We thank the editor and the two anonymous reviewers for the thorough review of our manuscript and their many helpful suggestions, which have contributed to improvements of the manuscript. We have carefully considered each comment, and the the manuscript has been revised accordingly. The following list addresses the raised points, describes our view, and explains the changes that have been implemented in the manuscript. Manuscript changes are shown using the track changes function.

Response to editor comments on "Bacterial production in subarctic peatland lakes enriched by thawing permafrost."

In addition, please provide more quantitative information for some of the comparisons discussed in the Results section. For example, on lines 288-289 you mention "The aCDOM(λ) spectra for the DOC from the upper two permafrost core samples were almost identical, but differed greatly from those for the bottom-core samples". Differed by how much? Similar throughout the manuscript. Also, please provide the errors in your measurements (e.g., error in estimates of DOC or S_275295, etc.).

More details have been added to the Results section and errors have been added to Results in some cases, and directly into the Methodology for others.

Response to referees' comments on "Bacterial production in subarctic peatland lakes enriched by thawing permafrost."

Reviewer 1 comments

1) The manuscript would benefit from some clearer statements of goals, questions, and rationale, from the abstract to the end. It reads very much like a descriptive study and somewhat of a list of analyses and results. I think anything you can do to more clearly articulate goals, questions and rationale will improve the impact of your paper.

The aims and goals were clarified in the final paragraph of the introduction and a paragraph was added at the beginning of the discussion to better guide readers through the study objectives, findings and rationale.

2) There is a great deal of data in this paper, which is nice but it makes it a bit hard to follow main points and also seems that much of the data are underused in some cases. You may want to distill some of this down further to improve clarity of presentation. For example, I'm not sure the Fig 4 really illustrates anything key, and Fig 8 has some results that don't really seem to be discussed much. I would suggest trying to highlight the real nuggets, or at least guide the reader more through it.

A paragraph was inserted at the beginning of the discussion to improve clarity. Fig. 4 (now Fig. S1) has been moved to Supplemental Materials, however Fig. 8 (now Fig. 7) is considered to be a highly important experiment discussed within this paper. We have made efforts to better highlight its importance and to guide the reader.

3) I found it very unclear what the lake categories were in the statistics (I understand the location designation, but you allude to SAS versus the other two lake categories). How

were the categories established and why? To address a particular question?

A clarifying sentence was added to the methods to better explain the categories used, and lake categories are now mentioned specifically during presentation of statistical results. We have also made the statistical categories more clear by improving our communication of the study rationale as per the first comment.

4) Main points: I would suggest you try to revise to make these clearer. For example, your final paragraph gets to the really interesting inferences and implications- it would be great to see some of that earlier and better developed.

Sentences were added throughout the discussion to better highlight these points, along with the addition of the paragraph at the beginning of the Discussion (as explained above).

Specific comments: Line 21: define CT Line 34: delete one of the "no" Line 145: remove "," Line 167: should it be ug/L? Line 218: change sub-title to Bacterial abundance to match later terms Line 330: give p-value, and in this section, averages for all categories should be provided, not just for SAS lakes Line 339: can you provide some stratification data? Line 343: change "2and" to "and". Line 389: insert "bacterial" before "cell" Line 407: include "%" to the value of 50.1. Line 488: change "Less 30%" to "Less than 30%". Line 501: change "resulted" to "result" Line 523: may want to be consistent with notation, different in Results, and I think the usage here (all x106) is better Line 529: change "from." to "from" Line 555: include citation after "limitation"

These changes have been made. We thank you for your careful reading and for listing these errors so explicitly.

Table 1: I would suggest switching the order of chemical constituents so that they are organized from highest to lowest, not lowed to highest.

This was changed as per the comment.

Figure 8: the order of the treatments listed in the legend should match the order that they appear in the figure.

This was changed as per the comment.

Reviewer 2 Comments

The authors sample numerous lake and adjacent terrestrial sites, from a series of different geographic regions. Overall, I found it hard to follow the naming conventions used in the manuscript, and found that I often had to flip back and forth with section 2.1, where the site abbreviations were laid out. I would urge the authors to consider a way that they might make their naming conventions more intuitive throughout the manuscript. Simply taking care to always refer to a site as 'peat thermokarst' 'mineral thermokarst' or 'rock basin' (or similar), in addition to the less intuitive abbreviations would be very

helpful.

More references to site types, as described by the reviewer, were added throughout the paper and to figure captions to better facilitate reader understanding, and to better guide readers through the results from the different geographic locations.

In addition, I wondered about the size fractionation results, and the fact that the fractionated samples (particularly at <35 and occasionally <3 microns) often show greater values than the total fraction. Of course, this is a concern, because (unless I am misreading the treatment) the various fractions represent just a subset of the 'total' fraction. The authors do spend a fair bit of time discussing some potential methodological reasons for these results in their Discussion. However, I wonder whether it would be best to limit the presentation of data to the 'total' and < 1 micron fraction, which ends up being the focus of the discussion, anyway. These results are also more intuitive, and seem more sensible overall. Alternatively, perhaps it is the difference in counting methods (flow cytometry vs. microscopy) between the total and fractionated samples that is leading to this offset in results. In any event, I would suggest a re-consideration of the presentation of this data.

The fact that the <35 and <3 micro size-fractions show greater values that the total sample provides support for demonstrating the presence of particle-attached bacterial communities in these lakes. Presentation of the four size fractions adds substantial information and helps to differentiate between lakes across the various subarctic regions.

Finally, I noticed a few typos and grammatical errors in the manuscript.

The manuscript was reviewed carefully and types and gramatical errors were corrected.

Line 29-31: It wasn't clear to me, in the abstract, that you were sampling three lake types – until this point the abstract addresses the peat thaw lakes only. More clarity on this point in the abstract would be helpful.

Reference to other lake types were added earlier in the abstract to clarify the extent of sampling.

Line 33: The enrichment experiment seems to out of nowhere a bit here. Perhaps just changing the wording slightly to say "An in situ experiment . . . relative to a control treatment" would make it clear to the reader that this hadn't been previously introduced in the abstract.

This change was made as per the comment.

Line 85: "marine snow": This is true, but marine snow is not terrestrially derived, and so the carbon quality is likely quite different from what you're investigating. Perhaps re-work the text slightly to reflect the fact that the importance of 'snow' for microbes in marine environments doesn't necessarily suggest that particles (and permafrost- derived particles) will be similarly important in Arctic lakes. A good reason for this study!

A sentence was added to clarify this key difference between marine snow and terrestrially-derived lake snow particles.

Line 134: Six, rather than five sites? Or perhaps I am mis-understanding the site descriptions?

The sites studied include five permafrost regions and one group of reference rock-basin lakes. We count this as a total of six sites. We clarified this within this paragraph, and also added references to the site types throughout the text as suggested by this reviewer to facilitate better understanding of the geographical regions and lake types studied.

Line 140: Two sets of lakes, or two lakes in the SAS valley? If two sets, then perhaps change subsequent wording to read "the SAS1 set of lakes was to the south . . ." or similar.

This sentence refers to two sets of lakes, for a total of 5 SAS lakes studied. This sentence was changed as suggested by the reviewer.

Line 163: 0.2 m? Units are missing here.

Units were added as per the reviewer comment.

Line 168: Could you provide more detail on how the active layer was sampled? A full core to 60 cm? Or was a simple shovel used? Understanding the depth of sampling, and method of sample acquisition would be useful.

More detail was added to the description of active-layer sampling.

Line 172: Define CDOM.

This was changed as per the reviewer comment.

Line 200: It would be useful to have a description of why these depths were chosen, relative to the active layer depth of 60 cm that is stated earlier. Related to this, as I read through parts of the Discussion, I felt it would be useful to have a better understanding of how thermokarst in this regions plays out. For example – how likely is it that soils (or, leachates) from 1.25 – 2.77 m depth are going to be available for transport to nearby lakes with thermokarst in this region? Is it reasonable to expect thaw or slumping to affect soils at this depth?

A sentence describing why these depths were chosen was added to the Methods in this section. The second aspect of this comment, regarding the justification of whether thawing or slumping at this depth and interactions with lake water was added to the discussion, with reference to Fig. 2.

Line 201: Could you provide the soil: water ratio? Was it constant?

No, the soil:water ratio was not constant. Instead, the results have been standardized to account for the differences in thawed volume of the permafrost core sediment and the amount of ultra-pure water that was added to samples. The nutrient and carbon concentrations provided are potential contributions from the melted ice released from the permafrost soil. This detail about the permafrost core nutrient and carbon concentrations will be added to the Methods section of the manuscript.

Line 248: Bacterial community specific growth rates. You're able to calculate a slightly different growth rate here than the more typical (per cell) value that's seen more commonly in the literature, because of the availability of average cellular carbon data. I might specify the units here to clarify that your cell-normalized growth rates are expressed in a slightly different way (d-1), and also state your abbreviation (BG). I also notice that through the text, you sometime refer to this as 'specific growth rates' or 'community growth rates' or 'community specific growth rates'. I think you mean the same thing by all of these? If so, it would be good to standardize the wording, or – better yet! – just consistently use "BG". In addition, provide your BP and BA abbreviations in this paragraph, and use these consistently in the text.

The units will be added and the terms 'specific growth rates', 'community growth rates', and 'community specific growth rates' will be changed to the abbreviated terms as recommended by the reviewer. The same adjustment has been made for BA and BP, as specified by the reviewer.

Line 328-338: Do you use the Mann-Whitney test for all of these comparisons? These look like comparisons between three groups to me, which suggests an ANOVA (or, non-parametric analog) followed by post-hoc comparisons. Is it possible to add these stats to Table 3?

These stats were not added to Table 3 as we prefer to keep the table results separate from our statistical analyses. We clarified the statistical methods that we used an ANOVA and have cleaned-up results slightly to improve reader understanding.

Line 341: "the other thaw lake types". Would "the mineral thaw lakes" be more accurate here?

The other thaw lake types include mineral thaw lakes and also lakes with varying combinations of mineral and peatland inputs. It would be inaccurate to say that all the lakes outside of the SAS peatland valley are mineral lakes. We have not changed the wording of this sentence, but have specific lake type more frequently throughout the manuscript, as recommended above, to clarify the differences between the lakes studied for readers.

Line 339-349: Were there interaction effects for any of these parameters? This might make the interpretation a bit more nuanced. It would be useful to state the presence (or absence) of significant interactions in the analysis, and if significant, provide some interpretation here.

We will add information regarding interaction effects and follow the suggestions

provided by the reviewer.

Line 361-364: I'm unclear on the meaning of this sentence – can it be re-worked for clarity?

Yes – this sentence was broken up for clarity and details were added to explain the two other categories referenced.

Line 422: "A rich potential source" would be more appropriate, given that you haven't measured water flow across this landscape.

This was changed as per the reviewer suggestion.

Line 430: "SAS waters": clarify that you're referring to lake waters here, rather than soil pore waters.

This was added as per the reviewer suggestion.

Line 439: Change "this element" to N, for clarity

This was changed as per the reviewer suggestion.

Line 447-448: The relatively high P could also indicate P enrichment in local rocks / till? This is also suggested by the higher P concentrations that you find at depth.

The sentence was changed to include this possibility as recommended by the reviewer.

Line 459-466: I found that this paragraph could use a bit of extra text to tie these findings from the literature back to your own work.

A sentence was added to better link this with the results of this study as per the reviewer comment.

Line 497 and onwards: These concerns about particle-based bacteria are certainly well-founded. It's worth considering these caveats when thinking about how to best present the fractionation data (as discussed in the overarching comments). I certainly agree with the assertion, however, that particle attachment is important in these systems.

Please see our comments above. We are pleased that the reviewer concurred with our conclusions about the importance particle attachment.

Line 562 – 563: Lakes in this region would be more similar to your mineral thermokarst lakes, I believe.

The reviewer could well be right, but we feel that we do not have sufficient information to reliably make this comparison.

1   Bacterial production in subarctic peatland lakes enriched by thawing permafrost

2

3   Bethany N. Deshpande[1], Sophie Crevecoeur[1], Alex Matveev[1], and Warwick F. Vincent[1]

4

5   [1]Centre for Northern Studies (CEN), Biology Department and Takuvik Joint International

6   Laboratory, Université Laval, Québec, QC, Canada

7   Running title: Bacterial production in thermokarst lakes

8   *Correspondence to:* B. N. Deshpande (bethany.deshpande.1@ulaval.ca)

9

10 **Abstract.** Peatlands extend over vast areas of the northern landscape. Within some of these areas,

11 lakes and ponds are changing in size as a result of permafrost thawing and erosion, resulting in

12 mobilisation of the carbon-rich peatland soils. Our aims in the present study were to characterize

13 the particle, carbon and nutrient regime of a set of thermokarst (thaw) lakes and their adjacent

14 peatland permafrost soils in a rapidly degrading landscape in subarctic Québec, Canada, and by

15 way of fluorescence microscopy, flow cytometry, production measurements and an in situ

16 enrichment experiment, determine the bacterial characteristics of these waters relative to other

17 thaw lakes in more mineral terrain and to non-permafrost-affected rock-basin lakes in the region.

18 The soil active layer in a degrading palsa (peatland permafrost mound) adjacent to one of the

19 lakes contained an elevated carbon content (51% of dry weight), low C:N ratios (17:1 by mass),

20 and large stocks of other elements including N (3% of dry weight), Fe (0.6%), S (0.5%), Ca

21 (0.5%) and P (0.05%). Two permafrost cores were obtained to a depth of 2.77 m in the palsa, and

22 computerized tomography CT scans of the cores confirmed that they contained high

23 concentrations (>80%) of ice. Upon thawing, the cores released nitrate and dissolved organic

24 carbon (from all core depths sampled), and soluble reactive phosphorus (from bottom depths), at

25 concentrations well above those in the adjacent lake waters. The active layer soil showed a range

26 of particle sizes with a peak at 229 μm, and this was similar to the distribution of particles in the

27 upper permafrost cores. The particle spectrum for the lake water overlapped with those for the

28 soil, but extended to larger (surface water) or finer (bottom water) particles. On average, more

29 than 50% of the bacterial cells and bacterial production was associated with particles >3 μm. This

30 relatively low contribution of free-living cells (operationally defined as the <1 μm fraction) to

31 bacterial production was a general feature of all of the northern lakes sampled, including other

32 thaw lakes and shallow rock-basin lakes (average $\pm$ SE of 25 $\pm$ 6%). However, a distinguishing

33   feature of the peatland thaw lakes was significantly higher bacterial specific growth rates, which

34   averaged 4 to 7 times higher values than in the other lake types. ~~The~~ An in situ enrichment

35   experiment showed no difference between organic carbon or phosphorus enrichment treatments

36   at day 5 relative to ~~the~~ a control treatment, however there was a significant, >100% increase in

37   bacterial growth rates between days 1 and 5 in the soil and the carbon plus phosphorus

38   enrichments. Collectively these results indicate that particles, nutrients and carbon are released by

39   degrading permafrost peatland soils into their associated thermokarst lakes, creating favorable

40   conditions for production by particle-based as well as free-living aquatic bacterial communities.

41   The reduced bacterial concentrations despite high cellular growth rates imply that there is strong

42   control of their population size by loss-related factors such as grazing and viral lysis.

43

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

45

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-

69   based bacteria play a major role. Several studies from estuarine- and marine-waters show that

70   particle-attached populations can account for 10 to 100 times more bacterial cells and activity

71   than free-living bacteria, depending on particle concentrations (Crump et al., 1999; Ghiglione et

72   al., 2007; Acinas et al., 1999; Lami et al., 2009). A study of seven freshwater ecosystems

73   including two marsh-systems showed that a small proportion of particle-attached bacteria (<10%)

74   was associated with >40% of the bacterial community activity, and it was hypothesized that lake

75   size may influence the presence of particulate matter for colonization via interactions between

76   sediments and the water column (Kirchman and Mitchell, 1982). In the turbid waters of the

77   Mackenzie River, which are strongly influenced by permafrost as well as fluvial erosion, more

78   than 90% of the total bacterial production was associated with particles >3 μm (Vallières et al.,

79   2008). Similarly, in the coastal waters of the Beaufort Sea, the >3 μm size-fraction often

80   accounted for >50% of total bacterial production (Garneau et al., 2006; Galand et al., 2008).

81   Other research has identified that a dominant portion (>50%) of bacterial cells were attached to

82   particles (Masin et al., 2012), especially in turbid systems with high concentrations of particulate

83   organic matter (Fletcher 1991; Lami et al., 2009).

84   Particle localisation of microbial processes has wide-ranging implications for trophic

85   processes in the water column and material fluxes to the sediments. In the oceanographic

86   literature, large particles are referred to as "marine snow", and many studies that have shown the

87   importance of these aggregates for food-web dynamics (Michaels and Silver, 1988; Alldredge

88   and Silver, 1988; Kiørboe, 2001). Similarly, there has been attention given to "lake snow",

89   although lake particulate matter is likely to be more of terrestrial origin, and therefore of

90   different chemical composition than marine snow. Grossart and Simon

91   (1993) found lake particle aggregates to be densely colonized by bacteria, with approximately

5

92 10^8 bacterial cells per mL, 100 times higher than concentrations in the bulk water. The presence

93 of particle-attached bacteria may also result in greater community diversity, as has been

94 demonstrated in studies of estuarine mixing zones (Crump et al., 1998; Waidner and Kirchman,

95 2007). A study by Ploug and Grossart (2000) identified a positive correlation between bacterial

96 production, particulate organic carbon and aggregate size. Size also affects sinking velocities

97 through Stokes' Law, and therefore the flux rates for transfer of materials from the pelagic zone

98 to the sediments (Ploug and Grossart, 2000).

99 Permafrost thaw lakes are rich in suspended particulate material as a result of permafrost

100 erosion (Breton et al., 2009; Watanabe et al., 2011). They are also continuously supplied with

101 organic as well as inorganic inputs from the thermokarst processes in their surrounding

102 catchments (Vonk et al., 2015), and there is increasing attention to the bacterial responses to such

103 inputs. In the Mackenzie River Delta region, a mesocosm assay showed decreased planktonic

104 bacterial production rates in response to permafrost soil enrichment, but a strong increase in

105 benthic bacterial production rates (Moquin and Wrona, 2014). In a set of subarctic thermokarst

106 ponds, late winter bacterial production was low and dominated by free-living bacterioplankton,

107 while much higher production rates in summer were dominated by particle-attached bacteria,

108 correlated with terrestrial carbon concentrations (Roiha et al., 2015). Permafrost peatland lakes

109 are known to be strong emitters of greenhouse gases with diverse microbiota (Liebner et al.,

110 2015), but little is known about the controls on their bacterial populations and productivity.

111 Our first aims in the present study were was to investigate the physical and geochemical

112 properties of permafrost peatland soils in order to better understand the allochthonous carbon,

113 nutrient and particle inputs interactions occurring between landscape level organic material,

114 bacterial communities, with to peatland thermokarst lakes and their potential effects on

6

115 ~~considered as sites for the associated biological~~bacterial activit~~yies. More specifically, we aimed~~

116 ~~to determine physical properties along with carbon and nutrient concentrations within permafrost~~

117 ~~peatland cores,~~Secondly, we aimed to determine the distribution of bacterial production between

118 the suspended and free-living size fractions in ~~subarctic~~ in these peatland lakes enriched with

119 particles from eroding permafrost. Our final aim was to~~, and lastly to investigate~~ experimentally

120 determine ~~their~~ the responses of peatland lake bacteria~~l communities~~ to permafrost soil inputs.

121 Two hypotheses were evaluated: firstly, that particle-attached bacteria account for the dominant

122 (>50%) fraction of the total microbial activity, and secondly that organic carbon and nutrients

123 originating from the erosion of permafrost soils promote bacterial metabolic activity and cellular

124 growth. We ~~focused~~ undertook this research ~~on a set of peatland lakes~~ in subarctic Québec and

125 first determined the chemical composition of the soil active layer and underlying permafrost in a

126 palsa (organic permafrost mound) that was adjacent to and eroding into a ~~one of the p~~peatland

127 thaw lake~~s~~. We examined the distribution of soil particle sizes and compared these with particle

128 distributions in permafrost peatland lakes, with comparisons of particle size spectra, nutrients and

129 organic carbon with other types of lakes in the region. We then measured bacterial abundance

130 (BA) and production rates (BP) associated with different size fractions in the peatland lakes and

131 other ~~s~~lakes, and tested the effects of phosphorus, carbon and soil enrichment on bacterial

132 concentrations and activity by way of an in situ incubation experiment.

2   Materials and methods

2.1   Study sites

135 The primary sampling sites were near Kuujjuarapik-Whapmagoostui (K-W, 55° 17' N, 77° 47'

136 W) in thermokarst lakes and their surrounding soils in the peatland palsa valley of the

7

137   Sasapimakwananistikw River (SAS; Fig. 1). Additional sampling for comparison took place in

138   thermokarst lakes in the mineral lithalsa (mineral permafrost mounds) valley of the

139   Kwakwatanikapistikw River (KWK) near K-W; glaciated rock-basin lakes, also near K-W, but

140   not influenced by permafrost (RBL); and lithalsa lakes up to 200 km further to the North (SEC,

141   BGR, NAS). This coastal region of northern Québec has experienced rapid climate change,

142   including an increase in mean annual temperatures from –4.2 °C for 1932–1960 to –2.6 ± 1.2°C

143   for 2001-2010, accompanied by changes in the permafrost landscapes, including expansion of the

144   tree line, changes to snow conditions, and various changes in thermokarst lakes frequency and

145   extent (Bhiry et al., 2011). A total of 15 lakes were sampled at five permafrost-affected the five

146   sites and one non-permafrost-affected area (Fig. 1; detailed location and depth information is

147   given in Table S1 in the Supplement).

148   The SAS valley is an area of sporadic permafrost (<2% frozen ground) mainly colonized

149   by *Sphagnum* and *Carex*, with dark brown and black colored thermokarst lakes (Arlen-Pouliot

150   and Bhiry, 2005; Fillion et al., 2014). This peat bog contains more than 50 isolated permafrost

151   mounds (palsas; Fig. 2) covered by a 60 cm soil active layer (Arlen-Pouliot and Bhiry, 2005;

152   Fillion et al., 2014). Two sets of lakes were sampled in the SAS valley: the SAS1 set of lakes was

153   located to the south and the SAS2 lakes were located to the north of the river. The SAS lakes are

154   stratified, heterotrophic lakes with anoxic zones throughout the majority of the water column, and

155   surface waters that are under-saturated in oxygen (Deshpande et al., 2015). These lakes have

156   abundant and active methanotrophic bacterial communities indicating their high methane supply

157   rates (Crevecoeur et al., 2015), and they, emit greenhouse gases to the atmosphere at flux rates

158   up to 10 13 mmol CH_4 m^{-2} d^{-1} and >200 240 mmol CO_2 m^{-2} d^{-1} (A. Matveev et al., unpublished

159   2016).

8

160   The valley of the Kwakwatanikapistikw River (KWK) is also in an area of sporadic

161   permafrost, located only 8 km from SAS. It is colonized by lichen-moss, shrub-tundra vegetation,

162   and forest patches in wind-sheltered areas (Arlen-Pouliot and Bhiry, 2005), and contains

163   numerous thermokarst lakes that vary in color from blue-green to brown. The SEC site (55°

164   42.067' N, 76° 38.604' W) was located 86.0 km north-east of K-W and the BGR site was located

165   near the Hudson Bay and the village of Umijuaq (56° 36.63' N, 76° 12.85' W), both in areas of

166   discontinuous permafrost. BGR1 appears to be a rapidly expanding lake, with a maximum depth

167   of 3.2 in 2006 (Breton et al., 2009) that had increased to 4.0 m in 2013 (Deshpande et al., 2015),

168   and 4.2 m in the present study. The Nastapoka River valley (NAS) contains thermokarst lakes

169   that were formed by thawing lithalsa mounds in this region of continuous permafrost. The non-

170   permafrost-affected, rock-basin lakes (RBL) in the K-W region are of similar area and shallow

171   depth (0.8 – 2.1 m) to the thermokarst systems, but with rock substrate catchments rather than

172   permafrost soils.

173   **2.2   Lake sampling and profiling**

174   Sampling took place during three consecutive summers from 2012 to 2014. At each visit, surface

175   water was sampled using sterile plastic containers. A Van Dorn sampler was used to retrieve

176   samples from the oxycline or the bottom waters, 0.2 m above the bottom sediments. Water

177   samples were analysed for soluble reactive phosphorus (SRP; detection limit of 0.5 µg P L^{-1}),

178   total nitrogen (TN; detection limit of 0.008 mg N L^{-1}), dissolved organic carbon (DOC; detection

179   limit of 0.05 mg DOC L^{-1}), Chlorophyll *a* (Chl *a*), and total suspended solids (TSS) according to

180   methods in Laurion et al., (2010). Ammonium and nitrate (including nitrite) concentrations were

181   measured in water from the SAS valley only using a Lachat autoanalyzer (detection limit of 10

182   µg N L^{-1}). Soil was sampled from the active layer directly next to a lake at each site and stored in

9

183 sterile plastic bags. Frozen samples of both water and soils were returned to Université Laval

184 (Laboratoire de géomorphologie et de sédimentologie, FFGG) to determine particle size

185 distribution via Laser Particle Size Analyzer (LA-950V2, Horiba Ltd., Japan).

186 For CDOM (colored dissolved organic matter) analysis, water samples from the surface

187 waters of the SAS lakes were filtered through sample-rinsed 0.47 mm, 0.2 μm pore size cellulose

188 acetate membrane filters and the filtrate was analyzed with the Varian Cary 100 UV-VIS

189 spectrophotometer. The absorbance scans were obtained from the spectrophotometer over the

190 wavelength range of 200-850 nm at natural pH using a 1-cm acid-cleaned quartz cuvette on dual

191 beam mode, at a speed of 240 nm min^{-1} with a slit width of 1 nm. The absorbance was measured

192 against ultra-pure water and corrected against the blanks prepared on site. Absorption coefficients

193 were calculated as $a(\lambda) = 2.303 \times A(\lambda)/L$, where $a(\lambda)$ is the absorption coefficient at a wavelength

194 λ, $A(\lambda)$ is the optical density (absorbance) for wavelength λ, and L is the path length of the

195 cuvette (m). Spectral slope parameters were also determined from absorbance at 275nm (a_{275})

196 and 295 nm (a_{295}) using the formula $a_{295} = a_{275}e^{-S(295-275)}$, where S (nm^{-1}) is the spectral slope

197 parameter (Fichot and Benner, 2012).

198 **2.3   Active layer and permafrost core sampling**

199 Triplicate soil samples were retrieved from the surface active layer of a palsa adjacent to

200 lake SAS1B on 3 August 2013; the soil was sampled from half way up the face of the palsa

201 (approximately 1 m above the lake surface) that was eroding and collapsing into the lake by

202 pushing tubes with an internal diameter of 6.0 cm and a length of 20 cm horizontally into the

203 palsa (Fig. 2). Subsamples were frozen and transported to Québec City for CHN (LECO

204 analyzer, CEN, Québec) and other geochemical analyses (ICP-AES; INRS-ETE, Québec).

10

205   Enrichment Factors (EF) for the soil samples were determined as per Gorham and Janssens
206   (2005):

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

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

211   Permafrost cores were sampled from two sites 15 m apart on large an organic-rich palsa
212   mound at the SAS2 site (Fig. 1) on 5 August 2013 using a portable drill system (Calmels et al.,
213   2005). For permafrost core sampling, a soil pit was dug into the palsa throughoutto the base of
214   the active layer. The permafrost cores were then retreivedretrieved using a portable drill system
215   (Calmels et al., 2005). The recovered cores were 10-cm in diameter, with lengths of 2.8 and 3.0
216   m. Samples were returned to the Centre for Northern Studies (Université Laval, Québec) and
217   maintained frozen. The frozen core was characterized by computerized tomography (CT)
218   scanning (Calmels and Allard, 2004) and later subsampled. Subsamples were 1.5-cm thick and
219   centered at depths of 1.25, 1.75, and 2.77 m from each of the two permafrost cores. Sample
220   depths were chosen to span the full-length of the permafrost core, and based on CT-scan results.
221   Each sub-sample was placed in a sterilized container filled with ultrapure Milli-Q water and
222   thawed for a period of 48-hours. Samples were then lightly shaken and then filtered through 0.47-
223   mm, 0.2-µm pore size cellulose acetate membrane filter. The filtrate and a blank (Milli-Q water)
224   were analysed for DOC, NO_3^- (including NO_2^-) and SRP (INRS-ETE, Québec). DOC was
225   analyzed using a Shimadzu 5000A TOC Analyzer (detection limits of 0.05 mg C L^{-1}). SRP and

226 NO_3^- were analyzed using a Lachat autoanalyzer (detection limit of 1 µg N and P L^{-1}). DOC,

227 SRP, and NO_3^- concentrations were normalized ~~as~~ to per ~~the~~unit volume of ice in the sample, to

228 determine the potential contributions from melted ~~core~~ ice. CDOM was analyzed as described

229 above. Unfiltered diluted samples were analyzed for particle-size distribution as described above.

230 Additional subsamples from throughout the core were analysed for total CHN content (LECO

231 analyzer, CEN).

2.4 Size-fractionation

233 Surface water was sampled from the pelagic zones of lakes BGR1, SEC, KWK12, SAS2A,

234 NAS1A and RBL4K for size fractionation. Phytoplankton and particle-attached bacterial

235 communities were filtered through a 35-µm Nitex screen. The bacteria were then further

236 separated into two size fractions: either by passing through a glass fibre filter (Pall Canada Ltd.)

237 with a nominal pore size of 3.0 µm, or by further filtration through a Whatman GF/B glass fibre

238 filter with a nominal pore size of 1.0 µm. Approximately 2.0 L was filtered for each size fraction,

239 and an unfiltered total community sample was also preserved for concurrent analysis.

2.5 Bacterial ~~community counts~~abundance

241 The bacterial communities in the size-fractionated samples were counted after staining with 4',6-

242 diamidino-2-phenylindole (DAPI). Samples were preserved with formaldehyde (3.7% final

243 concentration) in pre-washed plastic bottles, pre-rinsed with the sample and stored at 4°C for up

244 to 6 months. Samples were later shaken to break up larger particles and then filtered onto

245 Nuclepore black polycarbonate membranes (0.22 µm, 25 mm) placed on cellulose acetate

246 backing filters (0.7 µm, 25 mm) under low pressure. DAPI was added to 1.5 mL of sample (4 µg

247 mL^{-1} final concentration) and left to stain for 10 min before filtering until dry. Filters were

248 mounted on slides with coverslips and non-fluorescent immersion oil, and stored at -20°C until

249 counting on a Zeiss Axioskip 2 epifluorescence microscope, under UV light and 1000×

250 magnification with immersion oil. A minimum of 15 fields or 400 cells were counted of each

251 sample triplicate.

252   All other bacterial samples were counted via flow cytometer (FACSCalibur, BD

253 Biosciences Inc., USA) following the procedure described in Comte et al. (2016). Samples were

254 fixed with glutaraldehyde (1% final concentration) and stored at -80°C until analysis. Bacterial

255 samples were then shaken and a 500 μL aliquot was stained with the nucleic acid dye 50X SYBR

256 Green I (20 μL mL^{-1} final concentration; Life Technologies, Thermo Fisher Scientific, Waltham

257 MA, USA) for 10 min in the dark, and processed at the lowest flow rate (12 μL min^{-1}) using 1 μm

258 yellow-green microspheres (Polysciences Inc., Warrington PA, USA) solution as an internal

259 standard. Bacterial cells were enumerated based on fluorescence (FL1) and side-scatter

260 characteristics while excited at 488 nm, with data analyzed using the CellQuest Pro software with

261 manual gating.

262 **2.6   Bacterial production**

263 Bacterial production (BP) rates were measured via protein synthesis using radio-labelled leucine

264 incorporation (Kirchman, 2001). Triplicate microfuge tubes plus a killed control each containing

265 1.5 mL of sample and 40 nM of [4,5-^{3}H]leucine (60 Ci mmol^{-1}, PerkinElmer Inc.) were incubated

266 for 1 h at 15°C. After one hour, biomass production was halted by the addition of 100 μL of

267 trichloroacetic acid (100%) and stored at 4°C. Later, the samples were returned to the Takuvik

268 radio-isotope laboratory at Université Laval. Samples were processed using the centrifugation

269 method of Smith and Azam (1992) and then radio-assayed in a scintillation counter to measure

270 the ^{3}H-leucine uptake. Net bacterial C production was estimated using a conversion factor of 3.1

13

271   kg C per mole of leucine (Kirchman et al., 1993; Iriberri et al., 1990). Bacterial community

272   specific growth rates (BG, d^{-1}) were determined (as described in Kirchman 2001) via BG = BP/B,

273   where BP are bacterial production rates (μg C L^{-1} h^{-1}), and B is the bacterial biomass (fg C mL^{-1})

274   that was converted from bacterial cellular counts (cells mL^{-1}) to units of carbon using an average

275   cellular carbon content of 18 fg C $cell^{-1}$, as measured in the nearby KWK lakes (Roiha et al.,

276   2015).

277   **2.7   Enrichment experiment**

278   At lake SAS1B, the following treatments were added to triplicate 20 L containers of lake water:

279   43 μmol L^{-1} of glucose (G; to achieve an estimated 20% increase of ambient DOC based on

280   previous measurements), 1.8 μg L^{-1} of phosphorus (P; 10% enrichment of total P), glucose and

281   phosphorus together (G+P), and 6.2 mg L^{-1} of an aqueous suspension of the soil from the SAS1B

282   palsa face, sampled and analyzed as described above (S; equivalent to 20% increase in total

283   carbon relative to ambient DOC). A sample control was also prepared (C). Samples were taken

284   immediately after enrichment (t_0), and from each container after 5 days (t_5) of incubation in situ

285   in the near-surface waters of SAS1B. Chl *a*, ~~bacterial concentrations~~BA and ~~bacterial~~

286   ~~production~~BP rates were measured in each treatment.

287   **2.8   Statistical analysis**

288   Statistical differences were examined between the SAS peatland lakes and the other study lakes.

289   Environmental and bacterial variables for the comparison of lake waters were analysed by 1-way

290   ANOVA for three lake groups: the SAS lakes, the other thermokarst lakes, and the non-

291   thermokarst rock-basin lakes. A 2-way ANOVA was used to compare environmental and

292   biological differences between surface and bottom waters of ~~the various lake types~~the lake groups

293 mentioned above. For the size-fractionation data, a 2-way ANOVA was performed on pre-

294 standardized variables, with the factors of lake and size-fraction following the Shapiro normality

295 test. The enrichment experiment was analyzed via 2-factor repeated measures ANOVA, with

296 each replicate individually tracked. Variables before and after enrichment were also compared via

297 Holm-Sidak pairwise comparisons. ~~Bacterial community growth rates~~BG were normalized by

298 square route transformation, and ~~bacterial abundance~~BA was log transformed. Analyses were

299 done using GraphPad Prism (v. 6.0f, GraphPad Software Inc., USA) and SigmaPlot (v. 12, Systat

300 Software Inc., USA).

301 **3 Results**

302 **3.1 Active layer soil analyses**

303 The SAS active layer extended to 60 cm depth and contained 509 g kg^{-1} of carbon, or 50.9% of

304 the soil by mass, and 30 g kg^{-1} of nitrogen (Table 1). Several elements were present in substantial

305 concentrations, including phosphorus at a mean value ($\pm$SD) of 545 (19) mg kg^{-1}, iron at 6.0 (1.6)

306 g kg^{-1}, and calcium at 5.2 (3.4) mg kg^{-1}. The soil enrichment factors (EF) were used to compare

307 concentrations of soil elements with world medians (Bowen, 1979) to determine whether the

308 elements were derived uniquely from wind-blown mineral soil (EF $\leq$1), or were more likely to

309 accumulate due to multiple sources (EF $>>$1) (Gorham and Janssens, 2005). Several elements had

310 EF values <1, including K, Na, and Mg. For Al, Mn, Pb, Cr, Zn, and Ba, the EF values were

311 between 1 and 2. Phosphorus had an EF of 16, and S had the highest EF value of 132.

312 **3.2 Permafrost core analysis and comparison with lake water**

313 The frozen permafrost cores were composed mainly of organic matter intercalated with ice

314 (>80%) in the two upper levels, with high concentrations of sediment only in the deepest level at

15

315 ~2.77 m (Table 2). The soils throughout the core released water containing nitrate and high

316 concentrations of DOC, and the sediment-containing matter near the bottom of the cores

317 additionally released SRP at concentrations up to 30 times those measured in the SAS lakes.

318   The $a_{CDOM}(\lambda)$ spectra for the DOC from the upper two permafrost core samples were

319 almost identical, but differed ~~greatly~~ as much as 185 m^{-1} from those for the bottom-core samples

320 (Fig. S14). Mean v~~V~~alues (±SD) of $a_{CDOM}(440)$ ranged from 9.96±0.28 to 16.2±0.18 m^{-1} in all

321 permafrost core samples except the bottom of core A, which was 51.5±0.4~~0~~ m^{-1}. The spectral

322 slope parameter ($S_{275-295}$) ranged from 0.0087 to 0.014 nm^{-1} in the permafrost cores (mean for all

323 values of ~~x.xxxx~~0.0012±~~xx~~0.0018). For SAS lake water samples, $a_{CDOM}(\lambda)$ spectra were similar

324 to those observed from the permafrost core samples (Fig. S14)~~;.~~ $a_{CDOM}(440)$ ranged from

325 8.63±0.051 to 18.1±0.068 m^{-1}, and was consistently higher in bottom waters than in surface.

326 Spectral slope parameters ($S_{275-295}$) for the SAS water were within a notably smaller range than

327 for the permafrost cores, and ranged from 0.011 to 0.012 nm^{-1} (mean for all values of

328 ~~x.xxxx~~0.0115±0.0004~~xx~~)~~.~~.

3.3   Particle size distribution in soils and lakes

330 The particle-size distributions from the SAS permafrost cores followed a bimodal distribution as

331 observed in the SAS active layer soil and the SAS lake water (Fig. 4~~5~~). The maximum frequency

332 of particle size (PSmax) ranged from 152 to 200 μm for the permafrost layers at 1.25 and 1.75 m

333 for both duplicates. The bottom layer of core A had a distribution maximum of 67 μm while the

334 maximum for core B was 51 μm. The active layer soil was similar to the distribution of particles

335 in the upper permafrost cores, but with a maximum frequency at a slightly higher size (229 μm),

336 and an even distribution of particles from 80 to 300 μm. The particle spectrum for the SAS lake

337 water overlapped with those for the soil, but the surface water spectrum extended to higher sizes

16

and peaked at 394 µm, while the bottom water spectrum peaked at 200 µm and extended to finer particles (Fig 45).

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. 56). These curves also illustrate how the surface water was slightly enriched in larger particles that ranged from 229 to 2010 µm in diameter, while the bottom waters were enriched in finer particles that ranged from 39 to 200 µm.

Within-lake particle sizes showed highly variable distributions across the other lakes studied, with modes that ranged from 4 to 1337 µm (Table 3; Fig. 45). The smallest particles were identified in RBL4K, a rock-basin lake unaffected by permafrost, with a mode particle size of 4 µm. Of the thaw lakes, the lakes from areas of sporadic, degrading permafrost had larger particles than the continuous- and discontinuous-permafrost lakes. For example, the mode particle sizes in NAS1A, BGR1, and SEC were 102, 59, and 153 µm, respectively. In contrast, the particle-size modes in SAS2A and KWK12 were 300 µm and 592 µm, respectively.

The concordance of particle distributions between the lake waters and their adjacent soils varied among the other sample sites (Fig. 45). For example, the distribution of particles in KWK12 was strikingly similar to that of KWK active layer soil, while other lake samples tended to have modes than were higher than the mode observed in the soil, as in SAS. For example, the mode for BGR lake water was 59 µm, but 10 µm for the adjacent mineral soil. As at SAS, the distribution of soil and lake water particles at SEC was bimodal, and the particles encompassed a much wider range in soil than in the lakes.

17

3.4 Lake properties

The SAS lake surface waters differed significantly in their limnological properties from those of other thaw lakes and also from the rock-basin lakes (Table 3; 1-way ANOVA). The SAS lakes had a mean (±SD) surface DOC value of 11.5 ± 2.4 mg L^{-1}, that was significantly higher than the two other lake categories (p < 0.001) (Mann Whitney test, $p = 0.004$), with an average of 4.08 ± 1.4 mg L^{-1} for the other thermokarst lakes, and 10.6 ± 3.1 mg L^{-1} for the rock-basin lakes. The average surface Chl *a* concentration of 2.29 µg L^{-1} was also significantly higher for the SAS lakes (mean±SD = 2.29 ± 1.09 µg L^{-1}) relative to the other categories (other thermokarst lakes mean = 0.897 ± 0.43 µg L^{-1}; rock-basin lakes mean = 1.39 ± 0.50 µg L^{-1}; $p = 0.03$), as was surface TN, which averaged (±SD) 0.58 ± 0.10 mg L^{-1} in the SAS lakes, and 0.30 ± 0.08 and 0.61 ± 0.20 mg L^{-1} in each of the other two categories, respectively ($p \leq 0.0104$). TSS and maximum particle size (PSmax) values were variable within each lake type (Table 3), with no significant differences; the surface PSmax values were strikingly variable in rock-basin lakes, ranging over three orders of magnitude, but much more homogeneous among the SAS waters (mean of 384 µm with a CV of 37%).

The SAS lakes were well stratified and dDespite their shallow depths, the SAS lakes showed substantial differences between the top and bottom of the water column, which was also a feature of the other thaw lakes (Table 3). A two-way ANOVA for depth and the two thaw lake types (SAS versus the other thaw lakes) showed that overall there were significant increases at depth in SRP ($F = 23$; $p = 0.03$); TN ($F = 18$; $p = 0.02$) and Chl *a* ($F = 28$; $p = 0.03$), with no significant ($p > 0.05$) top-bottom differences in DOC, TSS or PSmax. Consistent with the 1-way analysis for all three lake types, this 2-way analysis (both depths) showed that SAS lakes had significantly higher concentrations of DOC ($F = 65$; $p < 0.0001$) and TN ($F = 32$; $p = 0.004$)

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383 relative to other thaw lakes. However, the SAS lakes had significantly lower concentrations of

384 TSS ($F = 23$; $p = 0.05$), which were especially high in NAS1A and BGR2, and there were no

385 significant differences ($p > 0.05$) between the two groups of thaw lakes in terms of SRP, Chl *a* or

386 PSmax.

387 Ammonium and nitrate were not analyzed routinely, but the surface waters of the SAS

388 lakes sampled during late June 2014 contained undetectable concentrations of nitrate (<10 µg N

389 L^{-1}) and substantial concentrations of ammonium: 64 (SAS1A), 58 (SAS1B), 49 (SAS2A), 60

390 (SAS2B) and 74 (SAS2C) µg NH_4^+-N L^{-1}. Much higher values were recorded in the anoxic

391 bottom waters of two of the lakes: 1021 (SAS1A) and 178 (SAS1B) µg NH_4^+-N L^{-1}, but values

392 were similar to surface waters in SAS2A (48 µg NH_4^+-N L^{-1}).

3.5 Bacterial abundance and productivity

394 ~~Bacterial abundance~~BA in the surface waters varied over an order of magnitude among SAS

395 lakes, from 0.2~~2.0 × 10~~^{5} to 3.1×10^6 cells mL^{-1}, and did not significantly differ from the other

396 lake types (Table 4; p >0.05). ~~Bacterial production~~BP rates varied by a factor of six among SAS

397 lakes, from 0.25 to 1.68 µg C L^{-1} h^{-1}, and as for cell concentration, there were no significant

398 differences among the categories of lakes. ~~Bacterial cellular growth rates~~BG were similarly

399 variable, ranging from 1.9 to 113 fg $cell^{-1}$ d^{-1}~~.; however f~~Four of the five ~~surface~~ values from SAS

400 surface waters were well above (factor of two or greater) any of the thermokarst or rock-basin

401 lakes ~~in~~ of the two other ~~lake~~ categories. ~~, and t~~Overall, the mean value for SAS waters was

402 significantly higher than the others ($F = 5.0$; $p = 0.026$).

3.6   Size-fractionated solids and associated bacteria

In SAS2A, the mass of suspended solids decreased sharply with filter size, and the <1 µm fraction contained only 5% of the total value (Fig. 67). Similar trends were observed in the other lakes, with the exception of NAS1A where almost all of the suspended solids passed through the 35 and 3 µm filters, and 34% even passed through the 1 µm filter. In terms of bacterial cells, highest counts were in the total or <35 µm fraction, with the exception of NAS1A, which peaked in the <3 µm fraction. Only 28% of the maximum counts occurred in the <1 µm fraction in SAS2A samples, and this fraction was similarly low in SEC (23%). Higher percentages of maximum occurred in the <1 µm fraction in RBL4K (43%), KWK12 (52%), BGR1 (52%) and NAS1A (87%).

The ~~bacterial production~~BP data showed a more striking pattern (Fig. 67). Total production was maximal in the unfiltered (total) or <35 µm fraction, but the <1 µm fraction accounted for only 26% of the maximum in SAS2A, and was even lower in most of the other lakes: 11% (NAS1A), 11% (RBL4K), 16% (KWK12), and 14% (BGR1). An average value of 39% was recorded in SEC. BG (bacterial ~~The cellular~~community specific growth rates ~~(BG)~~ were highly variable among size fractions, ranging from a minimum of 0.021 ± 0.0035 d^{-1} in the <1 µm size fraction of BGR1 to a maximum of 1.1 ± 0.032 d^{-1} in the <3 µm fraction of SEC (Fig. 6). In the SAS2A analysis, rates were two times higher in the <3 µm than in the <1 µm fraction. Similarly, in all of the other lake waters, highest ~~cellular growth rates~~BG were in fractions above 1 µm: Total (NAS1A); Total and <3 µm (BGR1); <3 µm (SEC); Total (KWK12) and Total and <35 µm (RBL4K). The free-living cell fraction (<1 µm) showed rates that were a small percentage of the production per cell in the unfiltered samples in RBL4K (27%); KWK12 (16%); NAS1A (8%) and BGR1 (16%).

20

3.7 Enrichment experiment

Over the course of the experiment (Fig. 78), there was no significant change in Chl *a* concentrations, either with time or among treatments (repeated measures ANOVA, $p > 0.05$). There was a significant drop in bacterial cell abundance in all treatments by day 5 (BA; effect of time F = 39; p = 0.025) but no significant change in production rates (BP, $p > 0.05$). Although there was no significant overall effect of time and treatment on bacterial growth rates (BG, carbon production rates per cell; $p > 0.05$), there was a significant interaction effect between time and treatment ($F = 4.9$; $p = 0.026$). Further analysis (Holm-Sidak pairwise comparisons) showed that while most of bacterial growth ratesBG had not changed statistically, there was a large significant increase between days 1 and 5 in the soil addition treatment (146% average increase; $t = 2.9$; $p = 0.034$) and in the carbon+phosphorus (G+P) enrichment (187% increase; $t = 3.34$; $p = 0.022$).

4 Discussion

4   The pPermafrost peatland soils analyzed here containeds abundant resources for bacterial development, including biologically-accessible carbon, nitrogen, and phosphorus. Degradation of the SAS permafrost peatland landscape iswas observed to be already underway, with the transfer of material from permafrost palsa mounds and surface soils into thermokarst lakes. This transfer iswas observableevident at the landscape level, from patterns of palsa size and degradation patterns (Fig. 2), as well as via within-lake evidence of similarities between particles, and at the microbial scale, via the abundant particle-attached bacterial communities whothat likely benefit from access to particles and flocculent matter. The favorable conditions available to bacterial communities in permafrost peatland thaw lakes resulteds in abundant bacterial communities with high BG. These bacterial communities areseemed −less likely to be not contrcontrolled by

21

449 bottom-up processes, as is ~~is more~~ commonly observed elsewhere (Pace and Cole 1994), ~~but are~~

450 ~~likely to be instead controlled~~than by top-down regulation.

4.1 Organic carbon enrichment

452 There is an estimated 1.048×10^6 km^2 of permafrost peatland in North America, half of which is

453 located in areas of sporadic or isolated permafrost like the SAS region of the present study

454 (Tarnocai et al., 2009). The surface soil and permafrost cores from the SAS region were abundant

455 in carbon, with ~50% C-content (by dry-weight) down to 2 m depth in the permafrost cores (Fig.

456 3), ~~. These values are~~ comparable to peatland soils elsewhere. A study of peat cores from five

457 North-American sites showed that the concentration was consistently around 50% C dry-weight

458 (Gorham and Janssens, 2005), as was also observed in the surface SAS1 active layer and in the

459 upper layers of the two permafrost cores. Similarly, a synthesis of peat data from 9 studies in the

460 northern hemisphere (Gorham et al., 2012) yielded a mean value (±SD) of 50.1 (2.9)%. These

461 carbon values are much higher than observed in other types of Arctic soils. For example, the

462 carbon content of active layer soil from a polygonal tundra of the Lena Delta ranged from 1.5 to

463 3% dry-weight (Höfle et al., 2013), an order-of-magnitude less than values in the SAS soil.

464 Lower carbon concentrations were also measured in a study of permafrost soils of the Arctic

465 tundra of Northwest Territories, which were 6.5% C (Moquin and Wrona, 2015), and in the

466 lithalsa mounds surrounding BGR1 (Fig. 1), where the carbon content of the active layer was less

467 than 1% (ADAPT, 2014).

468 The degrading palsas ~~are~~provided a rich potential source of organic carbon to their

469 associated lakes (Fig. 2). Paleoecological studies (Arlen-Pouliot and Bhiry, 2005; Fillion et al.,

470 2014) have shown that the peat in the SAS valley accumulated in bogs over a 1400 year period

471 from around 1800 to 400 years before the present, and was then uplifted in palsas during the

22

472   period of permafrost aggradation during the Little Ice Age, 400 to 200 years before present day.

473   From the end of the 19th century onwards, the SAS palsas have been thawing and eroding, with

474   the production and eventual infilling of associated thermokarst lakes (palsa lakes), and this

475   warming phase appears to have accelerated over the last two decades (Bhiry et al., 2011). ~~The~~

476   ~~degrading palsas are therefore a rich source of organic carbon to their associated lakes.~~ As shown

477   in the permafrost core analysis (Table 2), ~~this~~ the potential organic input to thermokarst lakes

478   includes not only particulate organic carbon but also DOC. Two contrasting scenarios have been

479   identified for the effects of thawing permafrost on carbon transport in northern catchments (Vonk

480   et al., 2015): (1) decreased net export of carbon as a result of increased flow path lengths,

481   residence times and decomposition in a deeper active layer, or (2) increased net export as a result

482   of thermal erosion and mobilisation of particulate and dissolved organic carbon. The SAS valley

483   is currently in the 'pulse phase' of carbon mobilisation, which as noted by Vonk et al. (2015), is

484   typically dominated by the export of particulate materials. However, the high DOC of the SAS

485   lake waters, significantly above that in the other lake types, also attests to a substantial export of

486   DOC from the SAS palsas to their associated lakes, and is consistent with the permafrost thaw

487   analyses. The low spectral slope values in the SAS lakes indicate a predominantly terrestrial

488   origin of DOC in these lakes (Fichot and Benner, 2012), and the similarity in slope values

489   between the permafrost cores and the lake waters also supports this close linkage between land

490   and water (Fig. S1).

491   **4.2   Nutrient enrichment**

492   In addition to carbon-enrichment, t~~T~~he SAS soil also likely represents a nutrient-rich substrate for

493   bacterial metabolic activity (Table 1). The soil N concentrations were low relative to C, reflecting

494   the stoichiometry of ancient moss tissue, however there were large standing stocks of ~~this~~

23

elementN, and the high ammonium levels in the lake water implies that nitrogen was in abundant supply for planktonic microbial growth processes. The SAS surface soil had nearly three times as much phosphorus and more than five times as much iron relative to concentrations found in other *Sphagnum* peat bogs (Gorham and Janssens, 2005). It also had 1.6 times the concentration of phosphorus and three times the amount of calcium when compared to permafrost soil from the Northwest Territories (Moquin and Wrona, 2015), though only a fraction (5%) of the magnesium observed in the latter study.

Part of the observed differences when compared to these other regions is related to the long-term history of the Hudson Bay region. Enrichment Factors (EF) indicated that phosphorus was above the global average for phosphorus concentrations in soil (EF=15.9), demonstrating long-term transfer of this elements from other sources, such as via atmospheric deposition or hydrological transfer (from surrounding rocks or terrestrial zones). The permafrost thawing analyses showed a release of nitrate but no evidence of soluble phosphorus release, except from the bottom-core samples that produced SRP concentrations that were 2- to 30-times above current lake water values (Table 2). 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.

24

517   Inorganic nutrient release from thawing and eroding permafrost has been documented at

518   sites elsewhere, but with large variations among regions and landscape types (Vonk et al., 2015).

519   Slumping of permafrost soils into Alaskan streams increases their inorganic as well as organic

520   concentrations (Bowden et al., 2008), but phosphorus adsorption onto clays may decrease SRP

521   concentrations in some mineral permafrost environments (Breton et al., 2009). Nitrate export

522   from the Kuparuk River catchment on the Alaska North Slope increased 5-fold between the late

523   1970s and early 2000s and may have been related to permafrost soil and vegetation effects

524   (McClelland et al., 2007). These processes may also operate in the peatland permafrost sites

525   studied here.

4.3   Particle enrichment

527   The SAS permafrost peatland lakes were rich in particulate material, with substantially larger

528   particles than non-permafrost-affected rock-basin lake RBL4K, and they contained some of the

529   largest particles amongst thermokarst lakes studied (Fig. 45). Much finer particles over a

530   narrower size range were recorded in the northern permafrost lakes NAS1A and BGR1, reflecting

531   their mineral permafrost catchments. The close correspondence between the active layer,

532   permafrost and lake particle size distribution at SAS2 (Fig. 56), is evidence that this richness of

533   particles in the peatland lakes is derived from the thermo-erosion of their associated palsas. The

534   small but conspicuous shift to larger particles in the SAS surface waters may indicate the

535   production of aggregates by flocculation that are maintained in the upper water column by virtue

536   of their low density and therefore slow sinking speeds. The production of flocs was observed

537   when SAS water was brought into the laboratory and stored in clear glass bottles without mixing

538   for several days (B. N. Deshpande, unpublished observations), and may be favored by the high

539   DOC concentration in these waters. In contrast, the deeper waters showed an increase in fine

540 particles, contrary to what might be expected from Stokes' Law based upon size relationships.

541 The origin of this difference is unknown at this time, but it could be the result of fine, high-

542 density mineral particles settling out from the overlying water column. The extreme thermal

543 stratification and physical stability of these waters (Deshpande et al., 2015; Przytulska et al.,

544 2016) indicates that only particles of small size or low density would be maintained in the water

545 column.

546 **4.4   Bacterial association with particles**

547 There was clear evidence that the high particle-loading of peatland SAS waters affected its

548 bacterial ecology. Less than 30% of the total cells BA and productivity BP rates were associated

549 with the free-living category, operationally defined here as passing through a 1 μm filter, and this

550 effect was even more pronounced for bacterial growth rates (BG), which were 50% lower in the

551 <1 μm than in the <3 μm fraction, implying much faster growth rates of bacteria on particles in

552 the size range 1-3 μm. In SAS2A, as in many of the other northern lakes, bacterial populations

553 and production appeared to be distributed across the full range of particle sizes (Fig. 6). This is

554 consistent with studies across a range of salt- and fresh-water environments showing that particle-

555 attached bacteria are favored in environments with a high availability of particulate habitats

556 (Lami et al., 2009; Kirchman and Ducklow, 1987; Kirchman and Mitchell, 1982).

557   There are several sources of experimental error that must be considered when interpreting

558 particle analyses of this sort. Firstly, it is difficult to obtain a reliable count of particle-based

559 bacteria. Our shaking of the samples would have broken up and released cells from larger

560 aggregates, but dislodging bacteria from particles is notoriously difficult. Even sonication is not

561 completely effective, and addition of a detergent along with sonication can resulted in a

562 pronounced increase in cell concentrations in sediment-laden waters (Yoon and Rosson, 1990). It

563   is therefore likely that the cell concentrations in the present study were underestimated, especially

564   in the >1 μm fractions. This would imply an even greater representation by particle-based cells to

565   the total community abundance, but it would also have led to an overestimation of the production

566   rates per cell biomass. Experiments based on size-fractionation by filtering are always

567   challenging because of the interactions between particle and the filters. Filtering water results in

568   the breakup of particles upon collision with the filter surface, causing two important effects: (1)

569   an increased bioavailability of organic particles (Amon and Brenner, 1996); and (2) potential

570   detachment of particle-attached bacterial from their organic-matter habitat. Filter blocking may

571   have also retained smaller fractions, including free-living cells. Although the exact rates per

572   fraction in the present study, as in all such studies, must be interpreted with caution, the

573   distribution of cells and activities across multiple fractions and the low values in the <1 μm

574   fraction point to the importance of particle-based bacteria in this system. This was not unique to

575   the organic-rich SAS waters, but was found in several of the other lakes. These results are

576   consistent with a previous study of five lakes in the mineral-rich KWK area, which showed a

577   substantially higher proportion of particle-attached bacteria (62±30% in the >3 μm size-fraction)

578   and high ~~productivity~~ BP (59~~±~~30 %) by these groups (Roiha et al., 2015). The ~~production-per-~~

579   ~~cell~~BG patterns are also consistent with data elsewhere; for example, Kirchman and Mitchell

580   (1982) found that particle-attached bacteria accounted for <10% of the total bacterial populations

581   but contributed substantially to total microbial activity.

582   **4.5   Controls on bacterial abundance and productivity**

583   Bacterial abundance in the thermokarst lakes sampled here ranged from 0.20 to 3.5×10^6 cells

584   mL^{-1}, which falls towards the higher end of the range for comparable aquatic ecosystems (Table

585   5). For example, in study of 16 lakes located in subarctic Sweden, bacterial concentrations ranged

586   from 0.4 to 2.4×10^6 cells mL^{-1} (Karlsson et al., 2001), and in a humic, boreal lake, bacterial

587   concentrations ranged from 1.2 to 1.7×10^6 cells mL^{-1} in winter (Tulonen et al., 1994).

588   The ~~bacterial production~~BP rates in the thermokarst lakes sampled here were also at the

589   high end of the range in comparable systems (Table 5), from~~.~~ 0.25 to 2.3 µg C L^{-1} h^{-1}, with an

590   average ($\pm$SD) of 0.92 ($\pm$0.46) µg C L^{-1} h^{-1}. These rates are more comparable with those observed

591   in southern Québec aquatic ecosystems, and productive systems elsewhere, for example the high-

592   nutrient Butron River, Vizcaya, Spain (Table 4). In this river, free-living bacteria had a

593   production rate of 5.8 µg C L^{-1} h^{-1}, with particle-attached communities contributing 2.97 µg C L^{-}

594   ^{1} h^{-1} of bacterial-production (Iriberri et al., 1990).

595   Such comparisons with other sites need to be made with caution because they rest on a

596   number of untested assumptions. Notably, we used a single factor for conversion between leucine

597   uptake to carbon production concentrations, and assumed a 2-fold isotopic dilution of leucine in

598   the natural environment, observed in certain subarctic ecosystems (Simon and Kirchman, 1988;

599   Simon and Azam, 1989) and as has been employed for a wide range of bacterial production

600   studies elsewhere (Judd et al., 2006; del Giorgio et al., 1997; del Giorgio and Bouvier, 2002).

601   However, given the wide-range of DOC concentrations and unique characteristics of thermokarst

602   lakes, it is likely that the true conversion factors would lie on a wider range, as found in Pulido-

603   Villena and Reche (2003). If ambient leucine concentrations follow the trend of measured total

604   DOC concentrations, then production rates may have been especially underestimated in the SAS

605   incubations. This should not have influenced the pattern amongst size fractions, however, as

606   noted above, errors associated with cell counts for the particle-associated fractions may have

607   affected the estimates of rates per biomass.

608   The enrichment experiment in the present study showed that there was no significant
609   effect of either glucose or phosphorus when added separately to the SAS peatland lake waters
610   (Fig. 7). These results imply that bacterial stocks and production were not strongly limited by
611   carbon supply, nor were they subject to primary phosphorus limitation. This contrasts with results
612   from the permafrost-influenced, turbid waters of the Mackenzie River, Northwest Territories
613   Canada, where short-term glucose enrichment resulted in a 4-fold increase in leucine uptake rates
614   (Vallières et al., 2008). They also contrast with enzymatic analyses of Greenland lakes that
615   implied strong primary phosphorus limitation (Burpee et al. 2016). Chl *a* levels also showed no
616   significant effect of enrichment, in contrast to such experiments in High Arctic lakes (Bonilla et
617   al., 2005). However, for the addition of glucose plus phosphorus, and also for the soil addition
618   treatment, there was a significant increase in ~~specific growth rates~~BG (Fig. 7). This implies a
619   combined stimulatory enrichment effect on bacterial production of the palsa permafrost soils
620   eroding into the SAS thermokarst lakes.

621   Other studies have shown that DOM-enrichment increased heterotrophic metabolism,
622   sometimes at the expense of autotrophic metabolic activity (Forsström et al., 2013). In an Arctic
623   tundra lake of the Northwest Territories, addition of permafrost soil resulted in decreased
624   bacterial production in the pelagic zone, but increased rates in the benthic zone (Moquin and
625   Wrona, 2015). A recent study of Arctic lakes in southwest Greenland found that microbial
626   populations were primarily phosphorus-limited, and that this P-limitation increased with the
627   availability of DOM (Burpee et al., 2016). In an area of discontinuous permafrost in northern
628   Sweden, addition of terrestrial carbon to aquatic bacterial samples resulted in a four- to seven-
629   fold increase in respiration rates, with only a small proportion of the available carbon $(1 - 12\%)$
630   contributing to cellular biomass and the dominant portion respired to CO_2 (Roehm et al., 2009).

All of the limnological and microbial measurements point to the SAS peatland lakes as favorable environments for ~~bacterial production~~BP. The ~~bacterial growth rates~~BG values show that SAS lakes were outliers amongst thermokarst lakes, with significantly elevated rates (Table 4). These rates are also on the higher end of observations made across a wide trophic range of lakes from other regions (del Gi~~r~~orgio et al., 1997; Smith and Prairie, 2004). The lack of response of cellular rates to either phosphorus or carbon added singly also implies sufficiency, and even although there was a significant rise in growth in response to soil and carbon+phosphorus (G+P), this was not translated into an increase in ~~population size~~BA (Fig. 7). In fact populations fell in all of the incubations, despite ~~bacterial community growth rates~~BG rates that remained the same or higher. In combination, these observations suggest that bacterial biomass in the SAS peatland lakes is controlled by top down processes rather than by bottom-up, substrate supply rates. This might involve viral lysis, as in planktonic bacterial systems elsewhere (e.g., Lymer et al., 2008) or it may be the result of intense grazing by bactivores. These waters contain high concentrations of zooplankton, including *Daphnia* (Bégin 2015) that can filter picocyanobacteria (Przytulska et al., 2015) and probably heterotrophic bacteria (Rautio and Vincent, 2006). Studies on SAS2A have shown that they contain abundant ciliates, heterotrophic nanoflagellates and mixotrophic phytoplankton (Przytulska et al., 2016), all of which may exert a control on bacterial densities. In these environments, enriched by soil particles, carbon and nutrients released from thawing and eroding permafrost, bacterial stocks may be ultimately capped by loss rather than gain processes.

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7 Tables

Table 1. Chemical properties of permafrost soil samples from the palsa surface at SAS1. Each 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)
C~~Mg~~	509 (10.9)~~0.339 (0.189)~~	Ba~~Cd~~	43.5 (10)~~0.12 (0.04)~~
N~~Na~~	30.0 (2.6)~~0.344 (0.123)~~	Mn~~Pb~~	24.5 (12)~~0.93 (0.46)~~
Fe~~K~~	6.04 (1.6)~~0.369 (0.178)~~	Cu~~Mo~~	6.5 (1.1)~~1.03 (0.18)~~
Ca~~P~~	5.23 (3.4)~~0.545 (0.019)~~	Zn~~Ni~~	5.8 (0.5)~~5.3 (0.8)~~
S~~Al~~	4.86 (0.52)~~3.67 (0.60)~~	Cr	5.8 (0.5)
Al~~S~~	3.67 (0.60)~~4.86 (0.52)~~	Ni~~Zn~~	5.3 (0.8)~~5.8 (0.5)~~
P~~Ca~~	0.545 (0.019)~~5.23 (3.4)~~	Mo~~Cu~~	1.03 (0.18)~~6.5 (1.1)~~
K~~Fe~~	0.369 (0.178)~~6.04 (1.6)~~	Pb~~Mn~~	0.93 (0.46)~~24.5 (12)~~
Na~~N~~	0.344 (0.123)~~30.0 (2.6)~~	Cd~~Ba~~	0.12 (0.04)~~43.5 (10)~~
Mg~~C~~	0.339 (0.189)~~509 (10.9)~~		

Formatted Table

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877 Table 2. Analysis from duplicate permafrost cores taken from palsas at the SAS2 study site. Gas,

878 ice, and sediment (Sed) proportions (%) are by volume. a_{CDOM} (m^{-1}) is the CDOM absorption at

879 440 nm. Dissolved organic carbon (DOC, in mg L^{-1}), soluble reactive phosphorus (SRP, in µg L^{-}

880 ^{1}), and nitrate-nitrogen (NO_3, in µg N L^{-1}) concentrations are potential contributions from melted

881 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

882

883 Table 3. Limnological properties of study sites. Zs, sample depth, soluble reactive phosphorus

884 (SRP, in µg L^{-1}), total nitrogen (TN, in mg L^{-1}), dissolved organic carbon (DOC, in mg L^{-1}),

885 Chlorophyll *a* (Chl *a*, in µg L^{-1}), total suspended solids (TSS, in mg L^{-1}); PSmax, maximum

886 frequency of particle size distribution (µm). The S samples correspond to surface at 0 m, and the

887 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

888

889 Table 4. Bacterial properties of study sites. Zs, sample depth, bacterial abundance (BA, in 10^6

890 cells mL^{-1}, bacterial production rate (BP, in µg C L^{-1} h^{-1}), and bacterial community specific

891 growth rates (BG, in d^{-1}). The S samples correspond to surface at 0 m, and the B samples

892 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

893

894   Table 5. Comparison of bacterial abundances (BA, 10^6 cells mL^{-1}) and production rates (BP, μg

895   C L^{-1} h^{-1}) from thermokarst lakes with other aquatic environments. * Trophic status based on Chl

896   *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*

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

897

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

Figure 67. 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 78. Planktonic variables in the 5-day experiment with amendments of phosphorus (P), glucose (G), glucose plus phosphorus (G+P), phosphorus (P), and palsa soil (S) to SAS1B lake

44

918   water. The control (C) is shown on both day 1 and day 5. Each value is the mean ± SD of

919   triplicate samples.

920

Figure 1. Map of the study regions and photos of the 6 study areas. NAS is a mineral-rich site located in an area of continuous permafrost. BGR and SEC are also mineral-rich sites, but located in areas of discontinuous permafrost. The KWK and SAS lakes are in areas of sporadic permafrost, but KWK is mineral-rich while SAS is in a peatland landscape. The rock-basin lakes (RBL) are not of permafrost-origin.
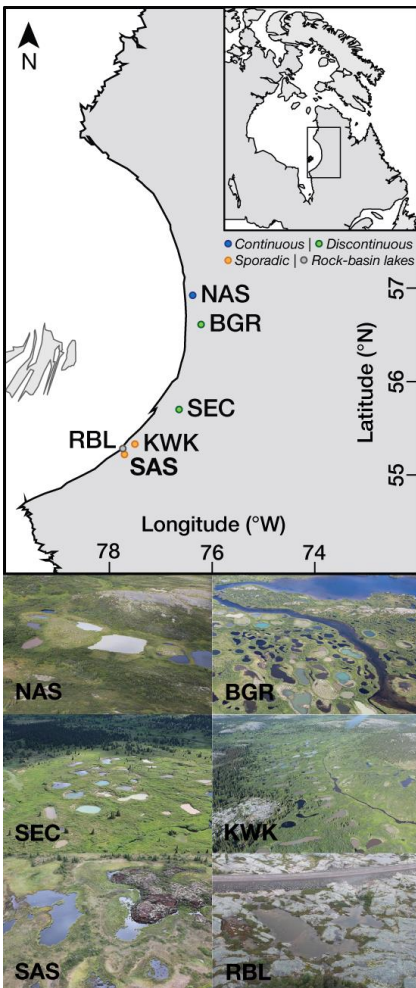
928   Figure 2. Palsas and their associated thermokarst lakes in the SAS peatland valley. Upper panel:

929   aerial view of the SAS1 area; lower panel ground-level view of SAS1B (photograph by

930   Alexander Culley).

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932

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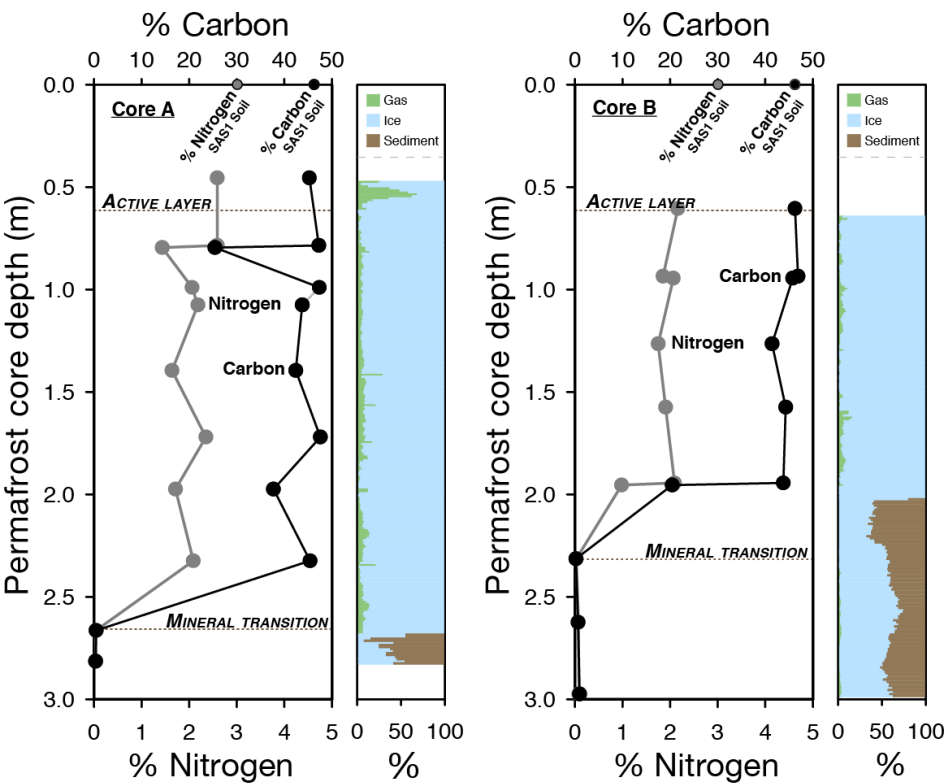
937 Figure 4. CDOM absorbance curve in SAS permafrost soil and lake water.
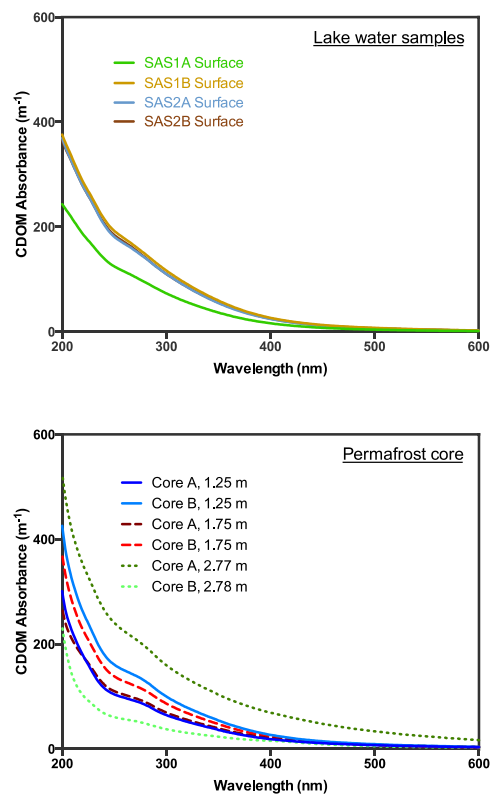
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944 samples.

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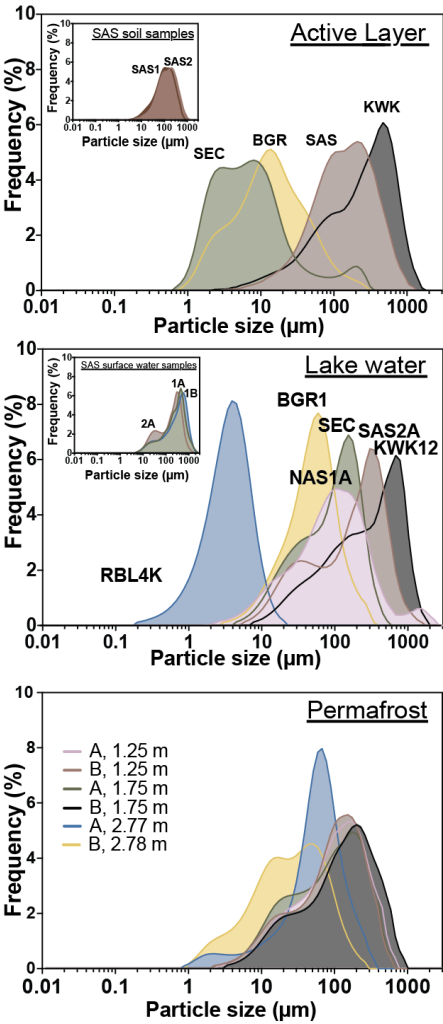
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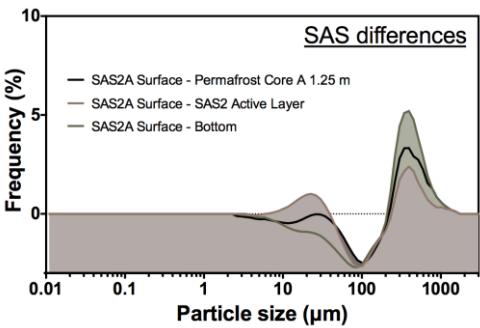
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952 production (BP), and bacterial cell-specific growth rates (BG) from five thermokarst lakes and

953 one rock-basin lake. Each is the mean ± SD of triplicate samples.

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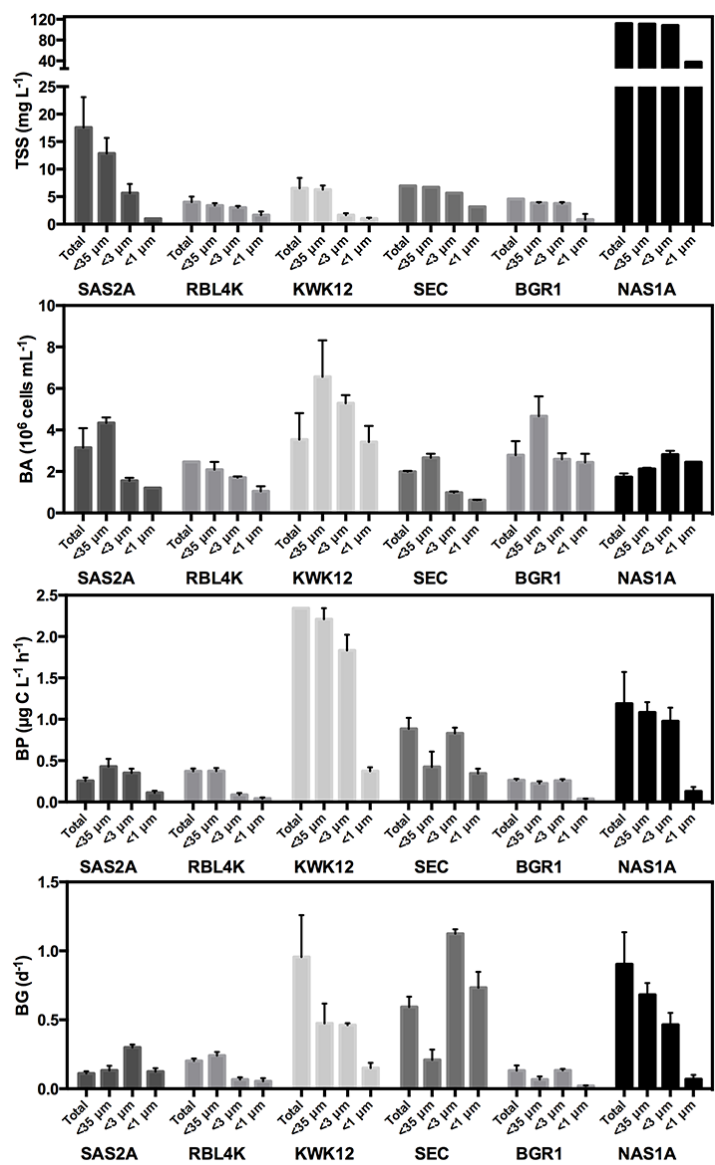
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956   glucose (G), glucose plus phosphorus (G+P), phosphorus (P), and palsa soil (S) to permafrost

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958   mean ± SD of triplicate samples.
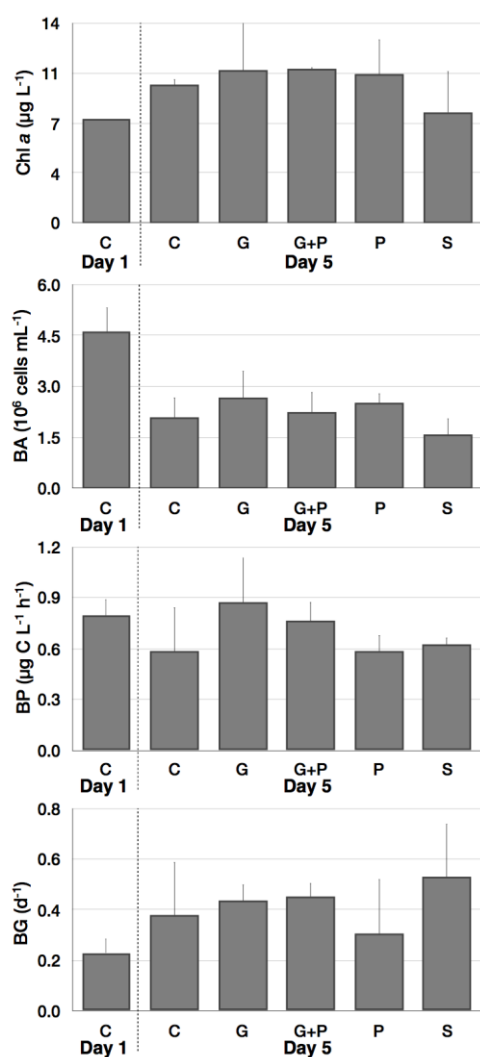
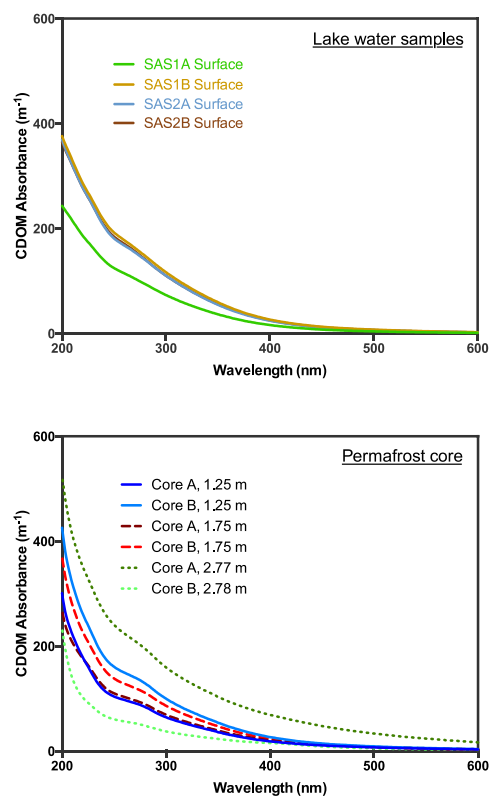959

960

961   Table S1. Physical properties of study sites. Zm, maximum depth (m); location given by latitude

962   (^{o}N), and longitude (^{o}W).

Lake	Zm	Latitude	Longitude
SAS1A	1.6	55.218800	77.707950
SAS1B	1.2	55.219013	77.707801
SAS2A	2.7	55.225018	77.696580
SAS2B	1.5	55.225212	77.696017
SAS2C	2.1	55.225083	77.694933
KWK12	2.7	55.330072	77.503849
SEC	3.4	55.701033	76.643850
BGR1	4.2	56.610833	76.215000
BGR2	1.1	56.610833	76.215617
NAS1A	3.2	56.923779	76.378293
NAS1H	3.6	56.924121	76.377038
RBL4K	0.7	55.331798	77.699393
POND9K	0.5	55.361083	77.650861
RBL9K	1.2	55.361083	77.650861
RBLOlsha	1.6	55.282452	77.739834

963
964

965 Figure S1. CDOM absorbance curves ~~in~~for SAS permafrost soil (thawed in Milli-Q water) and

966 lake water.

967