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# Carbon, nutrient and metal controls on phytoplankton concentration and biodiversity in thermokarst lakes of latitudinal gradient from isolated to continuous permafrost

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1 **Carbon, nutrient and metal controls on phytoplankton concentration**  
2 **and biodiversity in thermokarst lakes of latitudinal gradient from**  
3 **isolated to continuous permafrost**

4  
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19  
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27           **Abstract**

28           Shallow thaw (thermokarst) lakes abundant in regions of permafrost-affected peatlands  
29 represent important sources of carbon dioxide and methane emission to the atmosphere,  
30 however the quantitative parameters of phytoplankton communities which control the C cycle  
31 in these lakes remain poorly known. This is especially true considering the roles of permafrost,  
32 hydrochemical composition of lakes, lake sizes and season as major governing factors on  
33 phytoplankton abundance and biodiversity. In this work, we quantified phytoplankton  
34 characteristics of 27 thermokarst lakes (sizes ranging from 115 m<sup>2</sup> to 1.24 km<sup>2</sup>) sampled in  
35 spring, summer and autumn across a permafrost gradient (isolated, sporadic, discontinuous and  
36 continuous zone) in the Western Siberia Lowland (WSL). The biodiversity indices were highest  
37 during all seasons in lakes of the continuous permafrost zone and rather similar in lakes of  
38 isolated, sporadic and discontinuous permafrost zone. Considering all seasons and permafrost  
39 zones, the biomass and cell number of phytoplankton correlated with Dissolved Organic Carbon  
40 (DOC), phosphate, and some metal micro-nutrients (Ni, Zn). The strongest correlations were  
41 observed for *Cyanophyceae* during summer, with pH, Ni, Cu, Zn, Sr, Ba (cell number) and Cu,  
42 Zn, Ba (biomass), and during autumn, with DOC, K, Cr, Cu, Zn, Ba, Cd, Pb (biomass). Using  
43 a substituting space for time approach for climate warming and permafrost thaw and suggesting  
44 a shift in permafrost boundaries northward, we foresee an increase in cell number and biomass  
45 in continuous permafrost zone in spring and summer, and a decrease in phytoplankton  
46 abundance in the discontinuous and sporadic permafrost zones. The biodiversity of  
47 phytoplankton in the continuous permafrost zone might decrease whereas in other zones, it may  
48 not exhibit any sizably change. However, in case of strong deepening of the active layer down  
49 to underlying mineral horizons, and the release of some limiting nutrients (Si, P) due to  
50 enhanced connectivity of the lake with groundwater, the share of cyanobacteria and diatoms  
51 may increase.

## 52 INTRODUCTION

53 The change of aquatic biota in the Arctic under climate trends and permafrost thaw is at  
54 the forefront of environmental studies in high latitudes (Prowse et al., 2006; Roberts et al.,  
55 2017). Arctic warming is anticipated to result in massive carbon (C) mobilization from  
56 permafrost peat to atmosphere, rivers and lakes, thereby potentially worsening global warming  
57 via greenhouse gases (GHG) emissions (Vachon et al., 2021). The role of biotic component of  
58 inland waters, notably phytoplankton, is of crucial importance to understand whether the  
59 climate change can switch the lakes of permafrost zone from net source of carbon dioxide (CO<sub>2</sub>)  
60 emission to C sinks (Elder et al., 2018; Bogard et al., 2019; Shirokova et al., 2020). In this  
61 regard, C-rich permafrost peatlands are especially important as they occupy around 3.7 million  
62 km<sup>2</sup> of Arctic and subarctic territories, mostly in Northern Eurasia, and contain huge amount of  
63 highly vulnerable carbon (415 Pg C) in soil and surface waters (Hugelius et al., 2020). In all,  
64 the frozen peatlands of Northern Hemisphere (Bolshezemelskaya Tundra, 0.25×10<sup>6</sup> km<sup>2</sup>;  
65 western Siberia 1.05×10<sup>6</sup> km<sup>2</sup>; Hudson Bay Lowlands (1.1×10<sup>6</sup> km<sup>2</sup>); Northern Siberia and  
66 Eastern Siberia lowlands, 0.5×10<sup>6</sup> km<sup>2</sup>) account for 14 % of overall permafrost-affected regions  
67 worldwide and remain very poorly explored. These peatlands exhibit a disproportionally high  
68 contribution to C storage and exchange fluxes and present a prominent exception to well-  
69 studied aquatic and soil ecosystems on mineral substrates such as those investigated in Alaska  
70 and Scandinavia because the frozen peatlands 1) are developed on flat, low runoff terrain with  
71 long water residence time in lakes and ponds; 2) act as important C stock in the form of organic-  
72 rich histosols (peat soils); 3) emit substantial amount of CO<sub>2</sub> and methane (CH<sub>4</sub>) to the  
73 atmosphere from the surface of inland waters (Karlsson et al., 2021) and 4) exhibit high DOC  
74 and low pH in waters in contact with peat soils (Shirokova et al., 2021). These factors determine  
75 highly specific and still poorly known aquatic communities in dystrophic to mesotrophic  
76 peatland waters. Due to lack of nutrients and shallow photic layer, aquatic ecosystems of frozen

77 peatlands are likely to be very sensitive to permafrost thaw and can respond in totally unknown  
78 way to ongoing climate warming in terms in change of their C, nutrient and metal storage as  
79 well biodiversity and organisms adaptation strategies. However, in contrast to wide use of plant  
80 communities (i.e., Loiko et al., 2020; Yue et al., 2020) or microbial abundances (Song et al.,  
81 2021) as ecological indicators of permafrost development, the aquatic organisms are strongly  
82 understudied.

83         Western Siberia falls into the category of key targeting regions outlined in perspectives  
84 of biogeochemical studies in the Arctic (Vonk et al., 2019) as this region includes a continuous-  
85 discontinuous permafrost transition and experiences substantial thermokarst. As a result, this  
86 high-priority region is most susceptible to permafrost thaw thus affecting the biotic population  
87 of aquatic systems. The permafrost peatlands of WSL present unique hydrogeochemical surface  
88 water features that are capable shaping the abundance and diversity of the planktonic  
89 population. The majority of thaw ponds and lakes are located within the flat mound palsa of  
90 watershed divides and are thermokarst originated, i.e., formed after thawing of peat and mineral  
91 soil ice (Polishchuk et al., 2017, 2018). The thermokarst lakes are isolated, do not have distinct  
92 inlets and outlets and possess very small catchments, typically comparable to or less than the  
93 water's surface area. All lakes are shallow (< 1–1.5 m), devoid of fish and freeze solid during  
94 winter (Manasypov et al., 2015). Due to the dominance of peat rather than mineral deposits  
95 within the active (unfrozen) layer, the soil supra-permafrost water delivers high amount of  
96 allochthonous Dissolved Organic Matter (DOM) to these lakes (Raudina et al., 2018). This  
97 leads to a very shallow photic layer, restricted to the first few decimeters of the water column,  
98 due to high concentration of DOC ranging from 10 to 50 mg·L<sup>-1</sup> depending on lake size.  
99 Moreover, the concentration of dissolved inorganic carbon (DIC) is on average ten times lower  
100 than that of DOC and rarely exceeds several mg·L<sup>-1</sup>. This provides a very low buffering capacity  
101 for the lake waters. Finally, the acidic character of terrestrial organic matter subjected to water

102 leaching within the lake watershed (oligotrophic peat, moss biomass) leads to quite acidic  
103 waters ( $3 \leq \text{pH} \leq 6$ ), typically unfavorable for the phytoplankton development, although some  
104 acid-tolerant picocyanobacteria can thrive in humic waters (Jasser and Arvola, 2003; Jasser et  
105 al., 2009, 2013).

106         These environmental factors (acidic pH, high DOC, lack of stratification, total freeze in  
107 winter and peatland context) make the thermokarst lakes of western Siberia peatlands very  
108 different from other high-latitude or permafrost-affected lakes of Scandinavia (Forsström et al.,  
109 2005, 2007, 2009; Hay et al., 2000; Rautio et al., 2011; Albert et al., 2012), Northern European  
110 Russia (Trifonova, 1998; Laing & Smol, 2000), Qinghai Tibet Plateau (Jia et al., 2021; Li et  
111 al., 2021; Liang et al., 2021) and North America (Moore, 1978; Vincent, 2000; Milot-Roy &  
112 Vincent, 1994; Tang & Vincent, 1999; Tang et al., 1997; Sheath et al., 1986, 1996; Sheath &  
113 Steinman, 1982; Douglas & Small, 1994, 1995; Bergeron & Vincent, 1997; Bonilla et al., 2005;  
114 Thompson et al., 2012; Paterson et al., 2014; Lougheed et al., 2015; Lewis et al., 2016;  
115 Przytulska et al., 2017). Overall, compared to oligotrophic clearwater arctic lake waters,  
116 dystrophic, highly acidic and organic-rich lakes are still poorly studied from the view point of  
117 phytoplankton population with the exception of very few recent works on picoplankton  
118 (Przytulska et al., 2016) or periphyton (Bouchard et al., 2018) in subarctic Quebec. The poor  
119 knowledge on phytoplankton abundance and diversity in thermokarst lakes contrasts the  
120 increasing amount of work on bacterial and viral population and metabolism in these inland  
121 waters (i.e., Comte et al., 2016; Roiha et al., 2016; Crevecoeur et al., 2017; Vigneron et al.,  
122 2019, 2020; Levesque et al., 2019). At the same time, the role of photosynthetic microorganisms  
123 may be crucial in determining the net C balance of thermokarst lakes in terms of C  
124 emission/uptake. On the annual scale, the thermokarst lakes of permafrost peatlands are strong  
125 CO<sub>2</sub> emitters (i.e., Serikova et al., 2019). However, during summer, phytoplankton CO<sub>2</sub> uptake  
126 can reduce the pCO<sub>2</sub> in both nutrient-rich and nutrient-poor boreal lakes (i.e., Engel et al., 2019).

127 In order to estimate the relative importance of this processes in thermokarst lakes of frozen  
128 peatlands, quantitative measurements of phytoplankton abundance are needed.

129 In previous work, we investigated 20 thermokarst lakes located in discontinuous  
130 permafrost zones over 3 seasons demonstrating high phytoplankton biodiversity, dominated by  
131 green algae (Pavlova et al., 2016). The number of cells and biomass of cyanobacteria were  
132 partially controlled by DIC, whereas the number of diatoms and green algae was linked to DOC,  
133 Fe and Si concentration. However, permafrost (and climate) control on phytoplankton  
134 abundance and diversity in the thermokarst lakes remains totally unknown. This does not allow  
135 prediction of the possible evolution of phytoplankton communities under climate change  
136 scenarios. Here we present results of an extended study of 27 lakes located along the permafrost  
137 gradient, from isolated/sporadic zones in the forest-tundra, discontinuous (peat palsas) to  
138 continuous permafrost zone of polygonal tundra, sampled over three main hydrological seasons.  
139 We aimed at inventorying their phytoplankton population and testing environmental factors  
140 possibly controlling the microorganism population number and biomass as well as the  
141 abundance of individual taxons. We hypothesize primary control of lake water hydrochemistry  
142 on phytoplankton abundance and we expected a decrease in biomass and biodiversity  
143 northward, from isolated to continuous permafrost zone, following a decrease of the water  
144 temperature. At the same time, because studied lakes exhibit the highest pH and DIC in the  
145 continuous permafrost zone (Manasypov et al., 2020), this trend can be reversed in case of water  
146 acidity control on phytoplankton development. It is important to note that there is no latitudinal  
147 trend in DOC and nutrient concentrations in thermokarst water bodies across the permafrost  
148 gradient of the WSL (Manasypov et al., 2020). We further attempted a ‘substituting space for  
149 time’ approach to foresee possible changes in phytoplankton population induced by a  
150 permafrost boundary shift northward. Obtained results should help constrain hydrochemical  
151 factors controlling autotrophic processes in the water column. Eventually, this should allow

152 evaluation the capacity of thermokarst lakes to act as source or sink of CO<sub>2</sub> under a climate  
153 warming scenario in western Siberia.

154

## 155 **2. STUDY SITE AND METHODS**

### 156 *2.1. Thermokarst lakes of western Siberia*

157 The thermokarst (thaw) lakes of the Western Siberia Lowland are developed on palsa peat  
158 bogs across the isolated, sporadic, discontinuous and continuous permafrost zones within the  
159 northern taiga, forest-tundra and tundra biomes (**Fig. 1**). The substrate of the lake watersheds is  
160 Late Pleistocene sand and clay deposits that are covered by a layer of peat 1 to 2 m thick. The  
161 physio-geographical and climatic conditions of studied sites are summarized in **Table 1**.

162 Water bodies ranged from 115 m<sup>2</sup> to 1.24 km<sup>2</sup> in diameter and had a similar depth of 1.0  
163 ± 0.5 m as measured in the field (Manasypov et al., 2020). The morphology, hydrology and the  
164 water balance of thermokarst lakes have been extensively studied in June, August, and October  
165 (Manasypov et al., 2015, 2020). Further hydrochemical characterization of thermokarst lakes  
166 and their overall abundance in western Siberia are provided elsewhere (Polishchuk et al., 2017,  
167 2018; Serikova et al., 2019). Given their dissolved nutrient concentration, the lakes can be  
168 considered as oligotrophic to weakly mesotrophic. However, small water bodies (< 1000 m<sup>2</sup>)  
169 are quite acidic (3 ≤ pH ≤ 4), and humic (> 20–30 mg·L<sup>-1</sup> of DOC) and thus can be considered  
170 as dystrophic. No thermal and redox stratification was detected during open water seasons in  
171 these shallow fully oxygenated water bodies. The development of thermokarst lakes of western  
172 Siberia follows a sequence of maturation stages, from permafrost depressions and subsidences  
173 (< 10 m<sup>2</sup>) to small, actively growing (via peat abrasion at the borders) thaw ponds (10-10,000  
174 m<sup>2</sup>) and large thermokarst lakes (> 10,000 m<sup>2</sup>) with stable shoreline (Audry et al., 2011;  
175 Pokrovsky et al., 2014). Large lakes (> 100,000 m<sup>2</sup>) are often subjected to drainage which  
176 occurs due to the thawing of the permafrost and the formation of soil subsidences in the valley

177 through which lake water flows. The soil stability decreases, which causes a deepening of the  
178 flow and the formation of erosion channels, through which the lake water is discharged. The  
179 thawed ground is washed away by a stream, which leads to a decrease in the water table of the  
180 lake. As a result, lacustrine sediments become exposed. Pioneer plant species colonize the  
181 relatively warm and nutrient-rich sediments, thus initiating the succession of vegetation and  
182 soil (see Loiko et al., 2020 and references therein for details). The initial herbs are replaced by  
183 mosses, and a new cycle “depression → thaw pond → thermokarst lake” initiates. Along this  
184 sequence of aquatic ecosystems, there is a systematic increase in pH and DIC and a decrease in  
185 pCO<sub>2</sub> and nutrients with an increase in the size of the water body (Shirokova et al., 2013, 2020;  
186 Manasypov et al., 2020; Zabelina et al., 2021).

187         Similar to previous design of the field work (Pavlova et al., 2016), 27 lakes have been  
188 sampled during three main hydrological seasons in 2016: 20 May–13 June, 8–24 August and  
189 25 September–8 October. The beginning of June, right after a massive ice break corresponded  
190 to “biological spring”; the middle of August exhibited the highest water temperatures and thus  
191 corresponded to biological “summer”, and the end of September - beginning of October  
192 corresponded to the beginning of the ice formation and can be considered as biological  
193 “autumn.” During our sampling campaign, we followed the change of seasons and moved from  
194 the south to the north in spring and from the north to the south in autumn, thus collecting lake  
195 water at approximately the same hydrological stage and biological season. Sampling and  
196 analyses of pH, Specific Conductivity (S.C.), Specific UV absorbance at 254 nm (SUVA),  
197 DOC, CO<sub>2</sub>, CH<sub>4</sub>, DIC, major anions (Cl and SO<sub>4</sub>), major cations (Na, Mg, Ca, K), macro-  
198 nutrients (P<sub>tot</sub>, P-PO<sub>4</sub>, N-NO<sub>3</sub><sup>-</sup>, N-NH<sub>4</sub><sup>+</sup>, Si) and selected micro-nutrients (B, Mn, Fe, Co, Ni,  
199 Cu, Zn, Rb, Mo, Ba) were performed as described elsewhere (Manasypov et al., 2020; Serikova  
200 et al., 2019).

201

## 2.2. Phytoplankton sampling and analyses

For phytoplankton analyses, a 500-mL bottle of lake water was collected from the central part of the lake (or the deepest part if it was close to the border) using a rubber boat, from the depth of  $30 \pm 10$  cm and immediately fixed with 4 % formalin Lugol's solution. The phytoplankton was concentrated by sedimentation (10-14 days for 500-mL volume). To insure that this pre-concentration allowed total recovery of all species, including the small-sized ones, the biomass yield was verified by centrifugation at 3500 g during 20 min. For consistency with previous studies of thermokarst lakes of permafrost peatlands (cf., Getsen et al., 1994; Trifonova et al., 1998; Patova et al., 2014), the phytoplankton was counted in a sedimentation plankton counting chamber (Guseva, 1959) analogous to commonly used Utermöhl technique (Lund et al., 1958), using AxioLab A1 and Axiovert 40 CFL trinocular inverted fluorescence phase contrast microscopes (Zeiss). The biomass was determined as algal volume for each lake and converted to wet weight assuming a density of  $1 \text{ g}\cdot\text{cm}^{-3}$  after approximating the geometry of the cell (Makarova & Pichkily, 1970). The phytoplankton diversity was evaluated using the Shannon-Weaver's index (SH) and Pielou's index (P) based on the biomass (Odum, 1971) and Simpson and Simpson's equitability indices (SI and SE) (Odum, 1971). The Saprobity index (S) was evaluated according to Sládeček (1973) and Barinova et al. (2006). In this study, we used classical taxonomic approach to represent phytoplankton variability across lakes and seasons, to insure the consistency with previous studies of phytoplankton in thermokarst (Trifonova, 1998; Bouchard et al., 2018; Paterson et al., 2014) and humic boreal (Forsström et al., 2005; Engel et al., 2019 ) lakes. Classification of identified algae into functional groups (i.e., Reynolds et al., 2002; Salmaso and Padisak, 2007; Kruk et al., 2010; Salmaso et al., 2015) was not possible because the studied habitats (shallow, non-stratified, non-turbid, acidic, dystrophic humic lakes) belong to none of the established codon except Q (small acidic, humic lakes). However, none of the representative of this codon (*Gonyostromum* spp, *Heterosigma*

227 spp; Padisak et al., 2009) has been identified in thermokarst lakes of western Siberia (Pavlova  
228 et al., 2016 and this study).

229 The data on the taxon concentrations were analyzed with best fit functions based on  
230 the Pearson correlation and one-way ANOVA with the STATISTICA version 8 software  
231 (StatSoft Inc., Tulsa, OK). Regressions and power functions were used to examine the  
232 relationships among the cell number, the biomass, the pH, DIC, DOC and nutrient concentration  
233 in the lake water. A criterion for a significant correlation between chemical and biological  
234 parameters was that the Pearson coefficients is at  $p < 0.05$ . Further identification of  
235 phytoplankton drivers in thermokarst lake waters included a Principal Component Analysis  
236 which allowed to test the effect of various hydrochemical parameters on total phytoplankton  
237 cell number and biomass and those of individual taxons. In addition to PCA, a Redundancy  
238 analysis (RDA) was used to extract and summarize the variation in a set of response variables  
239 in phytoplankton composition that can be explained by a set of explanatory variables  
240 (environmental climatic and hydrochemical factors). The RDA combines a PCA and multiple  
241 regression analysis and it was run in XLSTAT is a statistical software that works as an add-on  
242 to Excel.

243

### 244 **3. RESULTS**

#### 245 *3.1. Biodiversity of the phytoplankton*

246 The list of sampled lakes together with main hydrochemical parameters is provided in  
247 **Table S1 of the Supplement**. The dominant species during each period, representing more than  
248 10 % of total species number, are listed in **Table S2**, whereas the taxa distribution in lakes  
249 during three observation seasons, averaged over 4 permafrost zones are summarized in **Table**  
250 **2**. Based on the three sampling campaigns conducted in 27 lakes across four permafrost zones,  
251 279 taxa of algae species were found. In June, August and October, we identified 42, 24 and 26

252 taxa in the isolated zone, 61, 48 and 39 taxa in the sporadic zone, 32, 71 and 45 taxa in the  
253 discontinuous zone and 75, 130 and 111 taxa in the continuous permafrost zone, respectively.  
254 The highest biodiversity was recorded among Charophyta (85 taxa representing from 13.7 % to  
255 35.2 % of total encountered forms in different permafrost zones), green algae (52 taxa  
256 corresponding to 12.4–22.2 % of total forms in different permafrost zones) and Cyanobacteria  
257 (40 taxa of 9.6 to 14.2 % forms in different permafrost zones). Although the sampling was  
258 always performed from the water column (20-40 cm depth), notable components of the  
259 identified algae were represented by benthic and periphytic forms of the classes  
260 Zygnematophyceae, Chlorophyceae, Cyanophyceae, Bacillariophyceae and others.

261 The measured biomass and biodiversity indices for individual lakes of each permafrost  
262 zones are illustrated in **Figure 2** whereas integral values (averaged over 4–10 lakes in each  
263 permafrost zone) of total cell number, biomass, Shannon, Pielu Simpson and Saprobity indices  
264 for each permafrost zone during three main seasons are shown in **Figure 3**. The total  
265 phytoplankton biomass was dominated by Chlorophyta, Cryptophyta and Dinophyta (30 %,  
266 22 % and 13 %, respectively) (**Figure 4**).

267 The biodiversity Shannon's index was the highest in the continuous permafrost zone,  
268 during all three season and it was rather similar across isolated, sporadic and discontinuous  
269 permafrost zones. This indicates the high species diversity and high and equal species cell  
270 number in thermokarst lakes of continuous permafrost zone during all seasons. The Simpson's  
271 index of diversity was also the highest in the continuous permafrost zones during spring and  
272 summer periods. In contrast, the Simpson's index of equitability was the lowest in the  
273 continuous zone and the highest in the discontinuous one (only in summer and autumn). This  
274 indicates 1) a low share of individual species in the total community structure of continuous  
275 permafrost lakes, consistent with Shannon indices, and 2) an enhanced influence of typical  
276 dominant species on the community structure in lakes of discontinuous permafrost zone.

277           3.2. *Phytoplankton cell number, biomass and their possible link to lake size and*  
278 *hydrochemistry of thermokarst lakes across the seasons and permafrost gradient.*

279           The lake surface area (which reflected the degree of lake maturity) correlated with  
280 neither biomass nor the cell number of phytoplankton ( $p < 0.05$ ), as illustrated for each season  
281 across all four permafrost zones in **Figure 5**. An overall lack of lake area impact on quantitative  
282 parameters of phytoplankton allowed consideration of the effect of other environmental  
283 parameters, notably the pH, pCO<sub>2</sub>, major ions, macro- and micro-nutrients via averaging all  
284 lakes in each region and season.

285           The mean value of the phytoplankton biomass ranged from 0.2 to 5 mg<sub>wet</sub>·L<sup>-1</sup> and  
286 exhibited a local maximum in the sporadic to discontinuous permafrost zone in spring and  
287 summer and in the sporadic zone in autumn (**Fig. 3**). The cell number varied from 500 cell·mL<sup>-1</sup>  
288 <sup>1</sup> in spring and autumn to 15,000 cell·mL<sup>-1</sup> in summer, had a maximum in sporadic to  
289 discontinuous permafrost zone in spring, and increased northward in summer and autumn.

290           A Pearson pairwise correlation allowed to test possible control of major components  
291 (pH, DOC, CO<sub>2</sub>), macro-nutrients (P, N, Si, K), micro-nutrients and toxicants on the total  
292 biomass and cell number of phytoplankton and those of individual taxons (**Table S3**).  
293 Considering total phytoplankton number and biomass across all seasons and permafrost zones,  
294 DOC, macro-nutrients (PO<sub>4</sub>, K), some lithogenic elements (Al, Cr), micro-nutrients (Zn, Ba)  
295 and potential toxicant (Cd) exhibited significant positive impact. The total cell number  
296 positively ( $R > 0.2$ ) correlated with water temperature, pH, PO<sub>4</sub>, P<sub>tot</sub> and Ni concentrations. The  
297 most pronounced effects were observed in summer and autumn, and the minimal impact was  
298 revealed in spring. Thus, in summer, total cell number strongly ( $R \geq 0.48$ ) correlated with PO<sub>4</sub>,  
299 P, Co, Ni, Cu, Zn and Ba. Such correlations were mostly pronounced for Cyanophyceae (pH,  
300 Ni, Cu, Zn, Sr, Ba with cell number and Cu, Zn and Ba with biomass). In autumn, Cryptophyta  
301 demonstrated the highest ( $R \geq 0.41$ ) correlations with DOC, PO<sub>4</sub>, K, Cr, Cu, Zn, Sr, Ba, and

302 Pb. The biomass of Cyanophyceae strongly ( $R \geq 0.58$ ,  $p < 0.01$ ) correlated with DOC, SUVA,  
303 K, Cr, Cu, Zn, Cd, Ba, Pb. Furthermore, during this period of the year, the biomass of  
304 Chlorophyta strongly increased with lake area,  $\text{NO}_3$  and V concentration. Overall, in autumn,  
305 total phytoplankton biomass sizably correlated ( $R \geq 0.42$ ) with DOC, nutrients ( $\text{PO}_4$ ,  $\text{NH}_4$ , K),  
306 lithogenic elements (Al, Cr), micro-nutrients (Cu, Zn, Ba) and potential toxicant (Pb).

307 In contrast to other seasons, the spring period did not reveal sizable links between  
308 phytoplankton quantitative parameters and lake water hydrochemistry (**Table S3**). Among all  
309 trace elements, only Pb exhibited significant ( $R \geq 0.55$ ,  $p < 0.01$ ) control on Bacillariophyta  
310 and Charophyta biomass and cell number, and strong control on the biomass of cyanobacteria  
311 ( $R = 0.98$ ,  $p < 0.001$ ). The latter was also positively correlated with  $\text{CO}_2$ ,  $\text{PO}_4$ ,  $\text{NO}_3$  and K  
312 concentration.

313 Principal Component Analysis (PCA) demonstrated a general lack of control of  
314 environmental parameters (lake depth, area (S),  $T_{\text{water}}$ , macro- and micro-nutrients) on total  
315 abundance and biomass of phytoplankton and of individual taxons. The PCA identified two  
316 factors that had generally low ability to describe the variance (10 to 5 %).

317 In spring, the 2<sup>nd</sup> factor acted on cell number, biomass, Bacillariophyta, Charophyta and  
318 Pb concentration (**Fig. 6**). The phytoplankton parameters were not associated to any factor in  
319 autumn, and in summer, the 2<sup>nd</sup> factor acted on cell number. None of the major and minor  
320 dissolved components of the lake water were linked to phytoplankton.

321 The RDA treatment did not provide additional insights into environmental control of  
322 phytoplankton concentration and biodiversity across the lakes, seasons and permafrost zones.  
323 After normalization, the main result was that the analyses are not statistically significant ( $p >$   
324  $0.05$ ). For example, during spring period, the biomass contributes  $< 30\%$  to the data inertia but  
325 it is linked to none of the predicting factor including the permafrost zones.

326

327 **4. DISCUSSION**

328 *4.1. General features of cell number and biodiversity evolution as a function of lake size*  
329 *and permafrost zone*

330 The lake area exhibited negligible control on both the biomass and the cell number of  
331 total phytoplankton and those of individual taxons. This contrasts the behavior of major  
332 hydrochemical parameters such as acidity, DOC, and pCO<sub>2</sub> that decreased with an increase in  
333 thermokarst lake size (Shirokova et al., 2013, 2020; Zabelina et al., 2020; Manasypov et al.,  
334 2020). This result suggests a rather homogeneous distribution of phytoplankton across all stages  
335 of lake growth and maturation, from small thaw ponds to large thermokarst lakes. Note that the  
336 water temperature at the lake bottom is unlikely to be a controlling factor of the phytoplankton  
337 development. Indeed, the shallow, well - mixed WSL lakes present no sizable thermal and  
338 chemical stratification (Shirokova et al., 2013; Manasypov et al., 2015, 2020). In addition, the  
339 photic layer depth of humic lakes sampled in this work (at 20-40 cm depth) rarely exceeds 0.5  
340 m; in this layer, the temperature was quite homogeneous.

341 Consistent with the generally weak control of lake size on phytoplankton abundance,  
342 the majority of hydrochemical parameters, including DOC, macro- and micro-nutrient  
343 concentration exhibited a rather weak effect on the total microorganisms number and biomass  
344 as well as those of individual taxons. The most pronounced control was revealed in autumn,  
345 when DOC, macro-nutrients (PO<sub>4</sub>, NH<sub>4</sub>, K) and some micro-nutrients (Cu, Zn, Cr, Ba)  
346 significantly correlated with the total biomass of phytoplankton, and in particular that of  
347 Cyanobacteria and Cryptophyta. For example, lakes from isolated permafrost zone (the most  
348 southern Kogalym site), dominated by Cryptomonadaceae, Peridiniaceae and Flagellata,  
349 demonstrated a 5-fold decrease in both cell number and biomass with a lake size increase over  
350 two orders of magnitude. In this zone, the active layer is very thick and a large amount of  
351 unfrozen peat is capable of interacting with lake water, thereby enriching it with limiting

352 nutrients. This was especially pronounced for small thaw ponds ( $\leq 1000 \text{ m}^2$  in size) which were  
353 subjected to maximal impact of peat abrasion at the border and feeded by shallow (subsurface,  
354 supra-permafrost) water.

355 A pronounced impact of certain macro-nutrients (N, P, K) and trace elements on the  
356 phytoplankton development in autumn could be originated from vegetation litter (K, N, P), peat  
357 (Cu, Zn, Ba, Pb), and deep soil mineral horizons (Al, Cr). This may be linked to enhanced  
358 mobilization of these elements from decaying plant litter at the surface and from deep (frozen)  
359 peat and mineral horizons, when the active layer was at its maximum. Another example is  $\text{CO}_2$ ,  
360  $\text{PO}_4$ ,  $\text{NO}_3$ , K and Pb control on Cyanophycea biomass during the spring. It is possible that this  
361 reflects the release of  $\text{CO}_2$ , P, N, K from vegetation biomass by melted snow (Broder and  
362 Biester, 2017; Manasyrov et al., 2020), and delivery of atmospherically-originated Pb from  
363 snow. The importance of snowmelt on Pb delivery to lakes is known from elemental mass  
364 balance estimation in the WSL (Shevchenko et al., 2017).

365 A first-order explanation of low environmental control on thermokarst lake  
366 phytoplankton abundance is the action of two factors: 1) inhibition of phytoplankton  
367 development by acidic, organic-rich peat waters (Pavlova et al., 2016 and references therein)  
368 and 2) promotion of possible bloom due to nutrient delivery from surface vegetation and  
369 thawing peat horizons (Shirokova et al., 2015). The latter is fairly well known from laboratory  
370 experiments on cyanobacterial growth on organic substrates obtained from moss and peat  
371 leachates (Shirokova et al., 2017). Overall, harsh conditions at the beginning of thaw in small  
372 water bodies (low pH, high DOC and shallow photic layer) were counterbalanced by enhanced  
373 delivery of nutrients, notably P and N, but also some micro-nutrients. Upon progressive lake  
374 size increase, initial dystrophic conditions are replaced by higher pH and lower DOC, thus  
375 leading to an increase in the photic layer. However, the delivery of main nutrients also  
376 drastically decreases as the ratio of lake circumference (and lake watershed) to lake volume

377 decreases, given very small watershed area of thermokarst lakes in western Siberia (Manasypov  
378 et al., 2020).

379 A tentative explanation of the association, in spring, between the 2<sup>nd</sup> PCA factor and  
380 cell number, biomass, Bacillariophyta, Charophyta and Pb concentration (**Fig. 6 A**) is that these  
381 algae (diatoms and chara) are delivered to the lakes from submerged supports (grass, mosses)  
382 of the lake watershed and within the lake border. During this period, Pb is massively delivered  
383 to the lakes due to its presence in melted snow and within the snow-water leached lichens and  
384 mosses (Shevchenko et al., 2017).

385 One of the hypotheses of this study was a decrease of biomass and biodiversity  
386 northward, from isolated to continuous permafrost zone. However, we discovered rather reverse  
387 trends, with maximal phytoplankton cell number (in summer) observed in the continuous  
388 permafrost zone. Most likely, elevated pH in this zone and sufficiently high water temperature  
389 during summer (16–17 °C, see **Table S1**) allowed for strong development of Chlorophyta,  
390 Cryptophyta, Cyanophyceae and Flagellata. In contrast, we do not have a straightforward  
391 explanation for local maxima of biomass in spring and autumn, observed in the sporadic  
392 permafrost zone (**Fig. 3 B**). One possibility is a maximal delivery of limiting macro- and micro-  
393 nutrients from the watershed to the lake in this permafrost zone. Indeed, it is known that the  
394 watershed export fluxes of some components (Particulate Organic Carbon (POC), DOC, Si, Fe,  
395 total dissolved phosphorus ( $P_{\text{tot}}$ ) and phosphate ( $PO_4$ )) also exhibit a maximum at the  
396 permafrost front boundary, in the discontinuous to the sporadic zone (Krickov et al., 2018;  
397 Pokrovsky et al., 2020). It is thus not excluded that freshly delivered from the lake watershed  
398 essential components are quickly consumed by autotrophic microorganisms and thus no  
399 correlations between phytoplankton parameters and these component concentrations are  
400 encountered in thermokarst lake waters.

401

402            *4.2. Comparison with other Arctic and subarctic lakes*

403            Among thermokarst lakes studied all over the world, such as from the Kolyma lowland  
404 (Walter Anthony et al., 2014), the Lena Delta (Boike et al., 2013), Northern Siberia (Khaliullina  
405 et al., 2016), Mackenzie Delta plain (Tank et al., 2009, 2011; Grosse et al., 2013; Walter  
406 Anthony & Anthony, 2013), Qinghai Tibet Plateau (Mu et al., 2016; Chen et al., 2021) and  
407 those north of Quebec (Laurion et al., 2010; Negandhi et al., 2013), only lakes of Canadian  
408 permafrost peatlands (Prsytska et al., 2016; Wauthy & Rautio, 2020) can serve as a first order  
409 analogue of WSL thermokarst lakes. However, such an analogy should be considered with  
410 caution given much higher DOC concentration and lower pH in the western Siberia lakes  
411 compared to the more oligotrophic Canadian water bodies. These factors create quite hostile  
412 environments in the WSL lakes for most phytoplankton, including cyanobacteria and diatoms.  
413 Furthermore, due to their very shallow (0.5–1.5 m) depth and good wind mixing, WSL lakes  
414 are not stratified and do not exhibit prolonged hypoxia or anoxia in the bottom waters during  
415 summer (Manasypov et al., 2015). This is unlike the Canadian thaw lakes (northern Québec)  
416 which are sizably deeper and influenced by underlying mineral deposits (Prsytska et al.,  
417 2016). The main source of solutes for thermokarst lakes of the WSL is thawed peat and surface  
418 vegetation (moss and lichen, Manasypov et al., 2017; Payandi-Rolland et al., 2020; Shirokova  
419 et al., 2021). This leads to acidic, Si-poor, and humic-rich nature of the lake water, which is not  
420 suitable for diatoms compared to the oligotrophic or ultra-oligotrophic lakes of other Arctic and  
421 subarctic regions on mineral substrates, including those of the Bolshezemelskaya tundra  
422 (Trifonova, 1998; Patova, 2014). For example, in most thermokarst lakes investigated in this  
423 study, the diatoms constituted only 6 to 10 % of the total taxon number (**Table 2**) and  
424 contributed only 7 % to the total biomass (**Fig. 4**). Low diatom abundance is consistent with  
425 quite low Si concentration in lakes across the WSL permafrost gradient (typically 200  $\mu\text{g}\cdot\text{L}^{-1}$

426 in isolated to discontinuous permafrost zone; 300 to 400  $\mu\text{g}\cdot\text{L}^{-1}$  in the continuous permafrost  
427 zone, Manasypov et al., 2020).

428         Similar to previous study of phytoplankton in the discontinuous permafrost zone during  
429 three seasons (Pavlova et al., 2016), the acidic environment of these lakes brought about the  
430 dominance of green algae (Chlorophyta) desmids which are typical for low pH boreal waters  
431 (Kosinskaya, 1960) and include a variety of genera *Botryococcus*, *Dictyosphaerium*,  
432 *Monoraphidium*, *Pseudosphaerocystis* and others). These results are in general agreement with  
433 prevalence of eukaryotic over prokaryotic picophytoplankton in shallow eutrophic lakes (Craig,  
434 1987; Mozés et al., 2006), boreal humic lakes (Jasser & Arvola, 2003), and in acidic dystrophic  
435 lakes (Stockner & Shortreed, 1991) which is partially linked to strong light extinction (Pick &  
436 Agbeti, 1991).

437         The majority of studied lakes in sporadic to discontinuous permafrost zone exhibited a  
438 a pH range between 4 and 6. In contrast, the lakes of the continuous permafrost zone (Tazovsky)  
439 exhibited the highest pH (up to 7.5–7.6) and were also accompanied by much higher cell  
440 number, Shannon's and Simpson's indices of diversity. Presumably, elevated pH and more  
441 abundant bicarbonate ions are beneficial for phytoplankton development. Indeed, the  
442 proportion of cyanobacteria and diatoms in the phytoplankton population (biomass) of western  
443 Siberia thermokarst lakes from isolated to discontinuous permafrost zone ranged from 3.5 % to  
444 2.3 % and 3.6 % to 12 %, respectively (**Fig. 4**). Only in less acidic thermokarst lakes from the  
445 continuous permafrost zone lakes, the proportion of cyanobacteria and diatoms in the  
446 phytoplankton biomass raised to  $7 \pm 6$  % (max. 48 %) and  $11 \pm 9$  % (max. 43 %), respectively.  
447 Such a low proportion of cyanobacteria and diatoms in thermokarst lakes of the WSL contrasts  
448 their dominance in other subarctic and High Arctic lakes and ponds (Milot-Roy & Vincent,  
449 1994; Sheath et al., 1996; Vézina & Vincent, 1997; Vincent, 2000; Vincent et al., 2000; Ratté-  
450 Fortin et al., 2020), including thermokarst lakes of Yakutia (Kopyrina et al., 2020). This can be

451 explained primarily by the pH regime. In fact, neutral pH, eutrophic shallow tundra lakes of the  
452 Bolshezemelskaya tundra (Trifonova, 1998) demonstrated dominance of cyanobacteria (75 %  
453 of the total biomass). The latter habitats are represented by a peat bog palsa permafrost-bearing  
454 region that can be considered as most similar to thermokarst lakes of western Siberia, although  
455 the pH of the Bolshezemelskaya tundra permafrost lakes is 1 to 2 units higher and the DOC is  
456 a factor of 2 to 3 lower than those of thermokarst lakes studied in this work. Consistent with  
457 this observation, in the WSL lakes the pH exerted positive control on the number of  
458 Cyanophyceae, which was especially pronounced during summer ( $R = 0.49$ ,  $p < 0.01$ ).

459

#### 460 *4.3. Consequences for CO<sub>2</sub> regime, DOC quality and permafrost boundary shifts*

461 Considering the range of phytoplankton biomass concentration in the thermokarst lakes  
462 during summer ( $0.5$  to  $3 \text{ mg}_{\text{wet}}\cdot\text{L}^{-1}$ ), together with the assumption of a doubling of the cell  
463 population every 2 days (as measured in the field, Shirokova et al., 2009) and the wet:dry ratio  
464 of 10:1, the primary productivity in the water column is equal to  $0.012$  to  $0.075 \text{ mg}\cdot\text{C}\cdot\text{L}^{-1}\cdot\text{day}^{-1}$ .  
465 This is significantly lower than the heterotrophic bacterioplankton respiration in thermokarst  
466 lakes of western Siberia ( $\sim 0.3 \text{ mg}\cdot\text{C}\cdot\text{L}^{-1}\cdot\text{day}^{-1}$ , Shirokova et al., 2013). Such a difference  
467 suggests net heterotrophic status of thermokarst lakes, i.e., CO<sub>2</sub> emission due to heterotrophic  
468 mineralization of allochthonous DOM. Indeed, all WSL lakes act as a strong CO<sub>2</sub> source for  
469 the atmosphere as indicated by a field study of the CO<sub>2</sub> emission in the WSL thermokarst lakes  
470 across a permafrost gradient (Serikova et al., 2019). However, in summer period, the day time  
471 CO<sub>2</sub> fluxes of large lakes may switch from emission to absorbance (Shirokova et al., 2020).  
472 The most likely reason for CO<sub>2</sub> uptake is photosynthesis of lake macrophytes and aquatic  
473 vegetation (i.e., submerged mosses) rather than the phytoplankton activity of the water column.

474 Another interesting results of phytoplankton quantification performed in the present  
475 work is an assessment of autochthonous DOC production (phytoplankton capacity to release

476 DOC into the lake water). It is known that the extracellular release of soluble  $C_{org}$  ranges from  
477 10 to 20 % of the particulate  $C_{org}$  produced by phytoplankton (Baines and Pace, 1991). Given  
478 the typical range of phytoplankton biomass concentration in thermokarst lakes of the WSL (0.5  
479 to 5  $mg \cdot L^{-1}$ ), the autochthonous DOC production is between 0.05 and 0.6  $mg \cdot L^{-1}$ . This is a  
480 negligibly small number relative to the allochthonous DOC reservoir in these lakes across the  
481 studied permafrost gradient (10 to 30  $mg \cdot L^{-1}$ , Manasypov et al., 2020). High concentration of  
482 allochthonous carbon is consistent with dominance of soil (humic and fulvic) chromoforic  
483 DOM in thermokarst lakes of western Siberia, as also reflected in the high value of  $SUVA_{254}$   
484 ( $4.0 \pm 0.7 L \cdot mg^{-1} \cdot m^{-1}$ , averaged over all permafrost zones; Manasypov et al., 2020).

485         Assuming that climate warming and permafrost thaw will produce a northward shift in  
486 the permafrost zones and applying a substituting space for time scenario, already tested for  
487 river, lake water, soil solutions and the GHG regime in the WSL (Krickov et al., 2018;  
488 Manasypov et al., 2014, 2020; Raudina et al., 2017, 2018; Serikova et al., 2019; Vorobyev et  
489 al., 2017), results of the present study suggest that phytoplankton biomass, cell number and  
490 community diversity in “southern” (isolated and sporadic zones) will not appreciably change.  
491 If the continuous permafrost zone disappears and discontinuous shifts northward, then one can  
492 expect a decrease in the cell number and biodiversity. An alternative scenario is that, due to  
493 thickening of the active layer, there will be an increase in groundwater connectivity leading  
494 primarily to thawing of currently frozen peat down to underlying mineral horizons. This may  
495 happen both at the lake border and in the lake sediments. As a result of enhanced mineral - lake  
496 water interaction across all permafrost zones, the pH of thermokarst lakes and ponds,  
497 determined by connectivity of lake water with mineral horizons, might increase upon the  
498 permafrost thaw. This, together with enhanced release of limiting nutrients (P, Si, Fe) from  
499 previously frozen soil minerals, may create favorable conditions for cyanobacterial and  
500 diatomous phytoplankton development in all permafrost regions.

501           **CONCLUSIONS**

502           A study of 27 shallow, acidic and organic-rich thermokarst lakes and thaw ponds across  
503 four permafrost zones of western Siberia permafrost peatlands, sampled over 3 main  
504 hydrological seasons demonstrated a lack of effect of the water body size on phytoplankton  
505 biomass and cell number. The dominant taxa in total biomass were Chlorophyta, Cryptophyta  
506 and Dinophyta, whereas Charophyta, Chlorophyta and Cyanophyceae accounted for the majority  
507 of species number without distinct control of season, lake size and permafrost zone. The  
508 biodiversity was the highest in the lakes of continuous permafrost zone and rather similar  
509 among other zones. The former exhibited the highest pH (across all seasons) and sufficiently  
510 high water temperature (during the summer), favorable for the phytoplankton development.

511           The phytoplankton biomass ranged from 0.2 to 5 mg<sub>wet</sub>·L<sup>-1</sup> and exhibited a local  
512 maximum in the sporadic to discontinuous permafrost zone in spring and summer and in the  
513 sporadic zone in autumn. The cell number varied from 500 to 15,000 cell·mL<sup>-1</sup>, had a maximum  
514 in the sporadic to discontinuous permafrost zone in spring, and increased northward in summer  
515 and autumn. There was an overall low controlling effect of lake water hydrochemistry on  
516 quantitative parameters of phytoplankton abundance. We hypothesize that rather harsh  
517 conditions at the beginning of thaw (low pH, high DOC and shallow photic layer) were  
518 counterbalanced by enhanced delivery of macro- and micro-nutrients from thawing peat and  
519 surface vegetation.

520           Thermokarst lakes of the WSL act as strong CO<sub>2</sub> emitters to the atmosphere due to the  
521 dominance of heterotrophic bacterial degradation of allochthonous DOM over the primary  
522 productivity of phytoplankton. Under a climate warming scenario, a thawing of peat permafrost  
523 and thickening of the active layer down to mineral horizons will lead to an increase in  
524 connectivity between the groundwater (mineral soils) and the lake. This may increase the lake  
525 water pH and some currently limiting nutrient concentrations. Such changes in lake

526 hydrochemistry may favor development of cyanobacteria and diatoms which are currently  
527 subordinate taxons relative to green and chara algae.

528

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535

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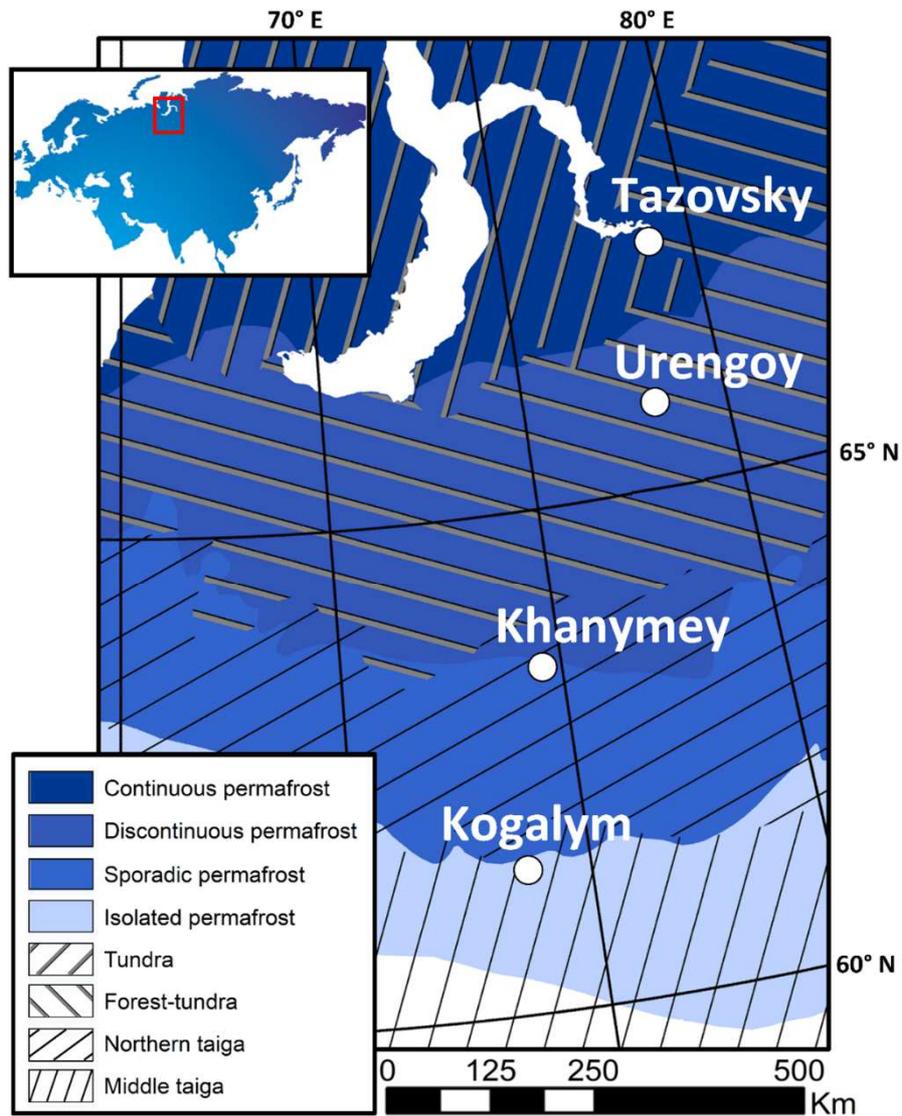
902 **Table 1.** The physio-geographical and climatic conditions of thermokarst lakes in four study sites of the Western Siberian Lowland. MAT is  
 903 mean annual air temperature.  
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Site	Coordinates	Permafrost zone	MAAT, °C	Mean annual precipitation, mm	Mineral substrate	Peat thickness, m	Seasonal thaw depth, cm	Lake average depth (summer), cm	Mean annual ice-free period, days	Melting date	Freeze-up date	Vegetation period, days
Tazovsky	67.4°N 78.7°E	Continuous	-9.1	363	clay loam and loam	0.2–1.5	44	90±35	111	25.05–10.06	12.09–30.09	93 (07.06–10.09)
Urengoy	66.0°N 78.3°E	Discontinuous	-7.8	453	loam and silt loam	0.3–1.2	49	36±25	118	20.05–05.06	20.09–05.10	96 (07.06–11.09)
Khanymey	63.8°N 75.6°E	Discontinuous/ Sporadic	-5.6	540	sand	0.7–1.1	40–90	45±27	137	15.05–05.06	25.09–07.10	107 (31.05–15.09)
Kogalym	62.3°N; 74.2°E	Isolated/ Sporadic	-4.0	594	sand	1.0–1.5	–	125±77	141	20.04–10.05	25.09–15.10	111 (29.05–17.09)

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**Table 2.** Taxa distribution in lakes during three observation seasons across the four permafrost zones.

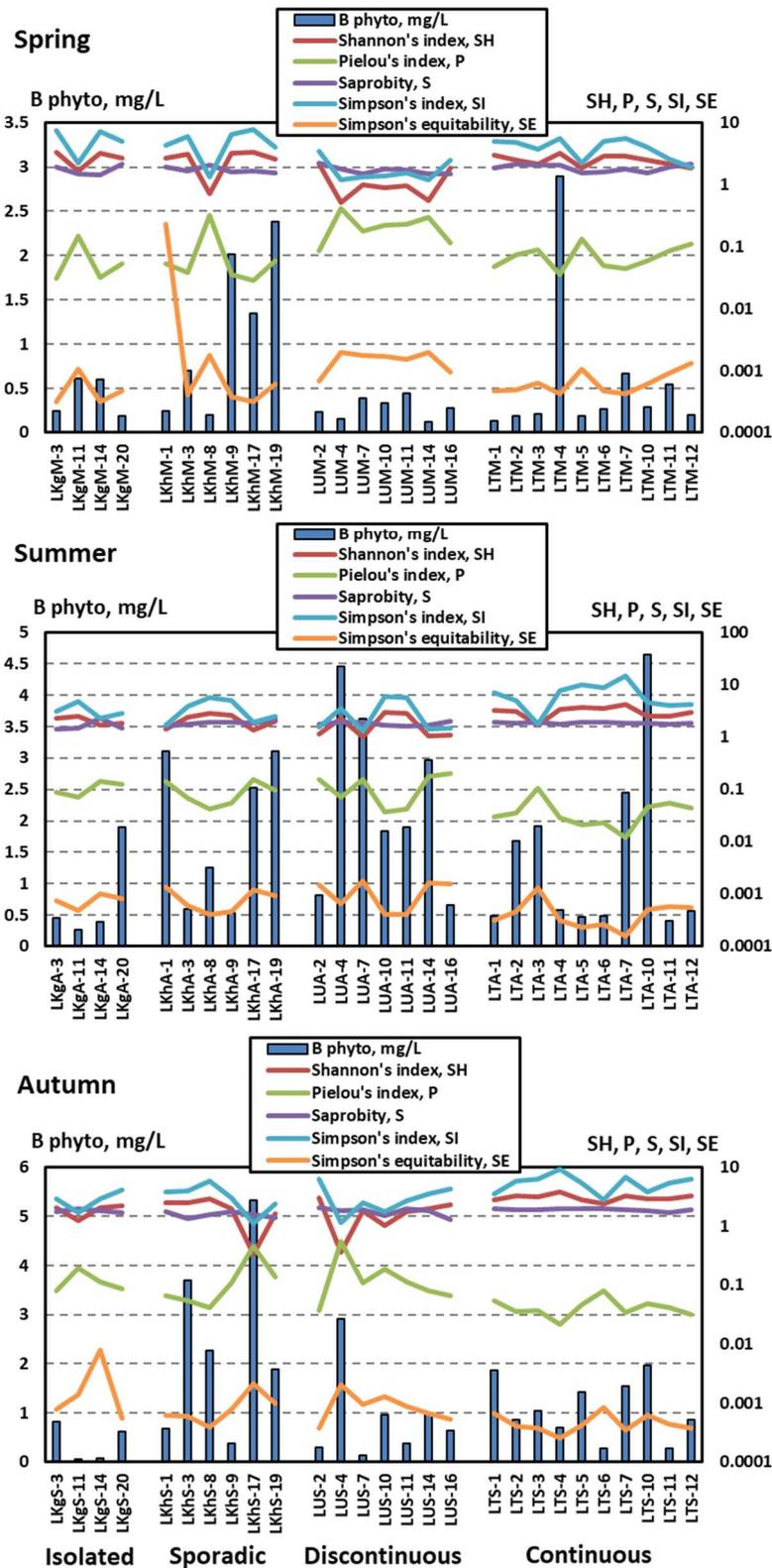
CONTINUOUS								
	Spring		Summer		Autumn		Total content	
		%		%		%		%
Cyanophyceae	8	10.7	25	19.2	12	10.8	30	14.2
Cryptophyta	8	10.7	8	6.2	10	9.0	19	9.0
Dinophyta	6	8.0	7	5.4	3	2.7	10	4.7
Chrysophyta	5	6.7	3	2.3	3	2.7	9	4.2
Bacillariophyta	8	10.7	6	4.6	11	9.9	14	6.6
Chlorophyta	17	22.7	31	23.8	25	22.5	47	22.2
Xanthophyta	1	1.3	2	1.5	1	0.9	4	1.9
Charophyta	18	24.0	36	27.7	35	31.5	61	28.8
Flagellata	1	1.3	1	0.8	2	1.8	2	0.9
Euglenozoa	3	4.0	11	8.5	9	8.1	16	7.5
Rhodophyta	0	0.0	0	0.0	0	0.0	0	0.0
<b>Total taxons</b>	<b>75</b>		<b>130</b>		<b>111</b>		<b>212</b>	
DISCONTINUOUS								
	Spring		Summer		Autumn		Total content	
		%		%		%		%
Cyanophyceae	3	9.4	9	12.7	2	4.4	14	13.3
Cryptophyta	4	12.5	6	8.5	3	6.7	8	7.6
Dinophyta	3	9.4	4	5.6	5	11.1	8	7.6
Chrysophyta	2	6.3	5	7.0	3	6.7	8	7.6
Bacillariophyta	6	18.8	5	7.0	4	8.9	9	8.6
Chlorophyta	3	9.4	7	9.9	8	17.8	13	12.4
Xanthophyta	1	3.1	1	1.4	0	0.0	2	1.9
Charophyta	6	18.8	29	40.8	17	37.8	37	35.2
Flagellata	2	6.3	2	2.8	1	2.2	2	1.9
Euglenozoa	2	6.3	3	4.2	2	4.4	4	3.8
Rhodophyta	0	0.0	0	0.0	0	0.0	0	0.0
<b>Total taxons</b>	<b>32</b>		<b>71</b>		<b>45</b>		<b>105</b>	
SPORADIC								
	Spring		Summer		Autumn		Total content	
		%		%		%		%
Cyanophyceae	7	11.5	4	8.3	2	5.1	9	9.6
Cryptophyta	6	9.8	3	6.3	3	7.7	7	7.4
Dinophyta	6	9.8	1	2.1	2	5.1	6	6.4
Chrysophyta	5	8.2	1	2.1	1	2.6	5	5.3
Bacillariophyta	6	9.8	6	12.5	3	7.7	10	10.6
Chlorophyta	10	16.4	9	18.8	9	23.1	20	21.3
Xanthophyta	0	0.0	1	2.1	0	0.0	1	1.1
Charophyta	17	27.9	18	37.5	16	41.0	30	31.9
Flagellata	2	3.3	1	2.1	2	5.1	2	2.1
Euglenozoa	2	3.3	3	6.3	1	2.6	3	3.2
Rhodophyta	0	0.0	1	2.1	0	0.0	1	1.1
<b>Total taxons</b>	<b>61</b>		<b>48</b>		<b>39</b>		<b>94</b>	
ISOLATED								
	Spring		Summer		Autumn		Total content	
		%		%		%		%
Cyanophyceae	8	19.0	2	8.3	0	0.0	10	13.7
Cryptophyta	5	11.9	4	16.7	4	15.4	10	13.7
Dinophyta	3	7.1	0	0.0	4	15.4	6	8.2
Chrysophyta	3	7.1	1	4.2	1	3.8	4	5.5
Bacillariophyta	7	16.7	4	16.7	6	23.1	13	17.8
Chlorophyta	6	14.3	7	29.2	4	15.4	13	17.8
Xanthophyta	3	7.1	1	4.2	0	0.0	3	4.1
Charophyta	5	11.9	4	16.7	3	11.5	10	13.7
Flagellata	2	4.8	1	4.2	2	7.7	2	2.7
Euglenozoa	0	0.0	0	0.0	2	7.7	2	2.7
Rhodophyta	0	0.0	0	0.0	0	0.0	0	0.0
<b>Total taxons</b>	<b>42</b>		<b>24</b>		<b>26</b>		<b>73</b>	



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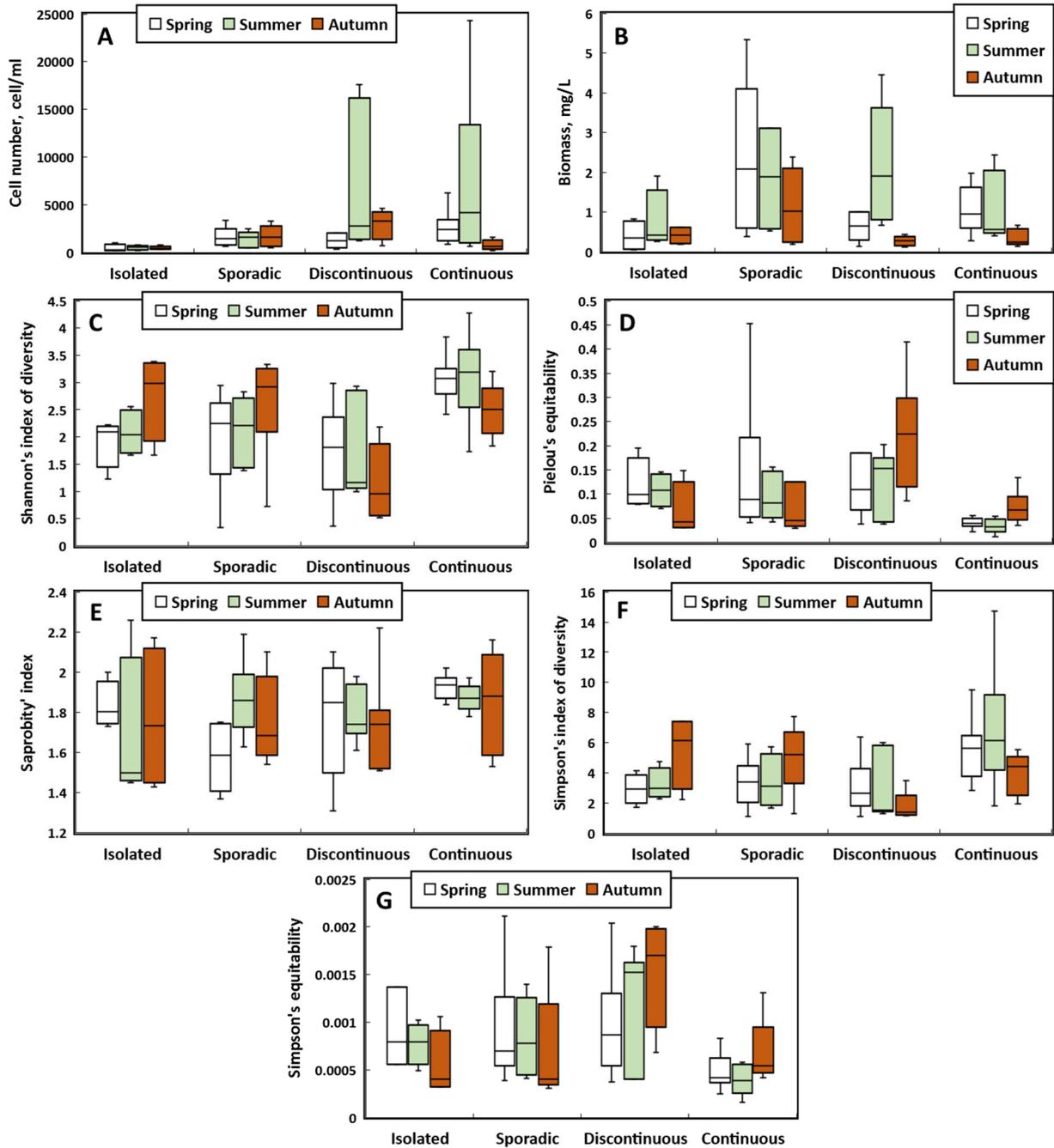
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912 **Figure 1.** Map of the study site. The area around the Tazovsky settlement (Continuous  
 913 permafrost zone), the area around the Urengoy settlement (Discontinuous permafrost zone), the  
 914 area around the Khanymey settlement (Sporadic permafrost zone) and the area around the  
 915 Kogalym city (Isolated permafrost zone).



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**Figure 2.** Quantitative parameters of phytoplankton abundance and biodiversity of individual lakes across four permafrost zones studied in spring (May), summer (August) and autumn (September). Abbreviations LKg, LKh, LU and LT stand for lakes sampled in isolated (Kogalym), sporadic (Khanymey), discontinuous (Urengoy) and continuous (Tazovsky) permafrost zones. See Table S1 for identification of lakes and their hydrochemical features.



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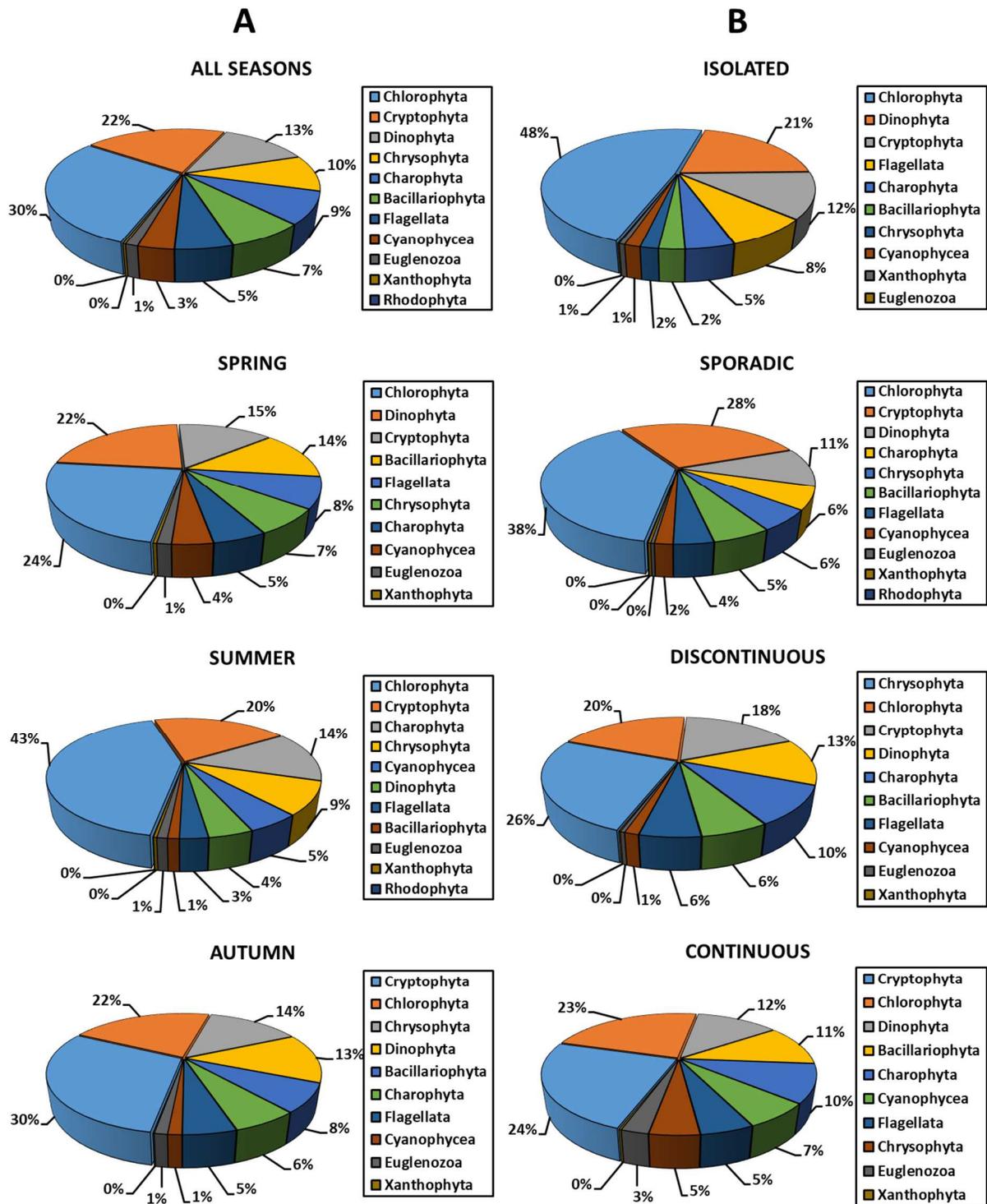
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926 **Figure 3.** Integral values (averaged from 4 to 10 lakes in each permafrost zone) of total cell  
927 number (A), biomass (B), Shannon (C), Pielou (D), Simpson (E) and Saprobity (F) indices for  
928 each permafrost zone during three main seasons.

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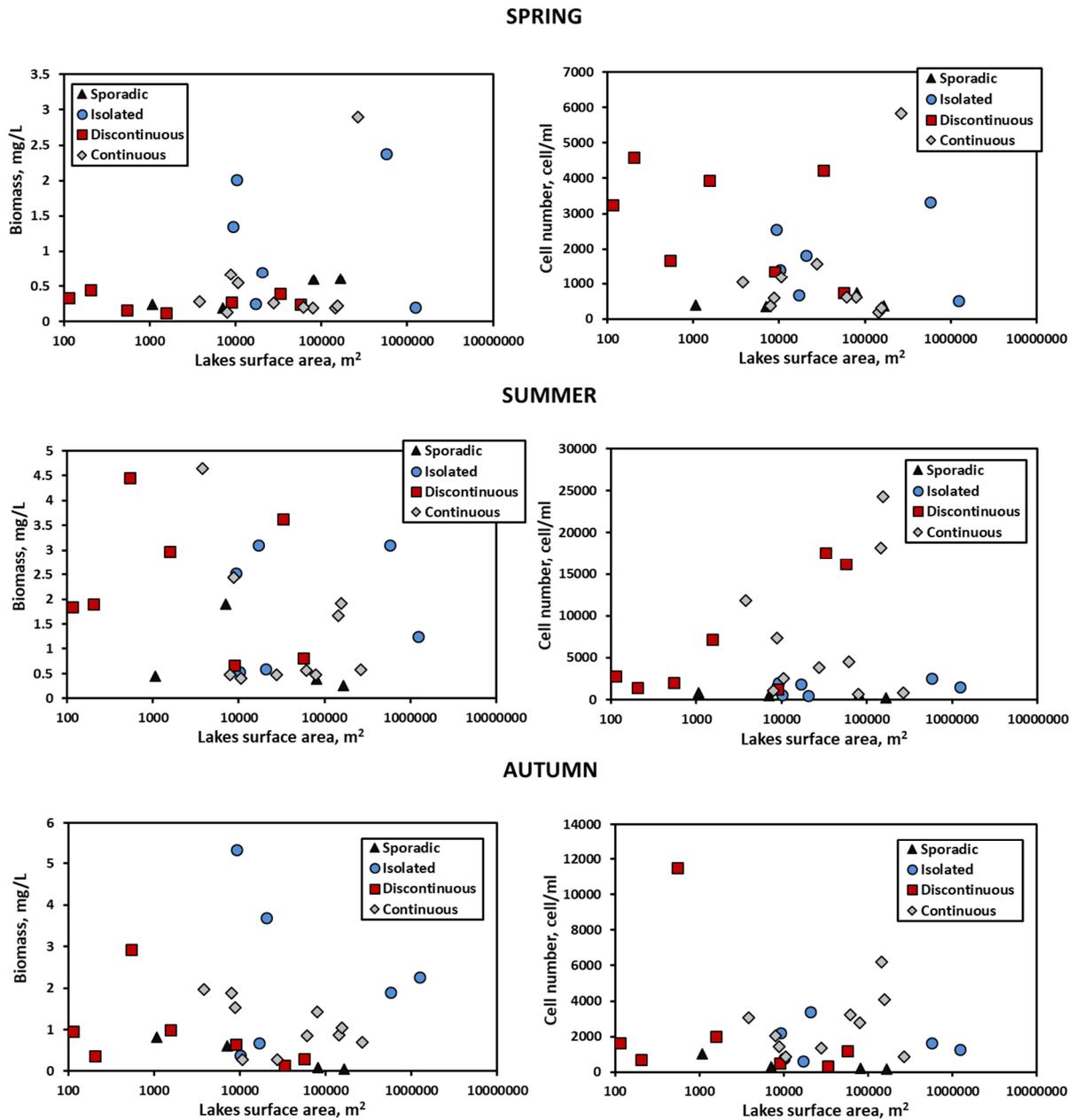
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**Figure 4.** Share of different taxa in overall phytoplankton biomass, averaged over all permafrost zones for different seasons (left column, **A**) and averaged over all seasons for four different permafrost zones (right column, **B**).

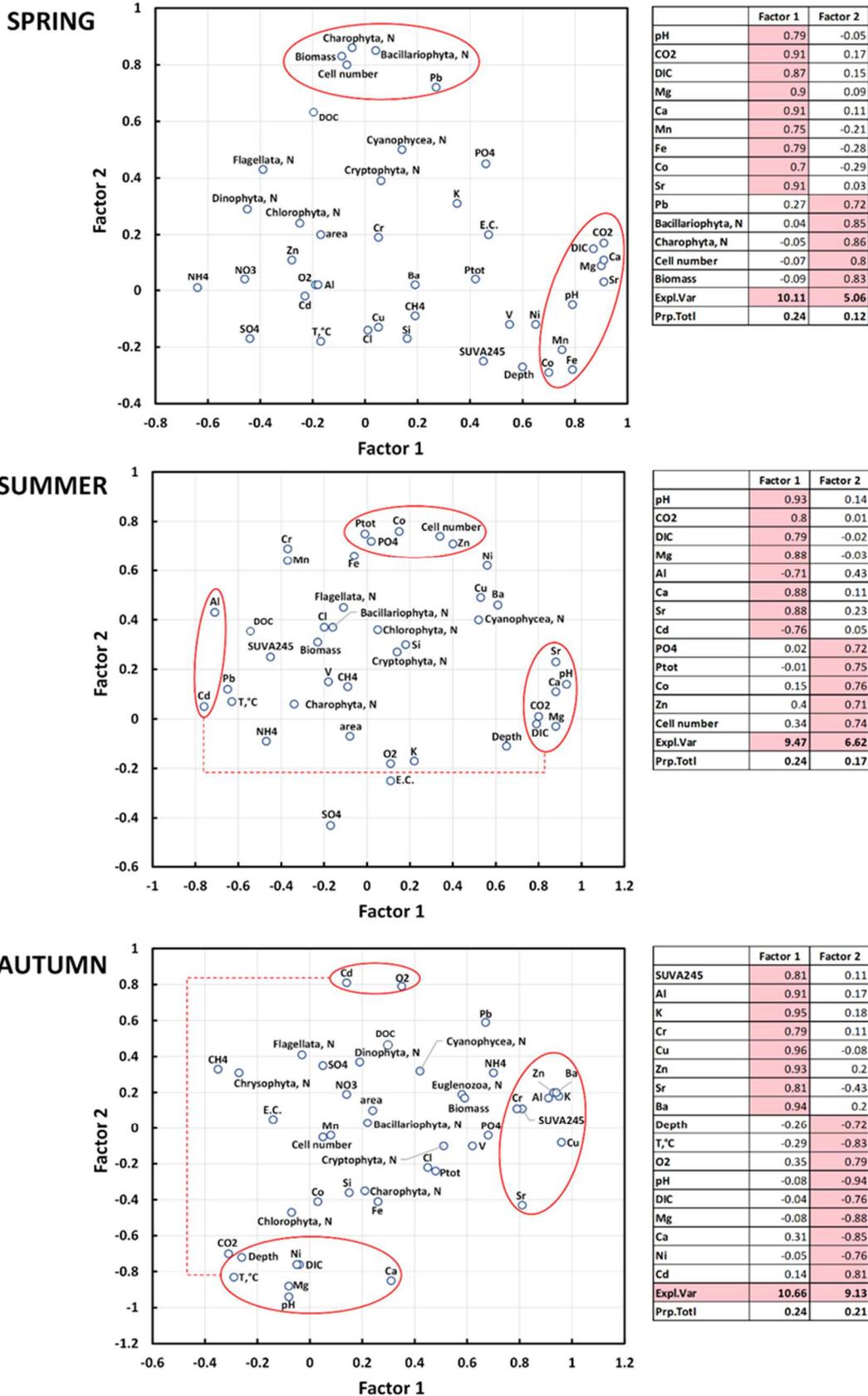


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941 **Figure 5.** Lack of lake size impact on phytoplankton biomass and cell number in thermokarst  
 942 lakes of western Siberia. The symbols represent the study sites of the four permafrost zones:  
 943 Kogalym (isolated), Khanymey (sporadic), Urengoy (discontinuous) and Tazovsky  
 944 (continuous).

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**Figure 6.** Results of PCA treatment of the whole database (all lakes, all permafrost zones) for spring (A), summer (B) and autumn (C). The red color denotes significant ( $p < 0.05$ ) link to the factor. Red ovals designate the components mostly affected by 1<sup>st</sup> or 2<sup>nd</sup> factor (based on statistical criterion).

## Environmental control on phytoplankton in thermokarst lakes of permafrost peatlands



DOC, macro-nutrients, lithogenic elements (Al, Cr) micro-nutrients (Zn, Ba) exhibited positive impact on phytoplankton abundance

