



HAL
open science

Laboratory growth capacity of an invasive cyanobacterium (*Microcystis aeruginosa*) on organic substrates from surface waters of permafrost peatlands

Dahédrey Payandi-Rolland, Liudmila Shirokova, Julien Larieux, Pascale Bénézeth, Oleg Pokrovsky

► To cite this version:

Dahédrey Payandi-Rolland, Liudmila Shirokova, Julien Larieux, Pascale Bénézeth, Oleg Pokrovsky. Laboratory growth capacity of an invasive cyanobacterium (*Microcystis aeruginosa*) on organic substrates from surface waters of permafrost peatlands. *Environmental Science: Processes & Impacts*, 2023, 25 (3), pp.659-669. 10.1039/d2em00456a . hal-04189443

HAL Id: hal-04189443

<https://hal.science/hal-04189443>

Submitted on 28 Aug 2023

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

26 **Abstract**

27 Within a global warming trend, invasive cyanobacteria, abundant in tropical and temperate
28 regions, can migrate northward and colonize thermokarst lakes in permafrost-affected
29 territories. Towards a better understanding of the cyanobacterial proliferation mechanism in
30 those lakes, we performed laboratory growth of typical invasive cyanobacteria, *Microcystis*
31 *aeruginosa*, onto various organic-rich solutions representative of permafrost peatlands.
32 Aqueous leachates of lichen, moss and peat were the most favorable substrates for massive
33 growth. The growth in the presence of all organic substrates produced a rise in solution pH by
34 two units and a sizable (30-50%) decrease in the concentration of dissolved organic carbon.
35 The observed increase of dissolved organic carbon aromaticity degree likely reflected
36 preferential cyanobacterial uptake of aliphatic, optically transparent organic substances.
37 Cyanobacterial growth over a bloom period can create a carbon sink (uptake of 2.5 and 8.3 g
38 C-CO₂ m⁻² d⁻¹) that can offset the net heterotrophic status of thermokarst lakes in the permafrost
39 peatlands, thus switching the lake status from C source to C sink. Therefore, predictions of the
40 future carbon exchanges with the atmosphere in surface waters of permafrost peatlands require
41 explicit accounting for the possibility of invasive cyanobacterial growth.

42

43 **1. Introduction**

44 On-going warming of the Arctic and subarctic surface waters is accompanied by more
45 frequent summer heatwaves inducing an increase in lakes water temperature up to 25-30 °C^{1,2}.
46 In this regard, thermokarst lakes, formed during massive and abrupt peat thaw in currently
47 frozen permafrost peatland, are especially interesting as they cover a sizable portion of land
48 surface in the Arctic and subarctic zone³⁻⁶. Due to their generally heterotrophic status, the
49 dominance of dissolved organic matter (DOM) and sediment respiration on primary production,

50 these lakes emit a sizable amount of CO₂ and CH₄ in the atmosphere, thus contributing to
51 positive feedback to climate warming at high latitudes ⁷⁻⁹.

52 A growing concern for all freshwater environments of the world is the development of
53 invasive cyanobacterial blooms primarily due to climate warming but also to an increase in
54 anthropogenic pressure ¹⁰⁻¹². The proliferation of these invasive microorganisms leads to
55 eutrophication of the water bodies, intoxication of native organisms and decreasing ecosystem
56 lakes' services ¹³⁻¹⁶. Phytoplankton and particularly cyanobacteria blooms are currently
57 observed in thermokarst lakes and will occur more frequently in the future due to global
58 warming ¹⁷⁻²¹. Indeed, main factors influencing the growth of cyanobacteria are light,
59 temperature and dissolved and suspended nutrient composition of the medium²². Arctic regions
60 can meet all those favorable conditions, naturally subjected to long period of sunshine during
61 summer season. The current global warming will increase global temperature and intensify
62 temperatures rise, especially in those regions where its impact is twice time faster than in other
63 regions of the world (e.g., arctic amplification phenomenon ^{23,24}). In addition, massive
64 permafrost thaw leads to the mobilization of nutrients from frozen peat layers ^{25,26} ; this is
65 especially true in the case of dispersed peat ice, which contains a sizable amount of low
66 molecular weight (and hence, potentially bioavailable forms) of dissolved organic matter
67 (DOM), phosphates, macro- and micro-nutrients ^{27,28} and carboxylic acids²⁹. These compounds
68 can become suitable substrates for cyanobacterial development, given that cyanobacteria are
69 capable to grow heterotrophically ³⁰⁻³² (mixotrophic combination of auto and heterotrophy).
70 Furthermore, it has been reported that post-wildfire precipitations increase the exports of
71 nutrient-enriched waters from burned areas ³³⁻³⁵ which can also lead to cyanobacterial blooms
72 and eutrophication ^{33,36,37} in temperate regions. In the high latitudes, these blooms can lead to a
73 net autotrophic status of thermokarst water bodies during summer periods ³⁸.

74 One such cyanobacterial species is *Microcystis aeruginosa*, which is the most common
75 genus forming freshwater cyanobacterial blooms³⁹ and the most common genera associated
76 with toxic blooms²². Its occurrence has already been noted in the Arctic/subarctic settings near
77 human activities, such as in Imandra Lake (Northern Europe) used as a cooling reservoir for a
78 nuclear power plant and for technical and drinking water supply⁴⁰, in sub-arctic lakes near
79 Saint Petersburg⁴¹, in Baltic sea⁴², as well as in other environments, from pristine to urban areas
80 through agricultural and industrial zones⁴³. The potential presence of *M. aeruginosa* in Arctic
81 and subarctic waters, the increasing number, frequency and extent of wildfires in those regions
82^{44,45}, and the favorable temperatures of surface waters reached during summer period could lead
83 to significant eutrophication. Despite the importance of this process, the environmental factors
84 controlling the proliferation of *M. aeruginosa* (temperature, insolation, inorganic nutrients,
85 dissolved organic matter) in Arctic and subarctic regions remain poorly constrained. Such a
86 lack of knowledge prevents foreseeing changes in thermokarst lakes' cyanobacterial
87 development, and notably assessing the future status of these lakes, *i.e.*, a possible switch from
88 a net heterotrophy (CO₂ emission to the atmosphere) to a net autotrophy (CO₂ uptake)^{8,38}. Note
89 that the C emission/uptake status of thermokarst lakes is one of the cornerstones of climate
90 warming's impact on the Arctic and subarctic water bodies⁷, allowing us to respond to the
91 question "Is there a positive or negative feedback of aquatic carbon (C) cycle to water
92 temperature rising and permafrost thaw?". Mains hypothesis are that *i*) both rising water
93 temperature and enhanced delivery of nutrients from frozen peat might trigger massive
94 phytoplankton bloom and *ii*) that the increase of tundra primary productivity will lead to
95 enhanced delivery of nutrients from plant litter leaching.

96 Towards better constraining the environmental factors governing cyanobacterial growth
97 in DOM-rich thermokarst lakes of permafrost peatlands, we performed laboratory growth
98 experiments using a typical invasive cyanobacteria, *M. aeruginosa*, and a series of natural

99 substrates, which are abundant in permafrost peatlands for which thermokarst lakes are fed by
100 precipitation (surface runoff) and shallow subsurface water input. To model the mains sources
101 of nutrients in those surface waters, we used aqueous leachates of peat (permafrost and active
102 layer) that can be the source of nutrients delivered *via* supra-permafrost flow, and tundra
103 vegetation (lichen and moss) that can deliver nutrient *via* runoff, together with original
104 thermokarst lake water, which combines nutrients from various sources. By encompassing a
105 large variety of natural DOM, we specifically aimed to (1) quantify the DOM uptake by
106 growing cyanobacteria; (2) identify the most suitable organic substrate for the growth of *M.*
107 *aeruginosa*, and (3) apply the obtained results for estimating the consequences of permafrost
108 thaw and water warming up on the carbon cycle in water bodies in these regions.

109 **2. Materials and Methods**

110 *2.1. Cyanobacteria origins and culture*

111 The cyanobacterium *Microcystis aeruginosa* (strain PMC 730.11) was obtained from
112 the National Natural History Museum (MNHN) in Paris. The strain used in this experiment
113 does not produce the microcystin cyanotoxin. Prior to the experiment, the cells were cultured
114 in a Z8 media (see details in **Figure S 1**) on a shaker under continuous light, at room temperature
115 (~20-25°C) and continuous air bubbling system for 7 days. At the end of the exponential –
116 stationary growth stage and prior to the experiments with natural substrates, cyanobacteria were
117 centrifuged to concentrate the biomass and rinsed 3 times using Milli-Q water to remove any
118 leftover of the Z8 culture broth and cell exometabolites. The development of cyanobacterial
119 biomass was monitored *via* measurements of the optical density at 680 nm (OD₆₈₀).

120

121 2.2. *Substrate: origins and use*

122 Organic substrates used in this experiment (ground vegetation, peat from the active layer
123 and permafrost, and thermokarst lake water) were collected in the Bolshezemelskaya Tundra
124 zone of North-East Europe (discontinuous permafrost area, see the description given in another
125 article ⁴⁶). All solid substrates were collected in the vicinity of the thermokarst lake. Vegetation
126 involved moss (*Sphagnum angustifolium*) and lichen (*Cladonia stellaris*) samples. Both of
127 these species are representative of boreal peatland ecosystems ⁴⁷ and their occurrence depends
128 on the microtopography of the peatland. Lichens are mostly spread on frozen mounds while
129 mosses mainly occur in depressions ⁴⁸. Peat was collected at two different depths: i) under the
130 first 2 cm of organic litter, within the active (unfrozen) layer, and ii) underneath the active layer
131 within the beginning of the permafrost (frozen horizon), *i.e.* between 30 to 40 cm depth. The
132 lake water was collected from a thermokarst lake (area of 1000 m²) and filtered on-site using a
133 sterile Millipore filtration unit (< 0.45 µm, Merck, France).

134 For all incubation experiments, we used only liquid substrates, *i.e.* aqueous leachates of
135 solid substrates described above (peats and vegetations). To prepare the leachates, the solid
136 phase reacted with sterile MilliQ water (10 g_{dry} L⁻¹) in aerobic conditions at room temperature
137 and under gentle mixing on a shaker. After 3 days of reaction, the suspension was centrifuged
138 at 4,500 g, filtered through a single use 0.45 µm Nalgene Rapid-Flow sterile filter units (Thermo
139 Fischer Scientific, France), and then used as a substrate in the experiment. Initial DOC
140 concentration in the leachates ranged between 10 and 60 mg L⁻¹, consistent with that occurring
141 in natural thaw ponds and depressions of the permafrost zone (10-100 mg L⁻¹) ^{49,50}.

142

143 2.3. *Incubation and sampling*

144 A scheme of the incubation set-up is given in **Figure 1**. Two types of reactors were
145 used: reactors with added cyanobacteria named “experimental reactors” (ER) and reactors

146 without added cyanobacteria (*i.e.*, control experiment) called “control reactors” (CR), both
147 placed under the same conditions.

148 Sterile 500 mL glass bottles with 300 mL of substrates were used as CR for each type
149 of substrate. In ER, a homogeneous suspension of the cyanobacteria was transferred into 500
150 mL sterile glass bottles, with substrates (300 mL) to obtain initial bacterial biomass of 1 g_{wet} L⁻¹.
151 ¹. Because of acidic conditions of most leachates, not favorable for cyanobacterial growth, the
152 initial pH of ER (prior to cyanobacteria addition) was adjusted between 5 and 6.5 using NaOH
153 solution (1N concentration). Experimental reactors were run in duplicates for each substrate.
154 Although it is common in biological experiments to use 3 to 5 replicates, we chose to run only
155 two replicates per substrates ER. In this configuration, all substrates (ER and CR) were run at
156 the same time to avoid *i*) variation of the “quality” of laboratory *Microcystis aeruginosa* strain,
157 *ii*) incubation temperature and luminosity variations, and also *iii*) for practical reasons of
158 sampling and analysis. Former works of our group in single bacterial culture experiments with
159 various natural substrates demonstrated adequate reproducibility of such laboratory growth
160 experiments^{20,51–56}.

161 Experimental (ER) and control (CR) reactors were placed under identical conditions *i.e.*,
162 aerated (the aeration was achieved *via* Biosilico® porous stoppers ; Thermo Fischer Scientific,
163 France), continuous light exposure and at 25 °C, which is an ideal growth temperature for
164 cyanobacteria⁵⁷. Note that such a temperature is frequently reached in thermokarst lakes waters
165 of permafrost peatlands during summer^{1,2,6,46}. To avoid the formation of cyanobacterial
166 aggregates at the bottom of the reactor, the suspension was stirred by a magnetic bar placed in
167 each reactor. A summary of the different types of reactors and substrates used in this experiment
168 is provided in **Table S 1**.

169 Note that, because natural leachates and lake water were filtered through a 0.45 µm and
170 not 0.22 µm pore size, they might contain their own native microbial community⁵⁸ (*i.e.* pico-,

171 nano- and a part of micro-phytoplankton). However, the amount of these “native” bacteria cells,
172 present in natural substrates and reported in literature, was several orders of magnitude lower
173 (10^4 - 10^5 cell mL⁻¹)^{6,46,59} than the initial concentration of *M. aeruginosa* ($1 \text{ g}_{\text{wet}} \text{ L}^{-1}$), $> 10^9$ cell
174 mL⁻¹ used in incubations.

175

176 *2.4. Analyses and treatment of experimental results*

177 Prior to the experiment, visual and UV-range absorbance of aquatic substrates were
178 measured between wavelength 200 and 800 nm, with a step of 1 nm. This allowed the
179 calculation of the Weight-Average Molecular Weight index in Da units (WAMW)⁶⁰ and the
180 specific UV absorbance index at 254 nm in L mg C⁻¹ m⁻¹ (SUVA₂₅₄)⁶¹ which was used to assess
181 the aromaticity of samples.

182 The experiments were terminated at different times of incubation, depending on the
183 amount of days needed to reach a steady state of cyanobacterial development (*i.e.* 13, 14, 16,
184 and 16 days for lake water, moss, lichen, and permafrost peat leachate incubations, respectively)
185 with the exception of the active layer peat leachate that was incubated over 29 days to achieve
186 the decline of the cyanobacterial population. A scheme of analyses performed on each sample
187 collected during incubation is presented in **Figure 1**. First, we sampled a homogenous
188 suspension of 10 mL from each reactor (under shaking). A non-filtered 4 mL aliquot was used
189 to measure pH (uncertainty of ± 0.01 pH units), conductivity ($\pm 0.1 \mu\text{S cm}^{-1}$) and optical density
190 at 680 nm (OD₆₈₀). The 680 nm wavelength was chosen to be a proxy of the cyanobacterial
191 biomass as this wavelength represents a spike in the absorbance spectrum of this cyanobacteria
192 ⁶² and as no overlap was observed at this wavelength between all substrates and the
193 cyanobacterial signal (tests done prior to the incubations). An aliquot of 6 mL was centrifuged
194 at 4500 g for 15 min and the supernatant was filtered through 0.45 μm before the measure of
195 UV absorbance at 254 nm (using a 10 mm quartz cuvette on a SpectroFlex spectrophotometer;

196 series 6600 – WTW). Dissolved organic and inorganic carbon (DOC and DIC) concentrations
197 in the filtrates were measured *via* Shimadzu TOC-VSC, with an uncertainty of 3%. Absorbance
198 at 254 nm wavelength has been defined as the best proxy for surface water DOC^{63,64} and the
199 calculated SUVA₂₅₄ index was used to assess the aromaticity of samples during the experiment.

200 Three indices were used to treat the results of the experiments: *i*) the total growth *ii*) the
201 apparent growth rate and *iii*) the DOC loss during the experiment. To estimate the total growth
202 and normalize the results, thus allowing the comparison between each substrate, we calculated
203 the percent of growth since the day 0 of the experiment:

$$204 \text{ Growth}_t(\%) = (OD_{680-ER_t} - OD_{680-ER_{t=0}}) \times \frac{100}{OD_{680-ER_{t=0}}} \quad (1)$$

205 where t represents the time of incubation. Apparent growth rate on each substrate was calculated
206 using a linear regression of the percent growth versus elapsed time of incubation, between the
207 last day of the adaptation phase to the last day of the exponential phase. Finally, the DOC loss
208 in ER was calculated relative to the initial conditions (day 0 of incubation) and subtracting the
209 DOC concentration in the control reactors from that in the experimental reactor at each
210 sampling time of the experiment:

$$211 \text{ DOC}_{loss_t} = (DOC_{ER_{t=0}} - DOC_{CR_{t=0}}) - (DOC_{ER_t} - DOC_{CR_t}) \quad (2)$$

212 where the units of DOC_{loss_t} and DOC concentration are mg L^{-1} and t corresponds to the time
213 of incubation.

214 3. Results and Discussion

215 3.1.M. *aeruginosa* growth on different substrates

216 The growth of *M. aeruginosa* in the presence of each substrate followed the same pattern
217 summarized in three main phases: adaptation, exponential growth and death (**Figure 2**). The
218 biomass development began with an adaptive period of time, which lasted between 20 (lake

219 ER) to 68 hours (lichen and permafrost peat ER) and was characterized by a weak decrease of
220 the cyanobacterial biomass. This period was followed by the exponential phase, during which
221 the population already adapted to the new conditions of the experiment and showed an increase
222 in biomass. This exponential phase lasted between 12 and 14 days (depending on the substrate).
223 The last phase could be monitored only for the active layer peat leachate. It consisted of the
224 decline of the population (the death phase), and lasted about 13 days.

225 The highest growth rate was achieved for the lichen leachate at 11 % biomass per hour between
226 day 3 and day 16 of incubation (**Table 1**). The growth rates in substrates followed the order
227 “lichen > active layer peat > permafrost peat > moss > thermokarst lake water”, with a minimal
228 growth rate at 2.2 % h⁻¹ for the lake water. Such differences in growth rates can be tentatively
229 explained by phenomena described in literature. Indeed, in natural settings, many factors can
230 inhibit the growth of cyanobacteria, such as a lack of nutrients, excessive light intensity⁶⁵,
231 water temperature⁵⁷ and the presence of toxic metals (Pb, Ni, Cd, Co, Zn)⁶⁶. On the other hand,
232 nutrient-rich and turbid water can promote cyanobacterial growth^{65,67}. The presence of humic
233 and fulvic acids (Ha and Fa) can be also beneficial for cyanobacteria, because these compounds
234 are capable of chelating the dissolved metals⁶⁶, thus alleviating their toxicity as well as
235 increasing the bioavailability of essential micro-nutrients. We hypothesize that the combination
236 of Ha and Fa, exhibiting high metal binding capacity, could be responsible for the difference in
237 the impact of different substrates on cyanobacterial growth rate. Indeed, the presence of both
238 Fa and Ha (WAMW respectively between 600 to 1000 Da, and between 1500 to 5000 Da)^{68,69}
239 at the pH of their maximal metal binding capacity (5-6 and 7-9, respectively)⁶⁸ can render
240 lichen, moss, active layer peat and permafrost peat leachate to be highly suitable substrate for
241 *M. aeruginosa* growth, especially at the beginning of experiment.

242 Considering thermokarst lake water substrate, weak growth of *M. aeruginosa* can be
243 explained by a competition with native phytoplankton (pico-, nano- or micro-phytoplankton

244 originated from 0.45 μm filtrated substrates leachates and filtrated lake water) that could have
245 outcompeted the introduced *M. aeruginosa* population. This hypothesis is supported by quick
246 increase of pH during the first two days of the experiment in the lake CR (**Figure 3**), which
247 could be a sign of a photosynthetic process as also evidenced from the pH evolution described
248 below.

249

250 *3.2. Chemical and biological consequences of cyanobacterial growth*

251 The pH evolution demonstrated an abrupt, over 2 to 3 units, rise during the first several
252 days of exposure (**Figure 3**). The maximal pH value, 10.0 to 10.3, was achieved in experiments
253 with lake water, moss and active layer peat leachates (**Figure 3A**). Note that in control
254 experiments, there was also some pH increase (**Figure 3B**), although the steady-state pH value
255 was 2-3 units lower than that in experiments with *M. aeruginosa*. Student test indicate that mean
256 differences between pH values of CR and ER (from each organic substrate) are significant
257 except for moss and lichen substrates (**Table S 2**). It is thus not excluded that some amount of
258 native cyanobacteria initially present in the substrates were photosynthesizing in the control
259 reactors as well. Note that, after approximately 7 days at the steady-state (stationary growth)
260 conditions, the pH of the active layer peat leachate ER decreased from 10 to 7, which was most
261 likely linked to cell lysis and cessation of photosynthesis.

262 Photosynthetically induced pH rises in experiments with added cyanobacteria (**Figure**
263 **S 2**) led to a sizable increase in DIC concentration, given that the reactors were open with
264 respect to the atmosphere and thus atmospheric CO_2 could be dissolved in alkaline fluids ⁷⁰
265 (**Figure S 3**).

266 The DOC concentration generally decreased starting from the very beginning of incubations
267 (**Figure 4**). The maximal loss of DOC ($81.8 \pm 1.0 \text{ mg L}^{-1}$) was achieved at the 5th day of

268 incubation in the moss ER. Maximum losses of DOC over the first 3 days in active layer peat,
269 lichen and permafrost peat ER were 29.5 ± 1.0 , 11.1 ± 0.6 and 1.1 ± 0.1 mg L⁻¹ respectively. It is
270 noteworthy that the control experiment also exhibited some decrease in DOC concentration
271 during entire incubation time. This decrease was less pronounced in permafrost peat and lake
272 CR (less than 2.9 mg L⁻¹ loss of DOC) but 10 times higher in moss CR (up to 111 mg L⁻¹ lost
273 in 14 days of incubations) than in active layer peat and lichen reactor (~12 mg.L⁻¹ DOC loss in
274 16 days) (**Figure S 4**).

275 The SUVA₂₅₄ was the highest in peat leachates and lake water, and demonstrated an
276 increase over the first 3 to 5 days of incubation (**Figure 5**). Such an increase may indicate the
277 uptake of optically-transparent, non-aromatic DOM by *M. aeruginosa*. Preferential uptake of
278 aliphatic compounds is known for the case of growth of other, non-invasive cyanobacteria such
279 as *Synechococcus* on moss leachate⁷¹. These authors reported that both autotrophic and
280 heterotrophic aquatic bacteria growing on moss leachate preferred not humic-like DOM, but
281 rather complex aliphatic and carboxylic acids. Note that some polyuronic acids such as decay-
282 resistant sphagnum (which is known to suppress microbial activity^{72,73}) may remain in solution
283 and contribute to the rise of SUVA₂₅₄ in the course of experiments. Overall, these observations
284 are consistent with former results that the soil and peat DOM are much less biodegradable than
285 the aquagenic DOM⁷⁴. Note that a decrease of SUVA₂₅₄ towards the end of experiment (**Figure**
286 **5**), and the slight increase in DOC after 10 days of experiment with peat and moss leachate
287 (**Figure 4**) could reflect a production of exometabolites of cyanobacteria, as well as cell lysis
288 which occurred at the declining stage of microbial development^{52,71}.

289

290 3.3. Pattern of cyanobacterial growth in active layer peat leachate ER

291 While other substrates experiments were stopped when a steady state of biomass
292 concentration was reached, the active layer peat ER was kept running for 29 days to monitor

293 all the growth phases of the cyanobacterium and assess the changes in physicochemical
294 parameters of the medium. As described in *section 3.1*, the growth of *M. aeruginosa* displayed
295 the same pattern in all ER, and included the adaptation and the exponential phases, followed by
296 the death phase (**Figure 6**). The discussion below will focus on the case of active layer peat,
297 because it is believed that the same behaviors are observed in all phases of other substrates.

298 The adaptation phase in experiments with active layer peat lasted for 44 hours, during which
299 the OD_{680 nm} dropped by 17 % h⁻¹ (**Figure 6A**) and the DOC concentration decreased by 39%
300 (from 55 to 22 mg L⁻¹, **Figure 6B**). This decrease is believed to be the result of DOC
301 biodegradation by the native heterotrophic microbial community as well as some heterotrophic
302 growth of cyanobacterium⁷¹. During this first phase, the SUVA₂₅₄ reached 3.9 ±0.4 L mg C⁻¹
303 m⁻¹ (**Figure 6C**) and the pH remained stable (~6.8) (**Figure 6D**). The combined decrease of
304 DOC and increase of SUVA₂₅₄ indicated a relative increase of aromatic carbon compounds due
305 to preferential biodegradation of aliphatic DOC. The second phase corresponds to an
306 exponential phase that lasted for 335 hours and during which the biomass of cyanobacteria
307 almost tripled (**Figure 6A**). The associated photosynthesis led to a drastic increase in pH from
308 6.8 to 9.6 with a maximum value reached after 209 hours of incubation (~10.3) (**Figure 6D**).
309 Concurrently, the DOC concentration increased by 11% between 44 (end of adaptation phase)
310 and 379 hours of exposure (**Figure 6B**) and SUVA₂₅₄ decreased from 3.9 to 2.6 L mg C⁻¹ m⁻¹
311 during this period (**Figure 6C**). The lysis of a part of *M. aeruginosa* cells are believed to be the
312 cause of the observed DOC increase. This provided new non-aromatic organic carbon to the
313 reactor leading to the relative decrease of SUVA₂₅₄. The death phase was characterized by a net
314 decrease of OD₆₈₀ (decline rate of -5.9 %·h⁻¹, **Figure 6A**), a slight increase of DOC (gain of
315 10%, **Figure 6B**), a decrease of SUVA₂₅₄ (from 2.6 to 2.0 L mg C⁻¹ m⁻¹, **Figure 6C**) and a pH
316 drop from 9.6 to 6.8 (**Figure 6D**). During this phase, cell lysis induced both the pH drop due to

317 the reduction of photosynthesis, and the DOC increase due to the release of cell content such
318 as cytoplasmic and various organic compounds to the aqueous solution ²⁰.

319

320 *3.4. Carbon capture potential during M. aeruginosa growth on natural organic*
321 *substrates and comparison with CO₂ evasion from thermokarst lake waters of*
322 *permafrost peatlands*

323 Over 15 days of incubation, the biomass of *M. aeruginosa* increased by a factor of 1.5
324 to 2, depending on the identity of the organic substrate (**Figure 2**). This translates into 1.5 to 2
325 g_{wet}.L⁻¹ produced during 10 to 15 days of incubation. Using results of the present laboratory
326 experiment and considering that the wet : dry biomass ratio of cyanobacteria is 8 to 10 ^{75,76}, and
327 that the carbon proportion in dry biomass is about 50%, the C uptake rate during cyanobacterial
328 growth ranges between 5 and 8.3 mg C L⁻¹ d⁻¹. By applying these results obtained under
329 laboratory conditions to observations made in natural environment, and considering that the
330 photic layer depth of surface waters in organic-rich permafrost peatlands is 0.5 to 1.0 m ^{6,77},
331 cyanobacterial growth over 2-weeks bloom period in the lake could create a C sink ranging
332 between 2.5 and 8.3 g C-CO₂.m⁻².d⁻¹. Such a high uptake rate can offset the net heterotrophic
333 status of thermokarst lakes (> 1000 m² area) in the permafrost peatlands (currently emitting
334 between 1 and 2 g C-CO₂.m⁻².d⁻¹) ^{6,8}. Therefore, during relatively short periods of summer
335 bloom, invasive cyanobacteria are capable of reversing the C balance of thermokarst lakes from
336 CO₂ source to C sink. At the same time, the estimations provided in the present study should
337 be considered as preliminary and likely conservative. The overall C balance of the aquatic
338 systems in permafrost peatlands will strongly depend on the relative proportion of large and
339 medium size thermokarst lakes and small thaw ponds and permafrost depressions. The latter
340 are known to be hot spots of C emissions ⁶, but at the same time, they are receiving the highest
341 input of terrestrial DOM from peat, moss and lichen leaching and degradation ^{55,56,59,77}. Taken

342 together, explicit provisions for possible invasive cyanobacterial proliferation in thermokarst
343 lakes and thaw ponds are needed for quantitative predictions of the future C exchanges with the
344 atmosphere in surface waters of permafrost peatlands. Such provisions are currently absent in
345 climate / biogeochemical models of permafrost regions.

346 It is noteworthy that after the bloom period, which mostly occurs in summer in Arctic and
347 subarctic regions, the generated biomass, if not buried in mineral sediments or in the form of
348 sapropel, may become a fresh source of labile DOM to surface waters. This newly imported C
349 source could be degraded by light (photodegradation) and heterotrophic bacteria
350 (biodegradation). Therefore, while during bloom period, the state of the thermokarst lake can
351 switch from source to sink of C to the atmosphere, the post-bloom period could become a time
352 of high OM degradation, thus creating sizable C emissions to the atmosphere, notably at the
353 end of summer period. Verification of this possibility, however, requires further experimental
354 and field work.

355 It is also necessary to point out that *M. aeruginosa* is a cyanobacterium that uses buoyancy
356 ecostrategy, *i.e.* when present in the euphotic part of the water column, the cells generate large
357 quantities of carbohydrates by photosynthesis⁷⁸. These carbohydrates act as a ballast and allow
358 the cells to sink to a darker part of the water column, where *M. aeruginosa* can consume these
359 extra carbohydrates by respiration and/or fermentation, which allows it to re-ascend towards
360 euphotic zone^{78,79}. In temperate regions, it has been shown that the decline of temperature in
361 autumn leads to the sinking of cyanobacteria towards the bottom of the lake, where they may
362 survive the winter⁶⁵. The effect of low temperature on the decrease of buoyancy capacity of *M.*
363 *aeruginosa* in non-turbulent waters has been also demonstrated by laboratories experiments
364^{80,81}. It is thus possible that, in the current context of global warming, the growth and blooms of
365 *M. aeruginosa* in thermokarst lakes could occur and lead to the dormancy of this

366 cyanobacterium in the bottom of lakes during winter therefore generating potential
367 recolonization of summer waters by this buoyancy mechanisms.

368

369 **4. Conclusions**

370 Laboratory growth of invasive cyanobacterium *Microcystis aeruginosa* demonstrated
371 its capacity to proliferate on various organic substrates, relevant to surface waters of permafrost
372 peatlands (lichen, moss and peat). The lichen leachate was by far the most favorable substrate
373 for *M. aeruginosa* bloom, producing a pH rise of 2 to 3 units and a two-fold increase in cell
374 biomass over two weeks of incubation in experimental reactors. Thermokarst lake water
375 appeared to be less favorable for cyanobacterial growth, although not hostile. The cyanobacteria
376 were capable of decreasing DOC concentration in aqueous leachate of organic compounds, *via*
377 preferentially consuming non-aromatic carbon. It follows that, at the conditions of proliferating
378 invasive cyanobacteria bloom, the C balance of thermokarst lake can be reverted from C source
379 (currently emitting CO₂ to the atmosphere) to C sink, fixing organic C in the form of
380 cyanobacterial biomass for a short period of time. However, the net effect of cyanobacteria on
381 the net balance of C in the lake may be seasonally dependent, *i.e.* after the bloom period, all
382 freshly created cyanobacterial biomass could be degraded and counterbalance the initial C-sink,
383 although this possible degradation needs to be verified by further work. Furthermore, variable
384 buoyant capacity of *M. aeruginosa* lead to surface – bottom migration allowing persisting of
385 this bacterium in Arctic and subarctic peatlands surface waters over several seasons. Upon on-
386 going climate warming in permafrost territories, accounting for possibility of invasive
387 cyanobacterial blooms may become an issue of concern when foreseeing the net C balance of
388 aquatic systems via modeling approaches.

389

390 **Data availability**

391 All research data are available with the following Mendeley data reference: DOI:
392 10.17632/mnb2g87h6v.3

393 **Conflict of interest**

394 The authors declare no conflict of interest.

395 **Acknowledgements**

396 Dahédrey Payandi-Rolland was supported by a fellowship from the French “Ministère de
397 l’Enseignement Supérieur, de la Recherche et de l’Innovation”. We acknowledge the main
398 funding from the RSF grant No 22-17-00253 to Liudmila S. Shirokova. Oleg S. Pokrovsky was
399 partially supported by the TSU Program Priority-2030. We thank Carole Causserand for all the
400 DOC and DIC analyses. We also thank Claude Yéprémian from the MNHN Paris for the
401 *Microcystis aeruginosa* strains and the indications on its broth culture fabrication (Z8 broth).

402 **Author contributions (CRediT)**

403 **D. Payandi-Rolland:** conceptualization, investigation, visualization, writing – original draft,

404 **J. Larieux:** investigation, **L.S. Shirokova:** supervision, validation, writing – original draft, **P.**

405 **Bénézeth:** supervision, validation, writing – original draft, **O.S. Pokrovsky:** conceptualization,

406 supervision, validation, writing – original draft. All authors read and approved the final

407 manuscript.

408 **References**

- 409 1 O. S. Pokrovsky, L. S. Shirokova, S. N. Kirpotin, S. P. Kulizhsky and S. N. Vorobiev, Impact
410 of western Siberia heat wave 2012 on greenhouse gases and trace metal concentration in
411 thaw lakes of discontinuous permafrost zone, *Biogeosciences*, 2013, **10**, 5349–5365.
412 2 L. S. Shirokova, O. S. Pokrovsky, S. N. Kirpotin, C. Desmukh, B. G. Pokrovsky, S. Audry
413 and J. Viers, Biogeochemistry of organic carbon, CO₂, CH₄, and trace elements in
414 thermokarst water bodies in discontinuous permafrost zones of Western Siberia,
415 *Biogeochemistry*, 2013, **113**, 573–593.
416 3 B. B. Cael and D. A. Seekell, The size-distribution of Earth’s lakes, *Sci. Rep.*, 2016, **6**, 29633.

- 417 4 Y. M. Polishchuk, A. N. Bogdanov, I. N. Muratov, V. Y. Polishchuk, A. Lim, R. M.
418 Manasypov, L. S. Shirokova and O. S. Pokrovsky, Minor contribution of small thaw ponds
419 to the pools of carbon and methane in the inland waters of the permafrost-affected part of
420 the Western Siberian Lowland, *Environ. Res. Lett.*, 2018, **13**, 045002.
- 421 5 Y. M. Polishchuk, A. N. Bogdanov, V. Y. Polishchuk, R. M. Manasypov, L. S. Shirokova,
422 S. N. Kirpotin and O. S. Pokrovsky, Size Distribution, Surface Coverage, Water, Carbon,
423 and Metal Storage of Thermokarst Lakes in the Permafrost Zone of the Western Siberia
424 Lowland, *Water*, 2017, **9**, 228.
- 425 6 S. A. Zabelina, L. S. Shirokova, S. I. Klimov, A. V. Chupakov, A. G. Lim, Y. M. Polishchuk,
426 V. Y. Polishchuk, A. N. Bogdanov, I. N. Muratov, F. Guerin, J. Karlsson and O. S.
427 Pokrovsky, Carbon emission from thermokarst lakes in NE European tundra, *Limnol.*
428 *Oceanogr.*, 2021, **66**, S216–S230.
- 429 7 J. Karlsson, S. Serikova, S. N. Vorobyev, G. Rocher-Ros, B. Denfeld and O. S. Pokrovsky,
430 Carbon emission from Western Siberian inland waters, *Nat. Commun.*, 2021, **12**, 825.
- 431 8 S. Serikova, O. S. Pokrovsky, H. Laudon, I. V. Krickov, A. G. Lim, R. M. Manasypov and
432 J. Karlsson, High carbon emissions from thermokarst lakes of Western Siberia, *Nat.*
433 *Commun.*, 2019, **10**, 1552.
- 434 9 K. M. Walter Anthony and S. A. Zimov, 2009, pp. U44A-02.
- 435 10 J. Huisman, G. A. Codd, H. W. Paerl, B. W. Ibelings, J. M. H. Verspagen and P. M. Visser,
436 Cyanobacterial blooms, *Nat. Rev. Microbiol.*, 2018, **16**, 471–483.
- 437 11 J. M. O’Neil, T. W. Davis, M. A. Burford and C. J. Gobler, The rise of harmful cyanobacteria
438 blooms: The potential roles of eutrophication and climate change, *Harmful Algae*, 2012, **14**,
439 313–334.
- 440 12 S. Suikkanen, M. Laamanen and M. Huttunen, Long-term changes in summer phytoplankton
441 communities of the open northern Baltic Sea, *Estuar. Coast. Shelf Sci.*, 2007, **71**, 580–592.
- 442 13 K. E. Havens, in *Cyanobacterial Harmful Algal Blooms: State of the Science and Research*
443 *Needs*, ed. H. K. Hudnell, Springer, New York, NY, 2008, pp. 733–747.
- 444 14 M. Nazari-Sharabian, S. Ahmad and M. Karakouzian, Climate Change and Eutrophication:
445 A Short Review, *Eng. Technol. Appl. Sci. Res.*, 2018, **8**, 3668–3672.
- 446 15 M. Olokotum, V. Mitroi, M. Troussellier, R. Semyalo, C. Bernard, B. Montuelle, W. Okello,
447 C. Quiblier and J.-F. Humbert, A review of the socioecological causes and consequences of
448 cyanobacterial blooms in Lake Victoria, *Harmful Algae*, 2020, **96**, 101829.
- 449 16 B. Qin, G. Gao, G. Zhu, Y. Zhang, Y. Song, X. Tang, H. Xu and J. Deng, Lake eutrophication
450 and its ecosystem response, *Chin. Sci. Bull.*, 2013, **58**, 961–970.
- 451 17 C. C. Carey, B. W. Ibelings, E. P. Hoffmann, D. P. Hamilton and J. D. Brookes, Eco-
452 physiological adaptations that favour freshwater cyanobacteria in a changing climate, *Water*
453 *Res.*, 2012, **46**, 1394–1407.
- 454 18 S. Kosten, V. L. M. Huszar, E. Bécares, L. S. Costa, E. van Donk, L.-A. Hansson, E.
455 Jeppesen, C. Kruk, G. Lacerot, N. Mazzeo, L. De Meester, B. Moss, M. Lürling, T. Nöges,
456 S. Romo and M. Scheffer, Warmer climates boost cyanobacterial dominance in shallow
457 lakes, *Glob. Change Biol.*, 2012, **18**, 118–126.
- 458 19 H. W. Paerl and V. J. Paul, Climate change: Links to global expansion of harmful
459 cyanobacteria, *Water Res.*, 2012, **46**, 1349–1363.
- 460 20 L. S. Shirokova, L. Kunhel, J.-L. Rols and O. S. Pokrovsky, Experimental Modeling of
461 Cyanobacterial Bloom in a Thermokarst Lake: Fate of Organic Carbon, Trace Metal, and
462 Carbon Sequestration Potential, *Aquat. Geochem.*, 2015, **21**, 487–511.
- 463 21 R. Sinha, L. A. Pearson, T. W. Davis, M. A. Burford, P. T. Orr and B. A. Neilan, Increased
464 incidence of *Cylindrospermopsis raciborskii* in temperate zones – Is climate change
465 responsible?, *Water Res.*, 2012, **46**, 1408–1419.
- 466 22 L. Giannuzzi, in *Algae*, ed. W. Yee, IntechOpen, London, 2018.

- 467 23 J. E. Overland and M. Wang, When will the summer Arctic be nearly sea ice free?, *Geophys.*
468 *Res. Lett.*, 2013, **40**, 2097–2101.
- 469 24 M. C. Serreze, A. P. Barrett, J. C. Stroeve, D. N. Kindig and M. M. Holland, The emergence
470 of surface-based Arctic amplification, *The Cryosphere*, 2009, **3**, 11–19.
- 471 25 S. V. Loiko, O. S. Pokrovsky, T. V. Raudina, A. Lim, L. G. Kolesnichenko, L. S. Shirokova,
472 S. N. Vorobyev and S. N. Kirpotin, Abrupt permafrost collapse enhances organic carbon,
473 CO₂, nutrient and metal release into surface waters, *Chem. Geol.*, 2017, **471**, 153–165.
- 474 26 M. R. Turetsky, B. W. Abbott, M. C. Jones, K. W. Anthony, D. Olefeldt, E. A. G. Schuur,
475 G. Grosse, P. Kuhry, G. Hugelius, C. Koven, D. M. Lawrence, C. Gibson, A. B. K. Sannel
476 and A. D. McGuire, Carbon release through abrupt permafrost thaw, *Nat. Geosci.*, 2020, **13**,
477 138–143.
- 478 27 A. G. Lim, S. V. Loiko and O. S. Pokrovsky, Sizable pool of labile organic carbon in peat
479 and mineral soils of permafrost peatlands, western Siberia, *Geoderma*, 2022, **409**, 115601.
- 480 28 A. G. Lim, S. V. Loiko, D. M. Kuzmina, I. V. Krickov, L. S. Shirokova, S. P. Kulizhsky, S.
481 N. Vorobyev and O. S. Pokrovsky, Dispersed ground ice of permafrost peatlands: Potential
482 unaccounted carbon, nutrient and metal sources, *Chemosphere*, 2021, **266**, 128953.
- 483 29 D. M. Kuzmina, A. G. Lim, S. V. Loiko, L. S. Shirokova, F. Julien, J.-L. Rols and O. S.
484 Pokrovsky, Dispersed ice of permafrost peatlands represents an important source of labile
485 carboxylic acids, nutrients and metals., *Geoderma*.
- 486 30 H. Ming, G. Yan, X. Zhang, X. Pei, L. Fu and D. Zhou, Harsh temperature induces
487 *Microcystis aeruginosa* growth enhancement and water deterioration during vernalization,
488 *Water Res.*, 2022, **223**, 118956.
- 489 31 M. Kong, J. Chao, W. Han, C. Ye, C.-H. Li and W. Tian, Degradation Characteristics of
490 Phosphorus in Phytoplankton-Derived Particulate Organic Matter and Its Effects on the
491 Growth of Phosphorus-Deficient *Microcystis aeruginosa* in Lake Taihu, *Int. J. Environ. Res.*
492 *Public Health*, 2019, **16**, 2155.
- 493 32 Y. M. El-Ayouty and S. Abd-El-Rahman, Structural variations in peptide toxins of
494 *Microcystis aeruginosa* grown on different carbon sources, *J. Nat. Toxins*, 1996, **5**, 39–47.
- 495 33 K. D. Bladon, M. B. Emelko, U. Silins and M. Stone, Wildfire and the Future of Water
496 Supply, *Environ. Sci. Technol.*, 2014, **48**, 8936–8943.
- 497 34 D. M. Kuzmina, Artem G. Lim, Sergey V. Loiko, and Oleg S. Pokrovsky, Experimental
498 assessment of tundra fire impact on element export and storage in permafrost peatlands, *Sci.*
499 *Total Environ.*, 2022, **853**, 158701.
- 500 35 H. G. Smith, G. J. Sheridan, P. N. J. Lane, P. Nyman and S. Haydon, Wildfire effects on
501 water quality in forest catchments: A review with implications for water supply, *J. Hydrol.*,
502 2011, **396**, 170–192.
- 503 36 K. Klose, S. D. Cooper and D. M. Bennett, Effects of wildfire on stream algal abundance,
504 community structure, and nutrient limitation, *Freshw. Sci.*, 2015, **34**, 1494–1509.
- 505 37 M. Odhiambo and J. Routh, Does Black Carbon Contribute to Eutrophication in Large
506 Lakes?, *Curr. Pollut. Rep.*, 2016, **2**, 236–238.
- 507 38 L. Hughes-Allen, Paleoenvironmental reconstructions and greenhouse gas characterization
508 in permafrost aquatic systems of Central Yakutia (Siberia), Université Paris-Saclay, 2022.
- 509 39 M. J. Harke, M. M. Steffen, C. J. Gobler, T. G. Otten, S. W. Wilhelm, S. A. Wood and H.
510 W. Paerl, A review of the global ecology, genomics, and biogeography of the toxic
511 cyanobacterium, *Microcystis* spp., *Harmful Algae*, 2016, **54**, 4–20.
- 512 40 D. B. Denisov, E. N. Chernova and I. V. Russkikh, in *Advanced Technologies for Sustainable*
513 *Development of Urban Green Infrastructure*, eds. V. Vasenev, E. Dovletyarova, R.
514 Valentini, Z. Cheng, C. Calfapietra, L. Inostroza and M. Leuchner, Springer International
515 Publishing, Cham, 2020, pp. 161–170.

- 516 41 E. Chernova, I. Russkikh, E. Voyakina and Z. Zhakovskaya, Occurrence of microcystins and
517 anatoxin-a in eutrophic lakes of Saint Petersburg, Northwestern Russia, *Oceanol. Hydrobiol.*
518 *Stud.*, 2016, **45**, 466–484.
- 519 42 E. Chernova, S. Sidelev, I. Russkikh, E. Voyakina and Z. Zhakovskaya, First observation of
520 microcystin- and anatoxin-a-producing cyanobacteria in the easternmost part of the Gulf of
521 Finland (the Baltic Sea), *Toxicon*, 2019, **157**, 18–24.
- 522 43 A. B. Caracciolo, L. Dejana, C. Fajardo, P. Grenni, M. Martin, G. Mengs, S. Sánchez-Fortún,
523 T. Lettieri, M. L. Saccà and L. K. Medlin, A new fluorescent oligonucleotide probe for in-
524 situ identification of *Microcystis aeruginosa* in freshwater, *Microchem. J.*, 2019, **148**, 503–
525 513.
- 526 44 J. L. McCarty, J. Aalto, V.-V. Paunu, S. R. Arnold, S. Eckhardt, Z. Klimont, J. J. Fain, N.
527 Evangeliou, A. Venäläinen, N. M. Tchepakova, E. I. Parfenova, K. Kupiainen, A. J. Soja, L.
528 Huang and S. Wilson, Reviews and syntheses: Arctic fire regimes and emissions in the 21st
529 century, *Biogeosciences*, 2021, **18**, 5053–5083.
- 530 45 Z. Zhang, L. Wang, N. Xue and Z. Du, Spatiotemporal Analysis of Active Fires in the Arctic
531 Region during 2001–2019 and a Fire Risk Assessment Model, *Fire*, 2021, **4**, 57.
- 532 46 L. S. Shirokova, I. Ivanova, R. Manasyrov, O. Pokrovsky, A. Chupakov, S. Iglovsky, N.
533 Shorina, S. Zabelina, M. Gofarov, D. Payandi-Rolland, A. Chupakova and O. Moreva, The
534 evolution of the ecosystems of thermokarst lakes of the Bolshezemelskaya tundra in the
535 context of climate change, *E3S Web Conf.*, 2019, **98**, 02010.
- 536 47 M. R. Turetsky, S. E. Crow, R. J. Evans, D. H. Vitt and R. K. Wieder, Trade-offs in resource
537 allocation among moss species control decomposition in boreal peatlands, *J. Ecol.*, 2008, **96**,
538 1297–1305.
- 539 48 I. I. Volkova, T. V. Callaghan, I. V. Volkov, N. A. Chernova and A. I. Volkova, South-
540 Siberian mountain mires: Perspectives on a potentially vulnerable remote source of
541 biodiversity, *Ambio*, 2021, **50**, 1975–1990.
- 542 49 O. S. Pokrovsky, R. M. Manasyrov, S. V. Loiko and L. S. Shirokova, Organic and organo-
543 mineral colloids in discontinuous permafrost zone, *Geochim. Cosmochim. Acta*, 2016, **188**,
544 1–20.
- 545 50 T. V. Raudina, S. V. Loiko, A. Lim, R. M. Manasyrov, L. S. Shirokova, G. I. Istigechev, D.
546 M. Kuzmina, S. P. Kulizhsky, S. N. Vorobyev and O. S. Pokrovsky, Permafrost thaw and
547 climate warming may decrease the CO₂, carbon, and metal concentration in peat soil waters
548 of the Western Siberia Lowland, *Sci. Total Environ.*, 2018, **634**, 1004–1023.
- 549 51 L. S. Shirokova, P. Bénézech, O. S. Pokrovsky, E. Gerard, B. Ménez and H. Alfredsson,
550 Effect of the heterotrophic bacterium *Pseudomonas reactans* on olivine dissolution kinetics
551 and implications for CO₂ storage in basalts, *Geochim. Cosmochim. Acta*, 2012, **80**, 30–50.
- 552 52 L. S. Shirokova, R. Bredoire, J.-L. Rols and O. S. Pokrovsky, Moss and Peat Leachate
553 Degradability by Heterotrophic Bacteria: The Fate of Organic Carbon and Trace Metals,
554 *Geomicrobiol. J.*, 2017, **34**, 641–655.
- 555 53 O. V. Oleinikova, L. S. Shirokova, E. Gérard, O. Yu. Drozdova, S. A. Lapitskiy, A. Yu.
556 Bychkov and O. S. Pokrovsky, Transformation of organo-ferric peat colloids by a
557 heterotrophic bacterium, *Geochim. Cosmochim. Acta*, 2017, **205**, 313–330.
- 558 54 O. V. Oleinikova, L. S. Shirokova, O. Y. Drozdova, S. A. Lapitskiy and O. S. Pokrovsky,
559 Low biodegradability of dissolved organic matter and trace metals from subarctic waters,
560 *Sci. Total Environ.*, 2018, **618**, 174–187.
- 561 55 D. Payandi-Rolland, L. S. Shirokova, P. Nakhle, M. Tesfa, A. Abdou, C. Causserand, B.
562 Lartiges, J.-L. Rols, F. Guérin, P. Bénézech and O. S. Pokrovsky, Aerobic release and
563 biodegradation of dissolved organic matter from frozen peat: Effects of temperature and
564 heterotrophic bacteria, *Chem. Geol.*, 2020, **536**, 119448.

- 565 56D. Payandi-Rolland, L. S. Shirokova, M. Tesfa, P. Bénézech, A. G. Lim, D. Kuzmina, J.
566 Karlsson, R. Giesler and O. S. Pokrovsky, Dissolved organic matter biodegradation along a
567 hydrological continuum in permafrost peatlands, *Sci. Total Environ.*, 2020, **749**, 141463.
- 568 57R. D. Robarts and T. Zohary, Temperature effects on photosynthetic capacity, respiration,
569 and growth rates of bloom-forming cyanobacteria, *N. Z. J. Mar. Freshw. Res.*, 1987, **21**,
570 391–399.
- 571 58J. F. Dean, J. R. van Hal, A. J. Dolman, R. Aerts and J. T. Weedon, Filtration artefacts in
572 bacterial community composition can affect the outcome of dissolved organic matter
573 biolability assays, *Biogeosciences*, 2018, **15**, 7141–7154.
- 574 59L. S. Shirokova, A. V. Chupakov, I. S. Ivanova, O. Y. Moreva, S. A. Zabelina, N. A.
575 Shutskiy, S. V. Loiko and O. S. Pokrovsky, Lichen, moss and peat control of C, nutrient and
576 trace metal regime in lakes of permafrost peatlands, *Sci. Total Environ.*, 2021, **782**, 146737.
- 577 60Y.-Ping. Chin, George. Aiken and Edward. O’Loughlin, Molecular Weight, Polydispersity,
578 and Spectroscopic Properties of Aquatic Humic Substances, *Environ. Sci. Technol.*, 1994,
579 **28**, 1853–1858.
- 580 61G. Abbt-Braun and F. H. Frimmel, Basic characterization of Norwegian NOM samples —
581 Similarities and differences, *Environ. Int.*, 1999, **25**, 161–180.
- 582 62W. Liang, J. Qu, L. Chen, H. Liu and P. Lei, Inactivation of *Microcystis aeruginosa* by
583 Continuous Electrochemical Cycling Process in Tube Using Ti/RuO₂ Electrodes, *Environ.*
584 *Sci. Technol.*, 2005, **39**, 4633–4639.
- 585 63J. K. Edzwald, W. C. Becker and K. L. Wattier, Surrogate parameters for monitoring organic
586 matter and THM precursors, *Journal-American Water Works Assoc.*, 1985, **77**, 122–132.
- 587 64M. Peacock, C. D. Evans, N. Fenner, C. Freeman, R. Gough, T. G. Jones and I. Lebron, UV-
588 visible absorbance spectroscopy as a proxy for peatland dissolved organic carbon (DOC)
589 quantity and quality: considerations on wavelength and absorbance degradation, *Environ.*
590 *Sci. Process. Impacts*, 2014, **16**, 1445–1461.
- 591 65R. Mur, O. M. Skulberg and H. Utkilen, in *Toxic Cyanobacteria in Water: A guide to their*
592 *public health consequences, monitoring and management*, eds. I. Chorus and J. Bartram, E
593 & FN Spon, 1999.
- 594 66N. Ohkubo, O. Yagi and M. Okada, Effects of Humic and Fulvic Acids on the Growth of
595 *Microcystis Aeruginosa*, *Environ. Technol.*, 1998, **19**, 611–617.
- 596 67J. D. Chaffin, T. B. Bridgeman, S. A. Heckathorn and S. Mishra, Assessment of *Microcystis*
597 growth rate potential and nutrient status across a trophic gradient in western Lake Erie, *J. Gt.*
598 *Lakes Res.*, 2011, **37**, 92–100.
- 599 68J. M. Garcia-Mina, Stability, solubility and maximum metal binding capacity in metal-
600 humic complexes involving humic substances extracted from peat and organic compost, *Org.*
601 *Geochem.*, 2006, **37**, 1960–1972.
- 602 69R. L. Malcolm, The uniqueness of humic substances in each of soil, stream and marine
603 environments, *Anal. Chim. Acta*, 1990, **232**, 19–30.
- 604 70W. Stumm and J. J. Morgan, *Aquatic chemistry: chemical equilibria and rates in natural*
605 *waters*, John Wiley & Sons, Inc, New York Chichester Brisbane Toronto Singapore, Third
606 edition., 1996.
- 607 71L. S. Shirokova, J. Labouret, M. Gurge, E. Gérard, I. S. Ivanova, S. A. Zabelina and O. S.
608 Pokrovsky, Impact of Cyanobacterial Associate and Heterotrophic Bacteria on Dissolved
609 Organic Carbon and Metal in Moss and Peat Leachate: Application to Permafrost Thaw in
610 Aquatic Environments, *Aquat. Geochem.*, 2017, **23**, 331–358.
- 611 72R. Aerts, J. T. A. Verhoeven and D. F. Whigham, Plant-Mediated Controls on Nutrient
612 Cycling in Temperate Fens and Bogs, *Ecology*, 1999, **80**, 2170–2181.

- 613 73 T. J. Painter, Lindow man, tollund man and other peat-bog bodies: The preservative and
614 antimicrobial action of Sphagnum, a reactive glycuronoglycan with tanning and sequestering
615 properties, *Carbohydr. Polym.*, 1991, **15**, 123–142.
- 616 74 H. V.-M. Nguyen and J. Hur, Tracing the sources of refractory dissolved organic matter in a
617 large artificial lake using multiple analytical tools, *Chemosphere*, 2011, **85**, 782–789.
- 618 75 C. Grimm, V. Mavromatis, A. Leis, O. S. Pokrovsky and E. H. Oelkers, The temporal
619 evolution of the carbon isotope composition of calcite in the presence of cyanobacteria,
620 *Chem. Geol.*, 2021, **584**, 120556.
- 621 76 C. Grimm, R. E. Martinez, O. S. Pokrovsky, L. G. Benning and E. H. Oelkers, Enhancement
622 of cyanobacterial growth by riverine particulate material, *Chem. Geol.*, 2019, **525**, 143–167.
- 623 77 R. M. Manasyrov, A. G. Lim, I. V. Krickov, L. S. Shirokova, S. N. Vorobyev, S. N. Kirpotin
624 and O. S. Pokrovsky, Spatial and Seasonal Variations of C, Nutrient, and Metal
625 Concentration in Thermokarst Lakes of Western Siberia Across a Permafrost Gradient,
626 *Water*, 2020, **12**, 1830.
- 627 78 R. H. Thomas and A. E. Walsby, Buoyancy Regulation in a Strain of *Microcystis*,
628 *Microbiology*, 1985, **131**, 799–809.
- 629 79 J. C. Kromkamp and L. R. Mur, Buoyant density changes in the cyanobacterium *Microcystis*
630 *aeruginosa* due to changes in the cellular carbohydrate content, *FEMS Microbiol. Lett.*, 1984,
631 **25**, 105–109.
- 632 80 J. Kromkamp, J. Botterweg and L. R. Mur, Buoyancy regulation in *Microcystis aeruginosa*
633 grown at different temperatures, *FEMS Microbiol. Ecol.*, 1988, **4**, 231–237.
- 634 81 J. You, K. Mallery, J. Hong and M. Hondzo, Temperature effects on growth and buoyancy
635 of *Microcystis aeruginosa*, *J. Plankton Res.*, 2018, **40**, 16–28.
- 636

637

638

639

640

641

642

643

644

645

646 **Tables and Figures**

647 *Tables*

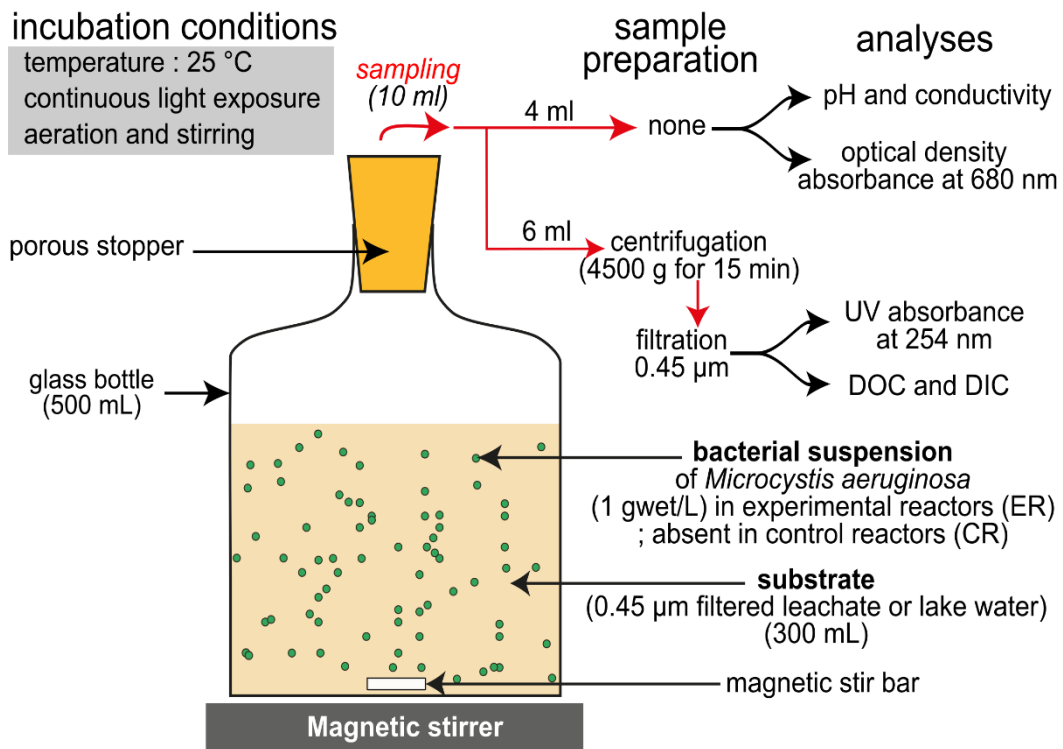
648 **Tab. 1:** Growth rates obtained by linear regression of the exponential phase in ER
 649 (experimental reactors) incubations of all substrates, and absorbance spectroscopy index of all
 650 substrates prior to the experiment.

Substrates	Growth rate parameters			DOM optical indices	
	Time for rate calculation, h	growth rate (% biomass h ⁻¹)	R ²	SUVA ₂₅₄ , L mg C ⁻¹ m ⁻¹	WAMW, Da
moss	44-331	7.6	0.95	0.1	510
lichen	68-379	11.4	0.89	1.9	1260
active layer peat	44-379	9.6	0.97	6.0	2800
permafrost peat	68-379	8.5	0.84	8.9	4400
lake water	20-317	2.2	0.49	4.7	2300

651

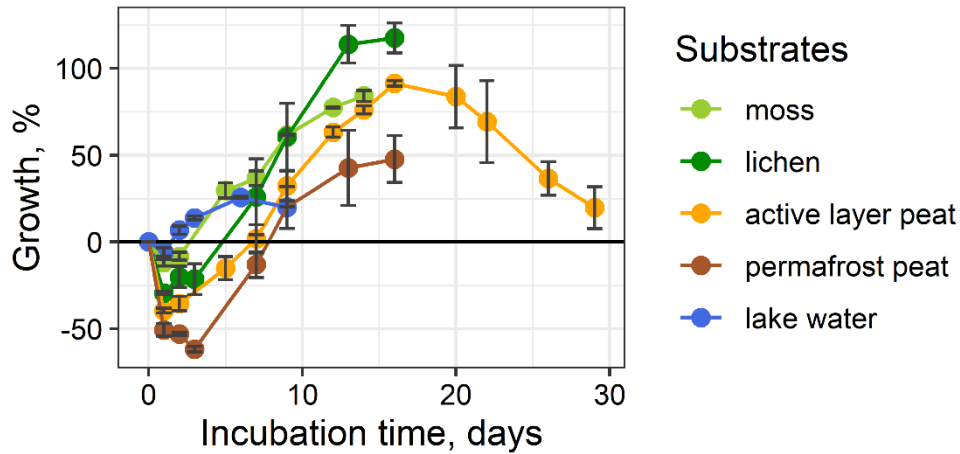
652

653 *Figures*



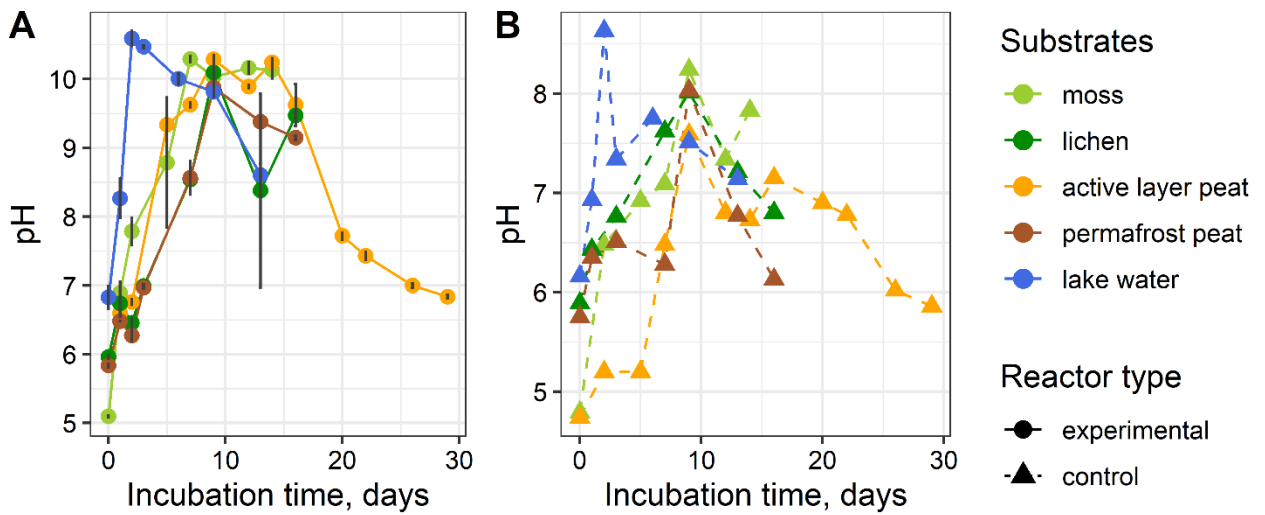
654

655 **Fig. 1:** Schematic of incubation set-up and various analyses performed during sampling.



656

657 **Fig. 2:** Percent of growth since day 0 of the invasive cyanobacterium *M. aeruginosa* on aqueous
 658 leachates of different organic substrates from permafrost peatlands and thermokarst lake
 659 water. The data represent the average of duplicates with error bars of standard deviations.

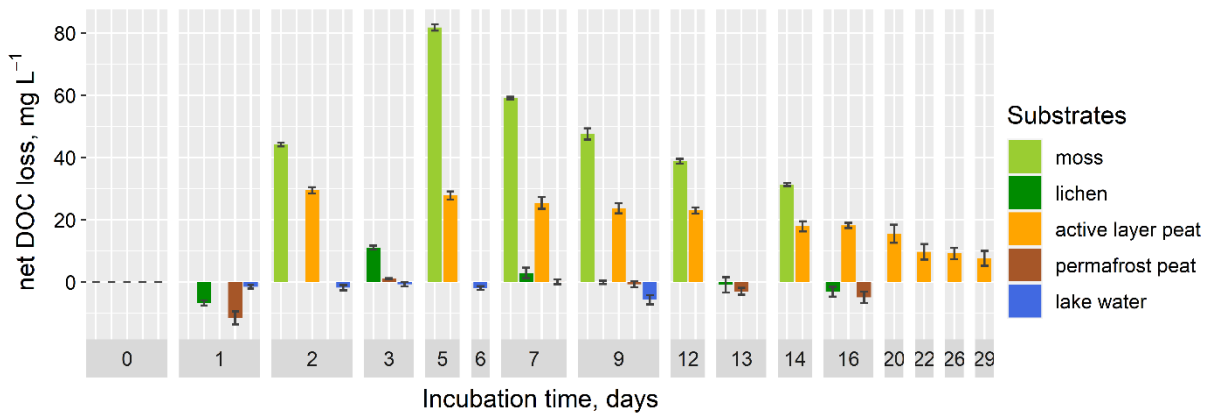


660

661 **Fig. 3:** Changes of pH in experimental (with added *Microcystis aeruginosa*; **A**) and
 662 control (**B**) reactors over incubation time.

663

664

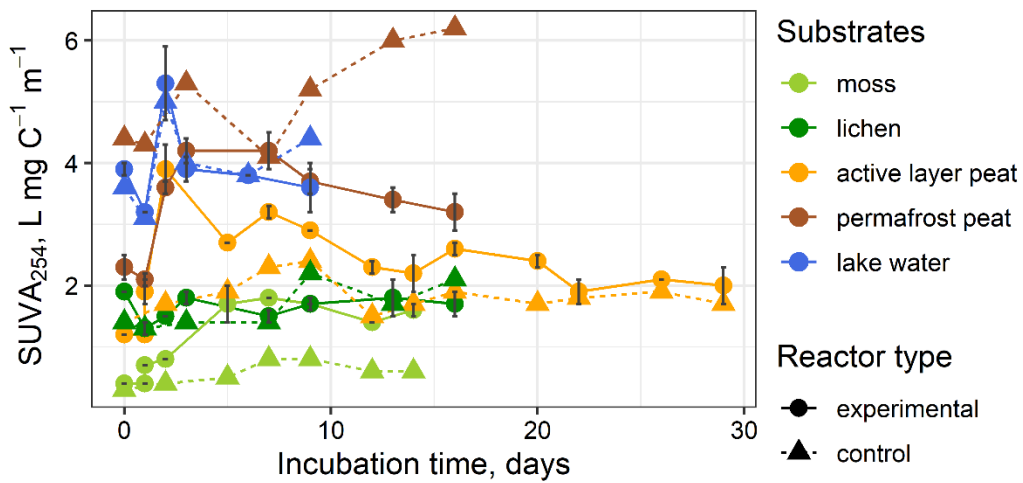


665

666 **Fig. 4:** Net DOC loss for all ER (experimental reactors) during the incubation relative to
667 DOC at day 0 of incubation (note that the DOC concentrations ER have been subtracted by
668 the DOC concentration in the related CR (control reactors) at the same day of experiment).

669

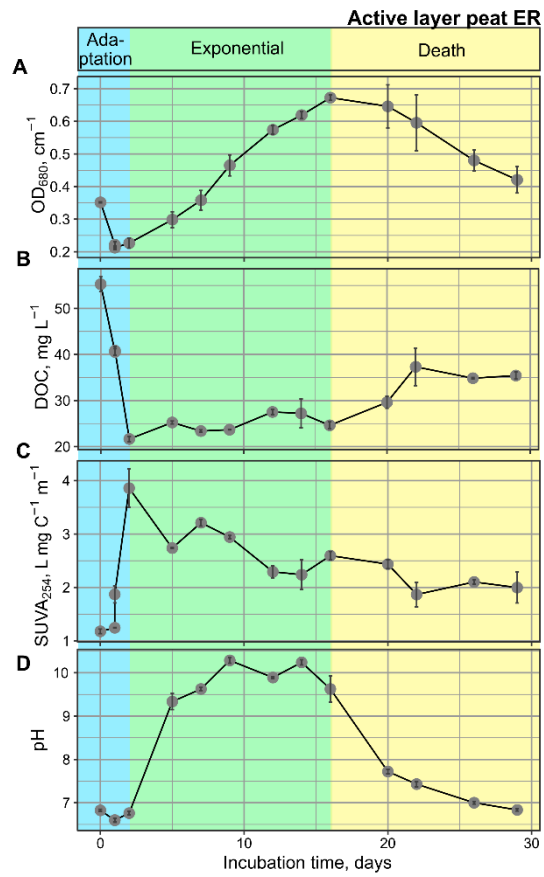
670



671

672 **Fig. 5:** SUVA₂₅₄ evolution during incubation of ER (experimental reactors) and CR
673 (control reactors).

674



675

676

677

678

Fig. 6: Cyanobacterial growth phases in active layer peat leachate ER (experimental reactors) through 29 days of incubations and associated evolution of (A) optical density at 680 nm, (B) DOC, (C) SUVA₂₅₄, and (D) pH.