cells mL^{-1}, and did not significantly differ from the other lake types

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359 (Table 4; p >0.05). Bacterial production rates varied by a factor of six among SAS lakes, from
360 0.25 to 1.68 µg C L^{-1} h^{-1}, and as for cell concentration, there were no significant differences
361 among the categories of lakes. Bacterial cellular growth rates were similarly variable, ranging
362 from 1.9 to 113 fg $cell^{-1}$ d^{-1}, however four of the five surface values were well above (factor of
363 two or greater) any of the lakes in the two other lake categories, and the mean value for SAS
364 waters was significantly higher than the others ($F = 5.0$; $p = 0.026$).

365 **3.6 Size-fractionated solids and associated bacteria**

366 In SAS2A, the mass of suspended solids decreased sharply with filter size, and the <1 µm
367 fraction contained only 5% of the total value (Fig. 7). Similar trends were observed in the other
368 lakes, with the exception of NAS1A where almost all of the suspended solids passed through the
369 35 and 3 µm filters, and 34% even passed through the 1 µm filter. In terms of bacterial cells,
370 highest counts were in the total or <35 µm fraction, with the exception of NAS1A, which peaked
371 in the <3 µm fraction. Only 28% of the maximum counts occurred in the <1 µm fraction in
372 SAS2A samples, and this fraction was similarly low in SEC (23%). Higher percentages of
373 maximum occurred in the <1 µm fraction in RBL4K (43%), KWK12 (52%), BGR1 (52%) and
374 NAS1A (87%).

375 The bacterial production data showed a more striking pattern (Fig. 7). Total production was
376 maximal in the unfiltered (total) or <35 µm fraction, but the <1 µm fraction accounted for only
377 26% of the maximum in SAS2A, and was even lower in most of the other lakes: 11% (NAS1A),
378 11% (RBL4K), 16% (KWK12), and 14% (BGR1). An average value of 39% was recorded in
379 SEC. The cellular growth rates (BG) were highly variable among size fractions (Fig. 6). In the
380 SAS2A analysis, rates were two times higher in the <3 µm than in the <1 µm fraction. Similarly,
381 in all of the other lake waters, highest cellular growth rates were in fractions above 1 µm: Total

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382 (NAS1A); Total and <3 µm (BGR1); <3 µm (SEC); Total (KWK12) and Total and <35 µm
383 (RBL4K). The free-living cell fraction (<1 µm) showed rates that were a small percentage of the
384 production per cell in the unfiltered samples in RBL4K (27%); KWK12 (16%); NAS1A (8%)
385 and BGR1 (16%).

386 **3.7 Enrichment experiment**

387 Over the course of the experiment (Fig. 8), there was no significant change in Chl *a*
388 concentrations, either with time or among treatments (repeated measures ANOVA, $p > 0.05$).
389 There was a significant drop in cell abundance in all treatments by day 5 (BA; effect of time F =
390 39; p = 0.025) but no significant change in production rates (BP, $p > 0.05$). Although there was
391 no significant overall effect of time and treatment on bacterial growth rates (BG, carbon
392 production rates per cell; $p > 0.05$), there was a significant interaction effect between time and
393 treatment ($F = 4.9$; $p = 0.026$). Further analysis (Holm-Sidak pairwise comparisons) showed that
394 while most of bacterial growth rates had not changed statistically, there was a large significant
395 increase between days 1 and 5 in the soil addition treatment (146% average increase; $t = 2.9$; $p =$
396 0.034) and in the carbon+phosphorus (G+P) enrichment (187% increase; $t = 3.34$; $p = 0.022$).

397 **4 Discussion**

398 **4.1 Organic carbon enrichment**

399 There is an estimated 1.048×10^6 km^2 of permafrost peatland in North America, half of which is
400 located in areas of sporadic or isolated permafrost like the SAS region of the present study
401 (Tarnocai et al., 2009). The surface soil and permafrost cores from the SAS region were abundant
402 in carbon, with ~50% C-content (by dry-weight) down to 2 m depth in the permafrost cores (Fig.
403 3). These values are comparable to peatland soils elsewhere. A study of peat cores from five

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404 North-American sites showed that the concentration was consistently around 50% C dry-weight
405 (Gorham and Janssens, 2005), as was also observed in the surface SAS1 active layer and in the
406 upper layers of the two permafrost cores. Similarly, a synthesis of peat data from 9 studies in the
407 northern hemisphere (Gorham et al., 2012) yielded a mean value (±SD) of 50.1 (2.9). These
408 carbon values are much higher than observed in other types of Arctic soils. For example, the
409 carbon content of active layer soil from a polygonal tundra of the Lena Delta ranged from 1.5 to
410 3% dry-weight (Höfle et al., 2013), an order-of-magnitude less than values in the SAS soil.
411 Lower carbon concentrations were also measured in a study of permafrost soils of the Arctic
412 tundra of Northwest Territories, which were 6.5% C (Moquin and Wrona, 2015), and in the
413 lithalsa mounds surrounding BGR1 (Fig. 1), where the carbon content of the active layer was less
414 than 1% (ADAPT, 2014).

415 Paleoecological studies (Arlen-Pouliot and Bhiry, 2005; Fillion et al., 2014) have shown
416 that the peat in the SAS valley accumulated in bogs over a 1400 year period from around 1800 to
417 400 years before the present, and was then uplifted in palsas during the period of permafrost
418 aggradation during the Little Ice Age, 400 to 200 years before present day. From the end of the
419 19th century onwards, the SAS palsas have been thawing and eroding, with the production and
420 eventual infilling of associated thermokarst lakes (palsa lakes), and this warming phase appears
421 to have accelerated over the last two decades (Bhiry et al., 2011). The degrading palsas are
422 therefore a rich source of organic carbon to their associated lakes. As shown in the permafrost
423 core analysis (Table 2), this organic input includes not only particulate organic carbon but also
424 DOC. Two contrasting scenarios have been identified for the effects of thawing permafrost on
425 carbon transport in northern catchments (Vonk et al., 2015): (1) decreased net export of carbon as
426 a result of increased flow path lengths, residence times and decomposition in a deeper active

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427 layer, or (2) increased net export as a result of thermal erosion and mobilisation of particulate and
428 dissolved organic carbon. The SAS valley is currently in the 'pulse phase' of carbon
429 mobilisation, which as noted by Vonk et al. (2015), is typically dominated by the export of
430 particulate materials. However, the high DOC of the SAS waters, significantly above that in the
431 other lake types, also attests to a substantial export of DOC from the SAS palsas to their
432 associated lakes, and is consistent with the permafrost thaw analyses. The low spectral slope
433 values in the SAS lakes indicate a predominantly terrestrial origin of DOC in these lakes (Fichot
434 and Benner, 2012), and the similarity in slope values between the permafrost cores and the lake
435 waters also supports this close linkage between land and water.

436 **4.2 Nutrient enrichment**

437 The SAS soil likely represents a nutrient-rich substrate for bacterial metabolic activity. The soil
438 N concentrations were low relative to C, reflecting the stoichiometry of ancient moss tissue,
439 however there were large standing stocks of this element, and the high ammonium levels in the
440 lake water implies that nitrogen was in abundant supply for planktonic microbial growth
441 processes. The SAS surface soil had nearly three times as much phosphorus and more than five
442 times as much iron relative to concentrations found in other *Sphagnum* peat bogs (Gorham and
443 Janssens, 2005). It had 1.6 times the concentration of phosphorus and three times the amount of
444 calcium when compared to permafrost soil from the Northwest Territories (Moquin and Wrona,
445 2015), though only a fraction (5%) of the magnesium observed in the latter study. Enrichment
446 Factors (EF) indicated that phosphorus was above the global average for phosphorus
447 concentrations in soil (EF=15.9), demonstrating long-term transfer of this elements from other
448 sources, such as via atmospheric deposition or hydrological transfer. The permafrost thawing
449 analyses showed a release of nitrate but no evidence of soluble phosphorus release, except from

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the bottom-core samples that produced SRP concentrations that were 2- to 30-times above current lake water values. This coastal region of eastern Hudson Bay was submerged beneath the Tyrell Sea from immediately after the retreat of the ice cap about 7900 years ago to emersion from the sea about 6000 years before the present, and previous paleoecological studies on the deeper strata of the SAS valley sampled in the bottom core show that these are ancient marine sediments (Arlen-Pouliot and Bhiry, 2005; Fillion et al., 2014). This would account for their higher phosphorus release relative to that from the upper core. Deep thawing of the palsas during the final stages of their collapse could therefore have a major P-enrichment effect on the associated thermokarst lake ecosystems.

Inorganic nutrient release from thawing and eroding permafrost has been documented at sites elsewhere, but with large variations among regions and landscape types (Vonk et al., 2015). Slumping of permafrost soils into Alaskan streams increases their inorganic as well as organic concentrations (Bowden et al., 2008), but phosphorus adsorption onto clays may decrease SRP concentrations in some mineral permafrost environments (Breton et al., 2009). Nitrate export from the Kuparuk River catchment on the Alaska North Slope increased 5-fold between the late 1970s and early 2000s and may have been related to permafrost soil and vegetation effects (McClelland et al., 2007).

4.3 Particle enrichment

The permafrost peatland lakes were rich in particulate material, with substantially larger particles than non-permafrost-affected rock-basin lake RBL4K, and they contained some of the largest particles amongst thermokarst lakes studied (Fig. 5). Much finer particles over a narrower size range were recorded in the northern permafrost lakes NAS1A and BGR1, reflecting their mineral permafrost catchments. The close correspondence between the active layer, permafrost and lake

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473 particle size distribution at SAS2 (Fig. 6), is evidence that this richness of particles in the
474 peatland lakes is derived from the thermo-erosion of their associated palsas. The small but
475 conspicuous shift to larger particles in the SAS surface waters may indicate the production of
476 aggregates by flocculation that are maintained in the upper water column by virtue of their low
477 density and therefore slow sinking speeds. The production of flocs was observed when SAS
478 water was brought into the laboratory and stored in clear glass bottles without mixing for several
479 days (B. N. Deshpande, unpublished observations), and may be favored by the high DOC
480 concentration in these waters. In contrast, the deeper waters showed an increase in fine particles,
481 contrary to what might be expected from Stokes' Law based upon size relationships. The origin
482 of this difference is unknown at this time, but it could be the result of fine, high-density mineral
483 particles settling out from the overlying water column. The extreme thermal stratification and
484 physical stability of these waters (Deshpande et al., 2015; Przytulska et al., 2016) indicates that
485 only particles of small size or low density would be maintained in the water column.

486 **4.4 Bacterial association with particles**

487 There was clear evidence that the high particle-loading of SAS waters affected its bacterial
488 ecology. Less 30% of the total cells and productivity were associated with the free-living
489 category, operationally defined here as passing through a 1 µm filter, and this effect was even
490 more pronounced for bacterial growth rates, which were 50% lower in the <1 µm than in the <3
491 µm fraction, implying much faster growth rates of bacteria on particles in the size range 1-3 µm.
492 In SAS2A, as in many of the other northern lakes, bacterial populations and production appeared
493 to be distributed across the full range of particle sizes. This is consistent with studies across a
494 range of salt- and fresh-water environments showing that particle-attached bacteria are favored in

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environments with a high availability of particulate habitats (Lami et al., 2009; Kirchman and Ducklow, 1987; Kirchman and Mitchell, 1982).

There are several sources of experimental error that must be considered when interpreting particle analyses of this sort. Firstly, it is difficult to obtain a reliable count of particle-based bacteria. Our shaking of the samples would have broken up and released cells from larger aggregates, but dislodging bacteria from particles is notoriously difficult. Even sonication is not completely effective, and addition of a detergent along with sonication can resulted in a pronounced increase in cell concentrations in sediment-laden waters (Yoon and Rosson, 1990). It is therefore likely that the cell concentrations in the present study were underestimated, especially in the >1 µm fractions. This would imply an even greater representation by particle-based cells to the total community abundance, but it would also have led to an overestimation of the production rates per cell biomass. Experiments based on size-fractionation by filtering are always challenging because of the interactions between particle and the filters. Filtering water results in the breakup of particles upon collision with the filter surface, causing two important effects: (1) an increased bioavailability of organic particles (Amon and Brenner, 1996); and (2) potential detachment of particle-attached bacterial from their organic-matter habitat. Filter blocking may have also retained smaller fractions, including free-living cells. Although the exact rates per fraction in the present study, as in all such studies, must be interpreted with caution, the distribution of cells and activities across multiple fractions and the low values in the <1 µm fraction point to the importance of particle-based bacteria in this system. This was not unique to SAS waters, but was found in several of the other lakes. These results are consistent with a previous study of five lakes in the KWK area, which showed a substantially higher proportion of particle-attached bacteria (62±30% in the >3 µm size-fraction) and high productivity (59 ± 30 %)

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518 by these groups (Roiha et al., 2015). The production-per-cell patterns are also consistent with
519 data elsewhere; for example, Kirchman and Mitchell (1982) found that particle-attached bacteria
520 accounted for <10% of the total bacterial populations but contributed substantially to total
521 microbial activity.

522 **4.5 Controls on bacterial abundance and productivity**

523 Bacterial abundance in the thermokarst lakes sampled here ranged from 0.20 to 3.5 × 10^6 cells
524 mL^{-1}, which falls towards the higher end of the range for comparable aquatic ecosystems (Table
525 5). For example, in study of 16 lakes located in subarctic Sweden, bacterial concentrations ranged
526 from 0.4 to 2.4 × 10^6 cells mL^{-1} (Karlsson et al., 2001), and in a humic, boreal lake, bacterial
527 concentrations ranged from 1.2 to 1.7 × 10^6 cells mL^{-1} in winter (Tulonen et al., 1994).

528 The bacterial production rates in the thermokarst lakes sampled here were also at the high
529 end of the range in comparable systems (Table 5), from. 0.25 to 2.3 µg C L^{-1} h^{-1}, with an average
530 (SD) of 0.92 (0.46) µg C L^{-1} h^{-1}. These rates are more comparable with those observed in
531 southern Québec aquatic ecosystems, and productive systems elsewhere, for example the high-
532 nutrient Butron River, Vizcaya, Spain (Table 4). In this river, free-living bacteria had a
533 production rate of 5.8 µg C L^{-1} h^{-1}, with particle-attached communities contributing 2.97 µg C L^{-1}
534 h^{-1} of bacterial-production (Iriberri et al., 1990).

535 Such comparisons with other sites need to be made with caution because they rest on a
536 number of untested assumptions. Notably, we used a single factor for conversion between leucine
537 uptake to carbon production concentrations, and assumed a 2-fold isotopic dilution of leucine in
538 the natural environment, observed in certain subarctic ecosystems (Simon and Kirchman, 1988;
539 Simon and Azam, 1989) and as has been employed for a wide range of bacterial production

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studies elsewhere (Judd et al., 2006; del Giorgio et al., 1997; del Giorgio and Bouvier, 2002). However, given the wide-range of DOC concentrations and unique characteristics of thermokarst lakes, it is likely that the true conversion factors would lie on a wider range, as found in Pulido-Villena and Reche (2003). If ambient leucine concentrations follow the trend of measured total DOC concentrations, then production rates may have been especially underestimated in the SAS incubations. This should not have influenced the pattern amongst size fractions, however, as noted above, errors associated with cell counts for the particle-associated fractions may have affected the estimates of rates per biomass.

The enrichment experiment in the present study showed that there was no significant effect of either glucose or phosphorus when added separately. These results imply that bacterial stocks and production were not strongly limited by carbon supply, nor were they subject to primary phosphorus limitation. This contrasts with results from the permafrost-influenced, turbid waters of the Mackenzie River, Northwest Territories Canada, where short-term glucose enrichment resulted in a 4-fold increase in leucine uptake rates (Vallières et al., 2008). They also contrast with enzymatic analyses of Greenland lakes that implied strong primary phosphorus limitation. Chl *a* levels also showed no significant effect of enrichment, in contrast to such experiments in High Arctic lakes (Bonilla et al., 2005). However, for the addition of glucose plus phosphorus, and also for the soil addition treatment, there was a significant increase in specific growth rates. This implies a combined stimulatory enrichment effect on bacterial production of the palsa permafrost soils eroding into the SAS thermokarst lakes.

Other studies have shown that DOM-enrichment increased heterotrophic metabolism, sometimes at the expense of autotrophic metabolic activity (Forsström et al., 2013). In an Arctic tundra lake of the Northwest Territories, addition of permafrost soil resulted in decreased

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563 bacterial production in the pelagic zone, but increased rates in the benthic zone (Moquin and
564 Wrona, 2015). A recent study of Arctic lakes in southwest Greenland found that microbial
565 populations were primarily phosphorus-limited, and that this P-limitation increased with the
566 availability of DOM (Burpee et al., 2016). In an area of discontinuous permafrost in northern
567 Sweden, addition of terrestrial carbon to aquatic bacterial samples resulted in a four- to seven-
568 fold increase in respiration rates, with only a small proportion of the available carbon (1 – 12%)
569 contributing to cellular biomass and the dominant portion respired to CO_2 (Roehm et al., 2009).

570 All of the limnological and microbial measurements point to the SAS peatland lakes as
571 favorable environments for bacterial production. The bacterial growth rates show that SAS lakes
572 were outliers amongst thermokarst lakes, with significantly elevated rates (Table 4). These rates
573 are also on the higher end of observations made across a wide trophic range of lakes from other
574 regions (del Girogio et al., 1997; Smith and Prairie, 2004). The lack of response of cellular rates
575 to either phosphorus or carbon added singly also implies sufficiency, and even although there
576 was a significant rise in growth in response to soil and carbon+phosphorus (G+P), this was not
577 translated into an increase in population size. In fact populations fell in all of the incubations,
578 despite bacterial community growth rates that remained the same or higher.. In combination,
579 these observations suggest that bacterial biomass in the SAS peatland lakes is controlled by top
580 down processes rather than by bottom-up, substrate supply rates. This might involve viral lysis,
581 as in planktonic bacterial systems elsewhere (e.g., Lymer et al., 2008) or it may be the result of
582 intense grazing by bactivores. These waters contain high concentrations of zooplankton,
583 including *Daphnia* (Bégin 2014) that can filter picocyanobacteria (Przytulska et al., 2015) and
584 probably heterotrophic bacteria (Rautio and Vincent, 2006). Studies on SAS2A have shown that
585 they contain abundant ciliates, heterotrophic nanoflagellates and mixotrophic phytoplankton

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586 (Przytulska et al., 2016), all of which may exert a control on bacterial densities. In these
587 environments, enriched by soil particles, carbon and nutrients released from thawing and eroding
588 permafrost, bacterial stocks may be ultimately capped by loss rather than gain processes.

589

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804 # 7 Tables

805 Table 1. Chemical properties of permafrost soil samples from the palsa surface at SAS1. Each
806 value is the mean (standard deviation) of triplicates.

Major constituents	Mean elemental concentration (SD) (g kg^{-1} dry weight)	Minor constituents	Mean elemental concentration (SD) (mg kg^{-1} dry weight)
Mg	0.339 (0.189)	Cd	0.12 (0.04)
Na	0.344 (0.123)	Pb	0.93 (0.46)
K	0.369 (0.178)	Mo	1.03 (0.18)
P	0.545 (0.019)	Ni	5.3 (0.8)
Al	3.67 (0.60)	Cr	5.8 (0.5)
S	4.86 (0.52)	Zn	5.8 (0.5)
Ca	5.23 (3.4)	Cu	6.5 (1.1)
Fe	6.04 (1.6)	Mn	24.5 (12)
N	30.0 (2.6)	Ba	43.5 (10)
C	509 (10.9)		

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808 Table 2. Analysis from duplicate permafrost cores taken from palsas at the SAS2 study site. Gas,
809 ice, and sediment (Sed) proportions (%) are by volume. a_{CDOM} (m^{-1}) is the CDOM absorption at
810 440 nm. Dissolved organic carbon (DOC, in mg L^{-1}), soluble reactive phosphorus (SRP, in µg L^{-1}), and nitrate-nitrogen (NO_3, in µg N L^{-1}) concentrations are potential contributions from melted
812 core ice. N/A* = sample was below detection limit.

Core	Depth (m)	Gas (%)	Ice (%)	Sed (%)	a_{CDOM}	DOC	SRP	NO_3
A	1.25	5	95	0	12.0	14.7	N/A*	42.1
	1.75	18	82	0	13.3	13.9	N/A*	36.5
	2.77	1	41	58	51.5	28.0	33.1	341
B	1.25	3	97	0	16.2	26.9	N/A*	62.2
	1.75	5	95	0	14.0	17.9	N/A*	63.1
	2.77	2	53	44	10.0	28.8	20.8	93.6

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814 Table 3. Limnological properties of study sites. Zs, sample depth, soluble reactive phosphorus
815 (SRP, in µg L^{-1}), total nitrogen (TN, in mg L^{-1}), dissolved organic carbon (DOC, in mg L^{-1}),
816 Chlorophyll *a* (Chl *a*, in µg L^{-1}), total suspended solids (TSS, in mg L^{-1}); PSmax, maximum
817 frequency of particle size distribution (µm). The S samples correspond to surface at 0 m, and the
818 B samples correspond to the maximum depth of each lake.

Lake	Zs	SRP	TN	DOC	Chl *a*	TSS	PSmax
SAS1A	S	1.01	0.58	10.4	3.31	5.31	452
	B	5.48	1.76	13.4	4.13	33.0	200
SAS1B	S	1.44	0.70	14.7	3.44	7.43	592
	B	2.18	0.89	14.6	6.22	11.3	262
SAS2A	S	1.42	0.42	8.50	0.94	17.6	300
	B	1.17	0.40	9.00	3.34	4.56	200
SAS2B	S	1.12	0.61	12.8	1.54	6.00	344
	B	8.34	1.88	22.0	7.78	16.5	1338
SAS2C	S	1.03	0.59	11.0	2.24	4.62	229
	B	5.76	1.71	21.0	1.84	15.8	229
KWK12	S	0.41	0.41	6.30	1.12	6.52	592
	B	1.78	0.63	7.60	6.24	27.1	200
SEC	S	0.75	0.26	2.90	1.02	6.97	153
	B	1.56	0.35	3.90	1.58	61.6	175
BGR1	S	0.42	0.24	2.40	0.49	4.57	59
	B	2.06	0.51	3.20	13.4	34.7	59
BGR2	S	1.85	0.38	5.10	0.92	30.8	229
NAS1A	S	4.18	0.25	3.80	0.32	112	102
	B	3.25	0.23	3.30	0.07	163	102
NAS1H	S	1.80	0.24	4.00	1.51	10.9	102
RBL4K	S	0.47	0.74	8.10	1.48	4.00	4
POND9K	S	4.84	0.81	15.1	1.16	3.22	13
RBL9K	S	3.66	0.54	10.2	0.88	1.28	200
RBLOlsha	S	1.09	0.36	9.10	2.05	1.46	175

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Biogeosciences Discuss., doi:10.5194/bg-2016-32, 2016
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820 Table 4. Bacterial properties of study sites. Zs, sample depth, bacterial abundance (BA, in 10^6
821 cells mL^{-1}, bacterial production rate (BP, in µg C L^{-1} h^{-1}), and bacterial community specific
822 growth rates (BG, in d^{-1}). The S samples correspond to surface at 0 m, and the B samples
823 correspond to the maximum depth of each lake.

Lake	Zs	BA	BP	BG
SAS1A	S	0.319	0.896	3.72
	B	2.59	1.074	0.550
SAS1B	S	0.203	0.855	5.58
	B	0.867	0.923	1.41
SAS2A	S	3.15	0.254	0.107
	B	1.57	1.676	1.42
SAS2B	S	0.321	0.804	3.32
	B	1.26	0.588	0.619
SAS2C	S	0.282	1.34	6.30
	B	1.99	0.547	0.364
KWK12	S	3.53	2.34	0.879
	B	1.55	1.164	0.996
SEC	S	1.98	0.885	0.593
	B	0.994	0.650	0.867
BGR1	S	2.79	0.264	0.125
	B	1.03	0.609	0.784
BGR2	S	1.89	1.312	0.920
NAS1A	S	1.71	1.188	0.921
	B	1.16	0.785	0.897
NAS1H	S	0.864	1.253	1.92
RBL4K	S	2.46	0.371	0.200
POND9K	S	2.64	0.791	0.397
RBL9K	S	2.78	0.597	0.285
RBLOlsha	S	0.819	0.849	1.37

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825 Table 5. Comparison of bacterial abundances (BA, 10^6 cells mL^{-1}) and production rates (BP, µg
826 C L^{-1} h^{-1}) from thermokarst lakes with other aquatic environments. * Trophic status based on Chl
827 *a* concentrations only.

Name	Location	Trophic status	BA	BP	Reference
Pääjärvi	Finland, in winter	Dystrophic	1.2 - 1.7	0.0083 - 0.096	Tulonen et al., 1994
16 ponds	Subarctic Finland	Oligotrophic	1.75 - 2.75	0.063 - 0.15	Roiha et al., 2012
Mesocosm of small tundra lake	Mackenzie Delta, Northwest Territories	Mesotrophic	--	0.16	Moquin and Wrona, 2015
SAS2A	*Subarctic Québec*	*Dystrophic, mesotrophic*	*3.1*	*0.25*	*This study*
BGR1	*Subarctic Québec*	*Oligotrophic*	*2.8*	*0.26*	*This study*
Stukely	Southern Québec	Mesotrophic*	2.7	0.30	del Giorgio et al., 1997
16 lakes	Subarctic Sweden	Oligotrophic, dystrophic	2.4 - 0.4	0.012 - 0.32	Karlsson et al., 2001
RBL4K	*Subarctic Québec*	*Oligotrophic*	*2.5*	*0.37*	*This study*
SEC	*Subarctic Québec*	*Oligotrophic, mesotrophic*	*2.0*	*0.88*	*This study*
SAS1A	*Subarctic Québec*	*Dystrophic, mesotrophic*	*0.32*	*0.90*	*This study*
NAS1A	*Subarctic Québec*	*Oligotrophic, dystrophic*	*1.7*	*1.2*	*This study*
SAS2C	*Subarctic Québec*	*Dystrophic, mesotrophic*	*0.28*	*1.3*	*This study*
Lovering	Southern Québec	Oligotrophic*	3.4	1.35	del Giorgio et al., 1997
Massawippi	Southern Québec	Mesotrophic*	3.0	1.69	del Giorgio et al., 1997
Magog	Southern Québec	Eutrophic*	3.38	1.88	del Giorgio et al., 1997
Central	Southern Québec	Mesotrophic*	3.3	2.15	del Giorgio et al., 1997
Brome	Southern Québec	Eutrophic*	3.4	2.24	del Giorgio et al., 1997
KWK12	*Subarctic Québec*	*Mesotrophic, dystrophic*	*3.5*	*2.34*	*This study*

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Waterloo	Southern Québec	Hypereutrophic*	5.9	3.81	del Giorgio et al., 1997

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8 Figure captions

Figure 1. Map of the study regions and photos of the 6 study areas.

Figure 2. Palsas and their associated thermokarst lakes in the SAS valley. Upper panel: aerial view of the SAS1 area; lower panel ground-level view of SAS1B (photograph by Alexander Culley).

Figure 3. Percent carbon and nitrogen by dry weight in two permafrost cores from SAS palsa mounds, and proportions of gas, ice, and sediment by volume.

Figure 4. CDOM absorbance curve in SAS permafrost soil and lake water.

Figure 5. Distribution of particle sizes in lake water and permafrost soil samples. Insert in the top panel shows the soil sample particle-size distribution for both SAS valleys. The insert in the middle panel shows the particle-size distribution in three SAS lakes: SAS1A, SAS1B, and SAS2A. The bottom panel shows the particle-size distributions from the SAS2 permafrost core samples.

Figure 6. Difference spectra between the frequency distribution of particles in surface lake water (SAS2A) relative to active layer soil, permafrost and bottom lake water.

Figure 7. Size-fractionated total suspended solids (TSS), bacterial abundance (BA), bacterial production (BP), and bacterial cell-specific growth rates (BG) from five thermokarst lakes and one rock-basin lake. Each is the mean ± SD of triplicate samples.

Figure 8. Planktonic variables in the 5-day experiment with amendments of phosphorus (P), glucose (G), glucose plus phosphorus (G+P), and palsa soil (S) to SAS1B lake water. The control (C) is shown on both day 1 and day 5. Each value is the mean ± SD of triplicate samples.

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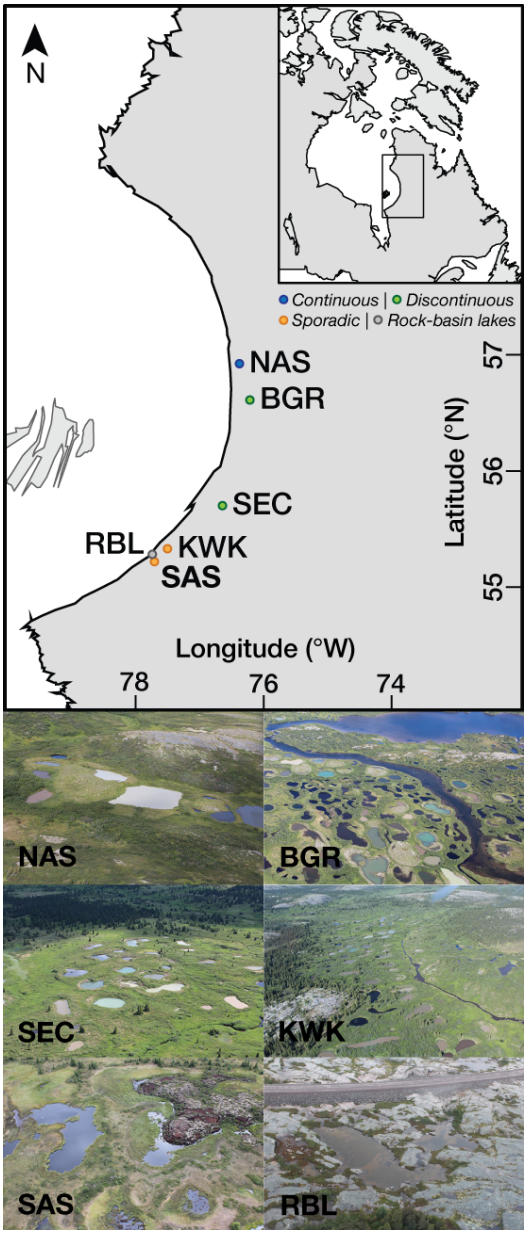
851 Figure 1. Map of the study regions and photos of the 6 study areas.



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856 Culley).

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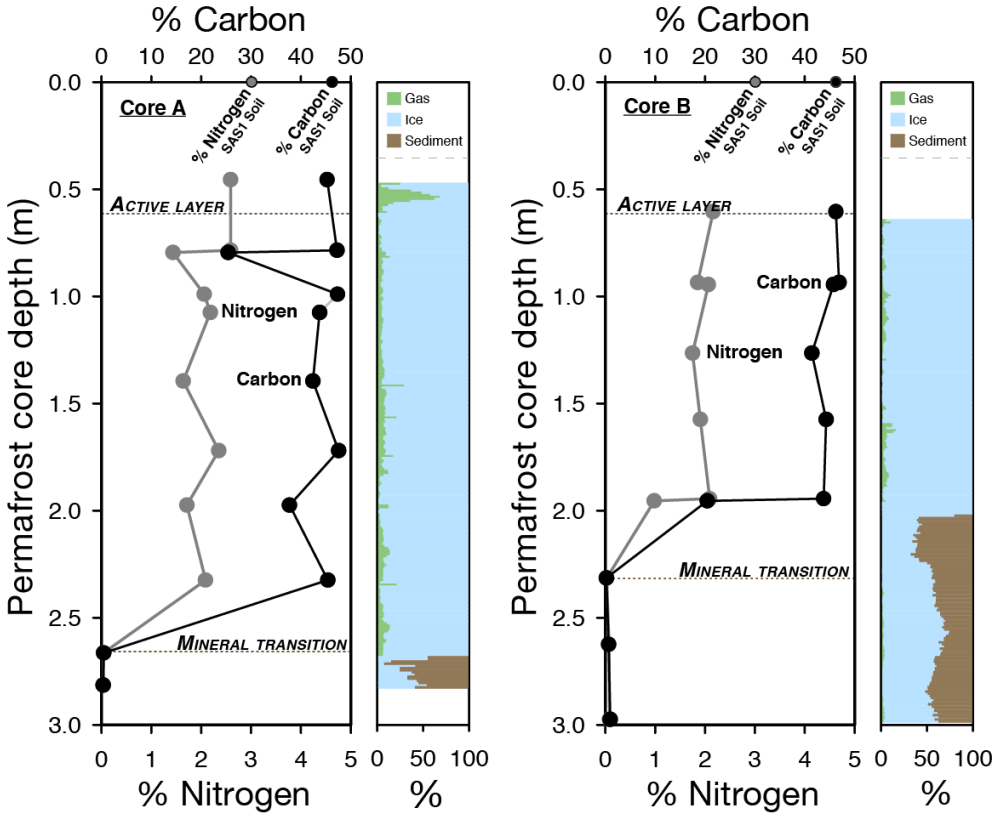

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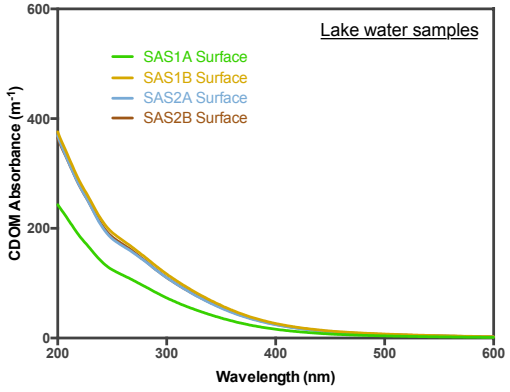
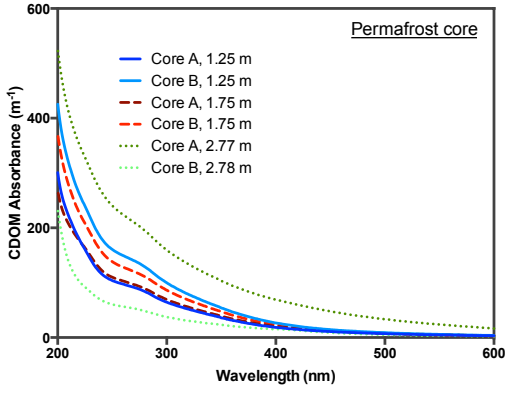
863 Figure 4. CDOM absorbance curve in SAS permafrost soil and lake water.





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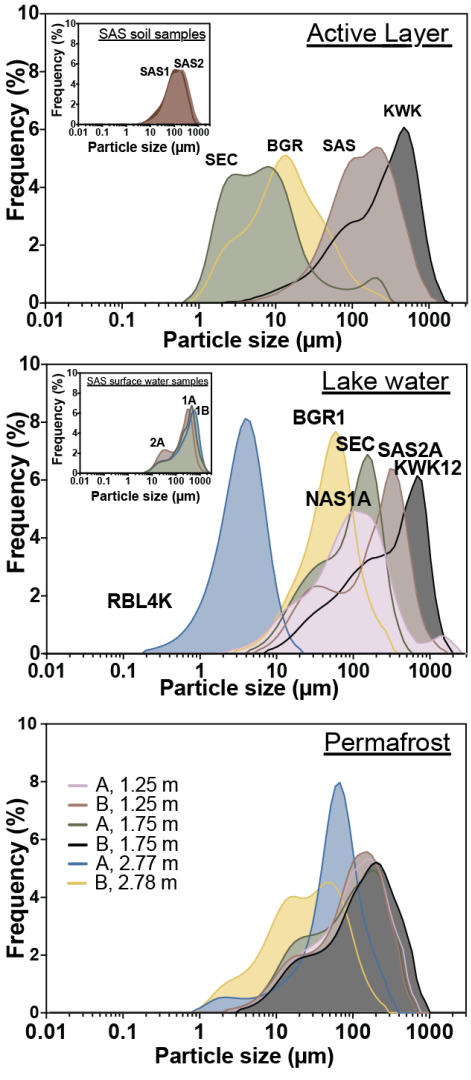
867 panel shows the soil sample particle-size distribution for both SAS valleys. The insert in the
868 middle panel shows the particle-size distribution in three SAS lakes: SAS1A, SAS1B, and
869 SAS2A. The bottom panel shows the particle-size distributions from the SAS2 permafrost core
870 samples.



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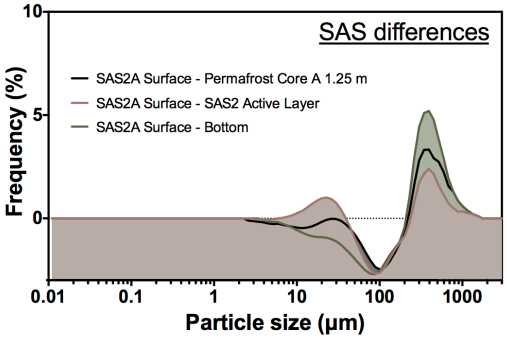
Biogeosciences Discuss., doi:10.5194/bg-2016-32, 2016
Manuscript under review for journal Biogeosciences
Published: 11 February 2016

873 Figure 6. Difference spectra between the frequency distribution of particles in surface lake water

874 (SAS2A) relative to active layer soil, permafrost and bottom lake water.



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Biogeosciences Discuss., doi:10.5194/bg-2016-32, 2016
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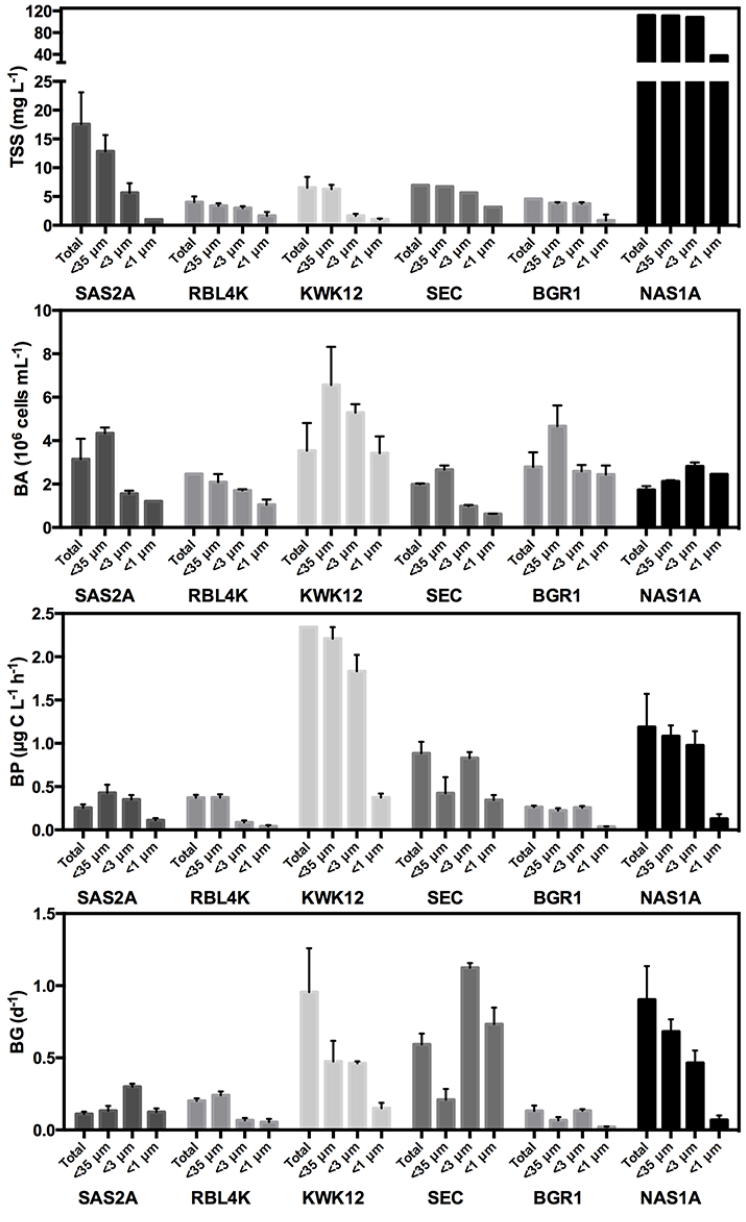
877 Figure 7. Size-fractionated total suspended solids (TSS), bacterial abundance (BA), bacterial
878 production (BP), and bacterial cell-specific growth rates (BG) from five thermokarst lakes and
879 one rock-basin lake. Each is the mean ± SD of triplicate samples.



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Biogeosciences Discuss., doi:10.5194/bg-2016-32, 2016
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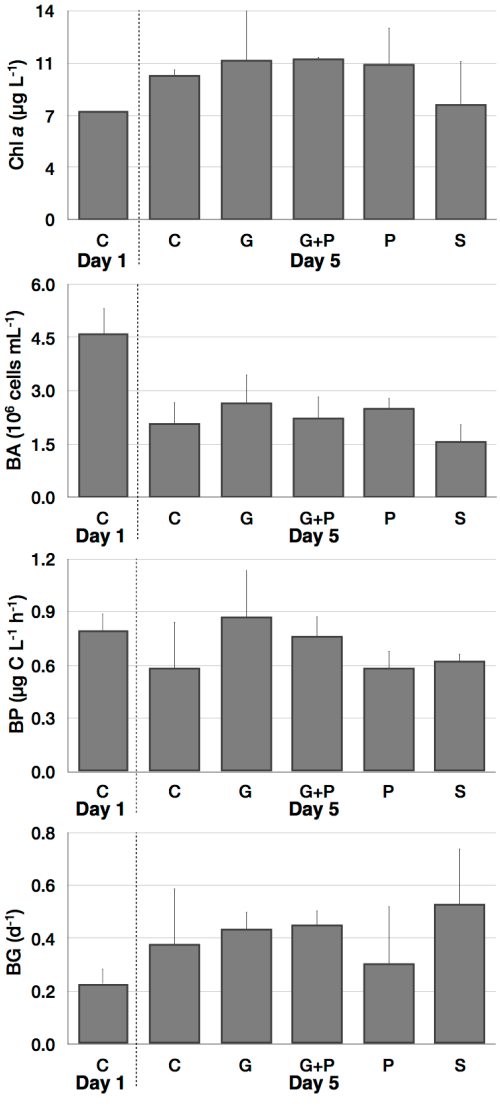
881 Figure 8. Planktonic variables in the 5-day experiment with amendments of phosphorus (P),
882 glucose (G), glucose plus phosphorus (G+P), and palsa soil (S) to SAS1B lake water. The control
883 (C) is shown on both day 1 and day 5. Each value is the mean ± SD of triplicate samples.



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