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Competitiveness of invasive and native cyanobacteria from temperate freshwaters under various light and temperature conditions

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Abstract

Some tropical cyanobacteria have spread to temperate freshwaters during the last decades. To evaluate their further development in temperate lakes we studied the temperature, and light, dependent growth of three invasive (Cylindrospermopsis raciborskii, Anabaena bergii, Aphanizomenon aphanizomenoides) and three native (Aphanizomenon gracile, Aphanizomenon flos-aquae, Anabaena macrospora) cyanobacterial species (Nostocales) from German lakes. We also included one potentially invasive (Aphanizomenon ovalisporum) Nostocales species. We conducted semi-continuous culture experiments and a microcosm experiment along a natural light gradient. Temperature data were used to design a model to simulate the development of selected species according to three temperature scenarios (past, present and future).

Native species had significantly higher growth rates than invasive species and the potential invader A. ovalisporum at low temperatures ($\leq 10^{\circ}$ C), while the opposite was true at high temperatures $(\geq 35^{\circ}C)$. Maximum growth rates of A. ovalisporum, A. aphanizomenoides and C. raciborskii were clearly higher than those of A. bergii and the native species. Regarding light-dependent growth, significant differences were found between single species but not between all native and invasive 29 50 species. The model simulation demonstrates a shift in dominance from the native A. gracile in the historic scenario to C. raciborskii populations in the future scenario, in which also the potential invader A. ovalisporum is able to establish populations in temperate lakes. Our findings suggest that any further temperature increase would promote the growth and development of Nostocales species in general, and that of the invasive species in particular, and would enable a more northward expansion of A. ovalisporum.

Introduction

In the course of global warming, many species could expand their range from lower to higher latitudes (Parmesan, 2006). In the case of prokaryotes including freshwater cyanobacteria it has been stated that 'Everything is everywhere, but, the environment selects' (Baas Becking, 1934), from which it was concluded that cyanobacteria were cosmopolitan (Fogg et al., 1973). Nowadays, it is well established that not only cosmopolitan cyanobacterial species, but also species with holarctic or pantropical distributions exist (Komárek, 1994; Hoffmann, 1996). Cylindrospermopsis raciborskii (Woloszynská) Seenayya & Subba Raju 1972 is a prime example of a cyanobacterial species that has spread from tropical and subtropical to temperate latitudes of the northern and 56 65 ₅₈ 66 southern hemisphere over the last decades (Padisák, 1997: Wiedner et al., 2007). In Germany, C. raciborskii is now widespread (Stüken et al., 2006) and accounts for a considerable proportion of the phytoplankton biovolume (Nixdorf et al., 2003; Mischke, 2003). Two other cyanobacteria, Anabaena bergii Ostenfeld 1908 and Aphanizomenon aphanizomenoides (Forti) Horecká &

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Komáreck 1979, were recently reported for the first time in German freshwaters (Stüken et al., 2006) and other temperate regions, e.g. North Carolina/USA (Moisander et al., 2002), Slovakia (Hindák, 2000) and Poland (Stefaniak and Kokocinski, 2005). These three invasive cyanobacteria of the order Nostocales are able to fix molecular nitrogen and can survive unfavourable conditions as akinetes (resting stages).

Such invasive species are of general ecological interest as they can have a major impact on community composition and ecosystem processes (Sala et al., 2000; Strayer et al., 2006). The successful establishment of an invasive species in a new habitat depends on its invasive potential and the invasibility of the native community (Lonsdale et al., 1999). In this context, the competitive potential of invasive species against native species that are overlapping in an ecological niche is of crucial importance. Since all three invasive species belong to the order Nostocales, their niche most likely overlaps with that of native Nostocales species. In temperate freshwaters, the invasive species are most abundant in polymictic shallow lakes (Stüken et al., 2006), where they co-exist with a great variety of native Nostocales of the genus Anabaena and Aphanizomenon, among which 27 84 Aphanizomenon gracile is the most frequent and abundant (Mischke and Nixdorf, 2003; Rücker et 29 85 al., 2007). However, the invasive species can also be found, albeit less abundantly, in stratified lakes (Stüken et al., 2006), where the most frequent Nostocales are Aphanizomenon flos-aquae and several taxa of the genus Anabaena.

Temperature and light intensity, the two abiotic factors that vary most between latitudes, are key 34 88 factors in the regulation of Nostocales growth and, presumably, of range expansion of tropical and subtropical species. Previous studies have shown that light is the main growth-limiting factor of Nostocales populations in temperate freshwaters, where they were out-competed by Oscillatoriales under light limitation and high nutrient conditions (Zevenboom, 1982; Scheffer, 1998; Wiedner et al., 2002). Light is also a growth-limiting factor for C. raciborskii populations in temperate waters 43 93 (Wiedner et al., 2007). Ecophysiological studies show that C. raciborskii require high light intensities (80 to 120 μ mol photons m⁻² s⁻¹) for maximum growth (Shafik et al., 2001; Briand et al., 2004); this is similar to the light intensities (100 to 110 μ mol photons m⁻² s⁻¹) required by Aphanizomenon species (Gentile and Maloney, 1969; Uehlinger, 1981). However, Padisák and 50 97 52 98 Reynolds (Padisák and Reynolds, 1998) consider C. raciborskii a shade-tolerant species due to its low light saturation parameter (I_K) .

⁵⁵/₅₆100 Cyanobacteria are known to have higher temperature optima than other phytoplankton species
 ⁵⁷/₅₈101 (Reynolds and Walsby, 1975; Paerl and Huisman, 2009). However, our knowledge about species
 ⁵⁸/₅₉102 specific differences in the temperature requirements within the cyanobacteria community is still
 ⁶⁰103 incomplete. Temperature plays an important role in the onset of Nostocales akinete germination in
 ⁶¹ spring (Kim et al., 2005; Rücker et al., 2009) and in their vegetative growth during the season.

2 105 Earlier increases in water temperatures in spring as well as a rise in the entire temperature amplitude 4 106 were found to promote the development of C. raciborskii in temperate freshwaters (Wiedner et al., 107 2007). Minimum temperatures, for example, required for growth of C. raciborskii, as determined in 108 field and laboratory studies, range from 15°C to 22°C (Dokulil and Mayer, 1996; Shafik et al., 9 109 2001; Mischke et al., 2003). The optimum growth temperature (T_{opt}) for C. raciborskii, as 10 determined in culture experiments, ranges from 29 to 31°C (Shafik et al., 2001; Briand et al., 2004), 11110 12 13111 which is slightly higher than that for Aphanizomenon and Anabaena species, namely, 20 to 28°C 14 15 112 (Foy et al., 1976; Uehlinger, 1981). However, as the published results are based on a mixture of 16 113 17 different field and culture studies and culture methods, data comparisons are difficult. So far, no 18114 direct comparison of C. raciborskii with other Nostocales species in terms of temperature and light-19 20115 dependent growth has been published. Moreover, there are only few studies available on the 21 22116 ecology of A. aphanizomenoides (Moisander et al., 2002; Stefaniak and Kokocinski, 2005), and 23 24¹¹⁷ none for A. bergii. Data about temperature-dependent growth of Aphanizomenon ovalisporum, a 25118 potentially invasive Nostocales species currently restricted to the Mediterranean region of Europe 26 27119 (Gkelis et al., 2005; Quesada et al., 2006), are restricted to strains from Lake Kinneret (Israel), 28 29 120 where Hadas and co-workers (Hadas et al., 2002) estimated that its T_{opt} ranges between 26 and 30 31 121 30 30°C. ³² 122 33 In summary, current knowledge about the temperature and light-dependent growth of invasive and 34123 potentially invasive species in relation to native Nostocales species is insufficient to assess their 35 36124 competitive potential and predict their development in temperate freshwaters as a consequence of

37 38 125 37 climate change. Therefore, the aim of the present study was to determine the temperature and light-³⁹₄₀126 dependent growth of three invasive and three native Nostocales species from German freshwater as 41 127 well as of one potentially invasive species. Three approaches were used: 42

- 43128 (i) Semi-continuous culture experiments to study temperature and light-dependent growth of 44 45 129 one to four different strains of each species
- 46 47 130 (ii) Microcosm experiment to assess the growth of one strain of each native and invasive species ⁴⁸131 along a natural light gradient in a shallow lake 49
- 50132 (iii) A simple mathematical model based on growth as a function of temperature (as determined 51 52 133 in the culture experiments) was created to simulate the seasonal course of biovolume
- 53 54 134 development and community composition for one native species (A. gracile), one invasive 55 135
- species (C. raciborskii) and one potentially invasive species (A. ovalisporum) at three 57136 different temperature scenarios: past, present and future.
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- 60 138 Method
 - 139 **Strains**

140 Strains of three invasive species (Cylindrospermopsis raciborskii, Anabaena bergii,

Aphanizomenon aphanizomenoides) and three native species (Aphanizomenon gracile,

42 Aphanizomenon flos-aquae, Anabaena macrospora) from Northeast Germany and one potentially

43 invasive Spanish species (A. ovalisporum) were used (Table I). German strains were isolated as

144 described by Preußel (Preußel et al., 2006), and the Spanish strain as described by Wormer

5 (Wormer et al., 2008).

⁴5147 **Culture experiments**

Temperature dependent growth of one strain of each species (Table I) was determined at seven temperatures between 10°C and 35°C at 80 μ mol photons m⁻² s⁻¹ for all species, and additionally at 40°C for *A. aphanizomenoides* (22C4-9) and *A. ovalisporum* (UAM290). Light dependent growth of all strains was determined at six or more light intensities between 17 and 57 μ mol photons m⁻² s⁻¹ at 15°C and 20°C (Table I).

Growth experiments were performed using 100 mL culture volume in 250 mL Erlenmeyer flasks,
which were continuously shaken at 80-100 rpm. Z8-medium (Haande et al., 2008) modified with
164 nM biotin, 30 nM cyanocobalamine and 119 nM thiamine hydrochloride was used for
culturing. The experiments were carried out in growth chambers (BINDER, KBW 400, Germany)
with dimmable illumination (OSRAM, Lumilux 18W/865XT Cool Daylight, Germany) simulating
12 h:12 h light:dark photoperiods. The cultures were grown in a semi-continuous fashion according
to the turbidostat principle (Paasche, 1975; Nicklisch, 1992). The biovolume was measured every
second day and the every second day increase of biovolume was removed by dilution with Z8. The
biovolume determination was carried out using a UV/VIS spectrophotometer (Lambda 2, Perkin
Elmer, USA) at 750 nm. The cultures were diluted every second day to an optical density (OD) of
0.1.

0.1.

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5 Growth rate and curve fitting

⁴⁸ 166 As biomass is correlated to OD, the specific growth rate (μ) was calculated from the change of 50 167 biomass over time (Δt): 51

$$\mu = \ln \left(\frac{X_{\Delta t}}{X_0} \right) \cdot \frac{1}{\Delta t} , \qquad (1)$$

⁵⁵ ⁵⁶ 169 where $X_{\Delta t}$ is biomass after cultivation time t, X_0 is biomass after dilution and Δt is the time between ⁵⁷ ⁵⁸ 170 two dilutions.

If biomass increase was equal to biomass loss after dilution, steady state was assumed. The mean
 specific growth rate as well as the standard deviation was calculated from at least three consecutive

2 173 measurements of the specific growth rates per steady state. This was done for each strain and at all

4 174 combinations of light and temperature.

Curve fitting of light-dependent growth rate was performed according to the exponential model of 175 176 Mitscherlich (Mitscherlich, 1909) modified using a β -factor describing photoinhibition:

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$$\mu(I) = A \cdot \left(1 - \exp\left(-\frac{(\alpha + \beta) \cdot (I - I_0)}{A}\right)\right) - \beta(I - I_0)$$
(2)
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$$A = \mu \max \cdot \left(\frac{\alpha + \beta}{\alpha + \beta \cdot \ln\left(\frac{\beta}{\alpha + \beta}\right)} \right), \tag{3}$$

20179 where μ is the specific growth rate, μ_{max} the maximum specific growth rate, α the initial slope at I =22180 I_0 with light intensity I and compensation light intensity I_0 . If the factor of photoinhibition, β , is $\beta = 0$, then $A = \mu_{max}$ and the enhanced exponential model reduces to the model of Mitscherlich. 24181 Irradiance at onset of light saturation, I_K , was calculated as $I_K = \mu_{max} / \alpha$. 26182

28¹⁸³ Curve fitting of the temperature-dependent growth rates was performed according to Jöhnk (Jöhnk 184 et al. 2008):

$$\mu(T) = \mu_{\max} \cdot \left(1 + b_i \left((R_{1i}^{T-T_{opt,i}} - 1) - \frac{\ln(R_{1i})}{\ln(R_{2i})} \cdot (R_{2i}^{T-T_{opt,i}} - 1) \right) \right),$$
(4)

³⁵186 where $\mu(T)$ is the specific growth rate at temperature T, μ_{max} the maximum specific growth rate at 37 38 187 optimal growth temperature $T_{opt,i}$ and b_i , R_{1i} , R_{2i} are parameters describing the form of the optimum ³⁹ 40¹⁸⁸ growth curve.

41 42¹⁸⁹ The slope, $\alpha(T) = \partial \mu / \partial T$, of the temperature-dependent growth curves was determined at 43 44 190 $T = 10^{\circ}C.$

45 191 46 The Q10 value, $Q10 = \mu(T+10)/\mu(T)$, is the rate of change as a consequence of increasing the 47 192 48 temperature by 10°C with $\mu(T+10)$ is the specific growth rate at a temperature increase of 10°C 49193 and $\mu(T)$ is specific growth rate at initial temperature. 50

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53195 **Microcosm experiment**

54 55 196 The microcosm experiment was carried out using a mixed culture including three native and three 56 57 197 invasive species (Table I). Pre-cultures were grown as batch cultures in 500 mL Erlenmeyer flasks ⁵⁸198 with a culture volume of 300 mL. Z8 medium was used as described above. The pre-cultures were 59 incubated at 21°C under 59 \pm 15 µmol photons m⁻² s⁻¹ provided by daylight fluorescent tubes 60 1 99 (Phillips TL-D 36W/25-740) with 10 h:14 h light:dark photoperiod. 200

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2 201 Approximately equal parts of biovolume (assessed from correlations between OD and biovolume, data not shown) of the pre-cultures were mixed and diluted to a final biovolume of 28 mm³ L⁻¹. The 4 202 203 pooled sample was filled in 2-L bottles (Nalgene) and incubated for four days at depths of 0.1, 0.2, 7 204 0.4, 0.6, 0.8, 1.0 and 1.6 m in a shallow experimental pond in the Scharmützelsee region. The 9 205 bottles were aerated daily. Subsamples from the starting suspensions and from each bottle were 10 11206 taken after 4 days of incubation and preserved for phytoplankton biovolume analyses. The 12 13207 biovolume was determined according to the method of Utermöhl (Utermöhl, 1958). $\frac{14}{15}208$ The mean water temperature during the experiment was 19.7 ± 0.4 °C. Global radiation was 16₂₀₉ 17 measured with a cosine-corrected quantum sensor (MQS-B, Heinz Walz GmbH, Germany). The 18210 vertical attenuation coefficient (K_d) was calculated using photosynthetically active radiation (PAR) 19 20211 measurements obtained at two defined depths with two spherical quantum sensors (LI-193 SA, LI-21 22²¹² COR Bioscience, USA). PAR at different depths was calculated from K_d , light intensity at the water ²³₂₄213 surface (I_0) and depth (z).

25214 The specific growth rate (μ) was determined as the change in biovolume from beginning to end of 26 27215 the experiment as described above (Eq. 1). Curve-fitting of light-dependent growth rates was 28 29 216 performed using Equation 2. The negative growth rate of A. *flos-aquae* at 254 μ mol photons m⁻² s⁻¹ ³⁰₃₁217 was not included in the fit. A. macrospora growth rates were not fitted as Eq. (2) was not suitable ³²218 33 for them.

35 36 220 **Simulation model**

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37 38 221 We used a simple model to point out the effects of differences in growth rates for different ³⁹₄₀222 Nostocales species on the seasonal course of population biovolume. In contrast to a simulation 41 223 model describing the full life cycle of Nostocales cyanobacteria (Jöhnk et al., 2010, unpublished 42 43224 data), we only included temperature-dependent growth (neglecting nutrient and light limitation) and 44 45 225 mortality rates from that model. Changes in pelagic population, $C [mm^3 L^{-1}]$, are thus described by 46 47 226 growth and loss processes:

$$\frac{48}{49227} \qquad \frac{dC}{dt} = \mu(T)C - [m + m_{dens}C]C \quad .$$
(5)

51 52 228 Temperature-dependent growth was simulated using growth functions $\mu(T)$ for three species, 53 54 229 A. gracile, C. raciborskii, and A. ovalisporum, determined by laboratory experiments (Eq. 4). ⁵⁵₅₆230 Model calibration provided a mortality rate $m = 0.06 \text{ d}^{-1}$ and a density-dependent loss rate, $m_{\text{dens}}C$, 57231 with $m_{\text{dens}} = 0.01 \text{ d}^{-1} \text{ Lmm}^{-3}$, which is equivalent to a carrying capacity of $K = \mu / m_{\text{dens}}$. Loss rates 58 ⁵⁹232 are in good agreement with data published by Reynolds (1984). Changing the mortality rates within 60 a feasible range does not significantly change the characteristics of the dynamics described 233 234 afterwards, although the size of the population densities changes in response to changing carrying

2 235 capacities. The populations were initialized at a threshold temperature of $T_{\text{threshold}} = 12^{\circ}\text{C}$, when 4 236 overwintering akinetes in the sediments are germinating (Rücker et al., 2009). In our simplified 237 model, this is represented by a starting population of

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$$C(t_{\text{start}}) = C_0$$
, where $t_{\text{start}} = \text{day}(T \ge T_{\text{threshold}})$. (6)

10²³⁹ Inoculum values, C_0 , for the three species were chosen as ratios of 1 to 1/3 to 1/10 of 10⁻⁴ mm³ L⁻¹, 11 240 representing spring conditions. 12

13241 The model is driven by seasonal changes in water temperature of a lake. Here, we chose the mean 14 15242 seasonal course (averaged over a period of 14 years, 1994 – 2007) of Lake Melangsee (Table I). $^{16}_{17}243$ Simulations for current mean water temperatures (CWT) were complemented by scenarios for 18 19²⁴⁴ historic (CWT minus 2°C) and future mean water temperatures (CWT plus 4°C) representing 20245 possible future climate change conditions. 21

23 24 247 Statistical analysis

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²⁵₂₆248 The investigated species were divided into four groups, native (A. gracile, A. flos-aquae, 27 249 A. macrospora), invasive (C. raciborskii, A. bergii, A. aphanizomenoides), deep oligotrophic lake 29250 (A. flos-aquae and A. macrospora) and shallow eutrophic to polytrophic lake species (A. gracile and 31251 invasive species), for the statistical analysis. A. ovalisporum was not included in the statistical 32 33²⁵² analysis. Statistically significant differences between the groups were assessed using the t-test for ³⁴₂₅253 independent samples and the Welch test of non-homogeneous variance. The Mann-Whitney U-test 36254 was used to compare growth rates at 35°C. All statistical tests were two-tailed.

Results 40256

41 42257 **Culture experiments**

43 44²⁵⁸ *Temperature-dependent growth*

45 46²⁵⁹ Native and invasive species differed significantly in their growth rates at very low (10°C) and very

high (35°C) temperatures (Fig. 1). At 10°C, native cyanobacteria grew at rates of 0.06 to 0.15 d⁻¹, 47260 48

49261 whereas invasive cyanobacteria did not grow. At 35°C, native cyanobacteria ceased to grow,

50 51 262 whereas the invasive cyanobacteria grew at rates of 0.09 to $0.32 d^{-1}$.

⁵²₅₃263 The growth curves of A. aphanizomenoides, C. raciborskii and A. bergii exceeded those of

54264 A. gracile, the main competitor of these invasive species in shallow lakes, at 16°C, 20°C and 31°C 55

(Fig. 1). Below these temperatures A. gracile grew faster than invasive species. Aphanizomenon 56265

57 58 266 aphanizomenoides and C. raciborskii had clearly higher maximum growth rates than native species ⁵⁹₆₀267 (Table II).

The invasive cyanobacteria had significantly higher Q10 values between 15 to 25°C ranging from 268

2.0 to 3.2 than native cyanobacteria with values of 1.4 to 1.7 (df = 4; t = 3.025; p \leq 0.05). Their 269

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growth curves had significantly higher initial slopes ($\alpha = 0.024$ to 0.035) than growth curves of native cyanobacteria ($\alpha = 0.010$ to 0.011) (df = 4; t = 5.151; p ≤ 0.01). Native and invasive species did not differ significantly in their *Q*10 values between 20 to 30°C (df = 2.210; t = 1.936; p > 0.05) and their T_{opt} (df = 4; t = 1.999; p > 0.05). Optimal growth temperatures of native and invasive species were not significantly different (df = 4; t = 1.999; p > 0.05). The lowest T_{opt} was measured for the two species from the deepest lake (*A. flos-aquae* and *A. macrospora*) (Table II). The Spanish strain (*A. ovalisporum*) did not grow at 10°C like the invasive species. Compared to all other species its growth curve is characterized by a low initial slope ($\alpha = 0.014$), by the highest growth rate at 35°C ($\mu = 0.34$), by the highest T_{opt} ($T_{opt} = 32.8$ °C) and highest *Q*10 values between 15 to 25°C (*Q*10 = 3.6) (Table II).

2281 Light-dependent growth

The highest maximum growth rates at 15°C were achieved by strains of *A. gracile* (Figs. 2 A and

3). Growth rates of all invasive species were significantly lower than those of *A. gracile* (df = 9;

t = 3.781; p \leq 0.01) but equivalent to those of *A. flos-aquae* and *A. macrospora* (df = 9; t = 0.667;

p > 0.05). The highest growth rates among the invasive species were achieved by the

1286 A. aphanizomenoides strains.

Initial slopes of the growth curves and I_K values did not differ significantly for the invasive species and *A. gracile* (p > 0.05) but significantly for *A. flos-aquae* and *A. macrospora* (p \leq 0.05). Initial slopes of the growth curves of the species from the oligotrophic deep lake were slightly higher than those of the species from eutrophic shallow lakes, and their I_K values were lower (Fig. 3).

At 20°C, *A. flos-aquae* and *A. macrospora* had significantly lower maximum growth rates, higher α and lower I_K values than the other species (p ≤ 0.001) (Figs. 2 B and 3).

A. gracile did not differ significantly from invasive cyanobacteria in their maximum growth rates at 20°C (df = 8; t = -0.891; p > 0.05) as well as in their α and I_K values (p > 0.05).

48 49²⁹⁶ Microcosm experiment

50 51²⁹⁷ In mixed culture, A. aphanizomenoides clearly reached the highest growth rates, followed by the 52298 other two invasive species, C. raciborskii and A. bergii, as well as by the native species, A. gracile, 53 54299 which had comparable growth rates (Fig. 4 A). The two species from the deep oligotrophic lake, 55 56 300 A. flos-aquae and A. macrospora, had the lowest growth rates. A similar pattern in growth was 57 58 301 found in the laboratory experiment at 20°C (Fig. 2 B). Slight differences between the two ⁵⁹302 approaches were reflected in the shape of the growth curves: The initial slope of the growth curve 60 of A. aphanizomenoides was distinctly higher and that of A. flos-aquae was distinctly lower in the 303 304 microcosm experiment (Fig. 4 B). Unlike the invasive species, the growth rates of the native species 2 305 declined at high irradiance levels. This kind of grouping was not observed in the laboratory 4 306 experiments. Growth rates of all strains determined in the microcosm experiment were lower than 307 those determined in the laboratory culture experiments.

9 309 Simulation of seasonal dynamics

Simulations show that compared to A. gracile, the biovolume of C. raciborskii is much lower at 11310 13311 lower historic temperatures (Fig. 5, upper panel), nearly equal at current temperatures (Fig. 5, 14 15³¹² middle panel), and higher at higher future temperatures (Fig. 5, lower panel). The potential invader 16₃₁₃ 17 A. ovalisporum is virtually absent in the colder scenario, reaching (undetectable) low values at 18314 current temperatures and blooms during future temperature increases, as can be expected based on 19 20 315 its higher T_{opt} (Table II). In the future scenario, the vegetation time of all three species is increased. 21 22³¹⁶

23 24³¹⁷ Discussion

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²⁵₂₆318 The aim of this study was to determine which of the native, invasive and potentially invasive 27₃₁₉ 28 species are stronger competitors under various temperature and light conditions. Our culture 29320 experiments clearly demonstrated that native cyanobacterial species were superior competitors at 30 31 321 low temperatures and invasive cyanobacterial species at high temperatures.

³² 33³²² The T_{opt} of native and invasive Nostocales species do not differ significantly. The T_{opt} of 27.8°C for ³⁴ 323 35 C. raciborskii coincided with values of 28 to 31°C reported for C. raciborskii isolates from different 36324 latitudes (Briand et al., 2004). This also holds true for the two native Aphanizomenon species, the 37 38325 T_{opt} of which were 24.7°C and 27.1°C in this study compared 25°C reported for A. flos-aquae ³⁹₄₀326 RALFS f. gracile LEMM. (Foy et al., 1976) and 28°C reported for A. flos-aquae var. klebahnii 41 327 42 ELENK. (Uehlinger, 1981) in other studies. In this study, A. ovalisporum had the highest T_{opt} of 43 328 44 32.8°C, which is also higher than T_{opt} of 26 to 30°C reported for strains from Lake Kinneret (Hadas 45 3 29 et al., 2002). This high T_{opt} is advantageous as ponds and reservoirs in the Mediterranean region can 46 47 330 reach temperatures over 30°C during summer months (A. Quesada, Madrid, personal 48 49³³¹ communication).

50 332 51 Overall, high T_{opt} values suggest that Nostocales tolerate the low temperatures of their habitats 52333 rather than are adapted to them. Tang and co-workers (Tang et al., 1997) published similar 53 54 334 observations for cyanobacteria from polar freshwater ecosystems. The T_{opt} of all Nostocales were 55 56 335 higher than the mean water temperatures of their habitats during their vegetation period. Therefore, 57 58³³⁶ all Nostocales would benefit from rising temperatures. This is in agreement with the recently 59337 confirmed concept of global expansion of cyanobacterial blooms favoured by global and regional 60 338 warming (Paerl and Huisman, 2009). Cylindrospermospis raciborskii, A. aphanizomenoides and 339 A. ovalisporum achieved the highest maximum growth rates at high temperatures. Hence, these

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2 340 three species would benefit most from any increase in water temperature. Below 20°C the lowest 4 341 growth rates were measured for A. ovalisporum. This may be the reason why A. ovalisporum is not 342 present in German freshwaters yet.

343 Contrary to our assumption, the invasive Nostocales species are not superior competitors for light. 9 344 Values of their light-dependent growth parameters (α , I_K) were similar to those of A. gracile. I_K 10 values for *C. raciborskii* (38 to 101 μ mol photons m⁻² s⁻¹) were much higher in the present study 11345 12 than those (15 to 26 μ mol photons m⁻² s⁻¹) reported in the literature (Shafik et al., 2001; Briand et 13346 14 15³⁴⁷ al., 2004). This might be due to differences in culturing methods since the low I_K values in the ${}^{16}_{17}348$ literature resulted from the exponential growth phase of batch cultures started at a much lower 18 349 19 trichome density (OD 750 nm ~ 0.002) and determined at higher temperatures ($25^{\circ}C$ and $27^{\circ}C$) 20350 than those in the semi-continuous culture experiments of our study. As we considered the relative 21 22 351 differences between native and invasive species, these absolute differences played a minor role in ²³₂₄352 our overall conclusions.

25₃₅₃ 26 Aphanizomenon flos-aquae and A. macrospora, the two species isolated from a deep oligotrophic 27354 lake, had a significantly lower optimal light intensity and were more stenoecious in regard to light 28 29 355 than the species from the eutrophic shallow lakes.

 $^{30}_{31}356$ The results of the microcosm experiment (at 19°C) are consistent with the main results of the ³²₃₃357 culture experiments (at 20°C): The most powerful competitors were A. aphanizomenoides, followed 34358 by C. raciborskii, A. gracile and A. bergii; A. flos-aquae and A. macrospora could not compete with 35 36359 the other species. This shows that results obtained for single strains using artificial irradiance in the 37 38 360 laboratory can be transferred to community level where species co-occur under natural light ³⁹₄₀361 conditions. Although this study is restricted to the effects of light and temperature on cyanobacterial 41 362 42 growth and competition, it can be noted that buoyancy enables the co-occurrence of Nostocales 43363 species with different light requirements. For example, under stratified conditions, Anabaena 44 45 364 species can adjust their buoyancy to maintain a near surface position, while C. raciborskii can 46 47 365 compete more effectively by remaining at greater depths. In shallow turbid waters, Nostocales 48 366 49 species can regulate their buoyancy only under calm weather conditions.

50367 Since there is increasing evidence that cyanobacterial populations are composed of different 51 52368 ecotypes or subpopulations (Becker et al., 2002; Johnson et al., 2006; Rohrlack et al., 2008), we 53 54 369 included different strains of each species (except for A. macrospora) in the light experiment to ⁵⁵₅₆370 estimate the variance in growth between strains. Figure 2 clearly illustrates that strains of some 57 371 58 species such as A. aphanizomenoides or A. flos-aquae show a nearly identical growth response at different light intensities while others, such as A. gracile vary considerably in their growth, 59372 60 373 especially at high light intensities. In our study differences between species were more pronounced 2 374 than differences between strains. However, variability between strains should be taken into account 4 375 when extending results obtained for one strain to the whole population.

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5 376 An interesting result of our study is the fact that A. aphanizomenoides reached the highest growth 6 7 377 rates in all experiments. This is contradictory to its low abundance in the field (Stüken et al., 2006). 8 9 378 Therefore, the development of A. *aphanizomenoides* field populations may be limited by other 10 11379 factors as nutrients, or it may just be at the beginning of its population development in German 12 13380 freshwaters.

14 15³⁸¹ Overall, our study showed that temperature has a major impact on the competition between native 16₃₈₂ 17 and invasive cyanobacteria. Our results suggest that native species can begin to build up 18383 populations earlier during the season. This is confirmed by field studies showing that populations of 19 20384 A. gracile occur earlier in the season from temperatures of 13°C (J. Rücker, Bad Saarow, personal 21 22³⁸⁵ communication), while populations of C. raciborskii occur later in the season when the water ²³₂₄386 temperature exceeds 17°C (Mischke, 2003; Wiedner et al., 2007; Dokulil and Mayer, 1996). Our 25387 results also suggest that C. raciborskii could outcompete A. gracile in summer when temperatures 26 27388 rise above 20°C. So far the population size of C. raciborskii does not exceed that of A. gracile 28 29 389 (Wiedner et al., 2008). However, this could change if the water temperature increases by a further ${}^{30}_{31}390$ 4.0°C in the future (scenario A1F1, IPCC 2007). Our simulation clearly demonstrates a shift from 32 391 33 past dominance by A. gracile to C. raciborskii in the future. The simulation also indicates that the 34392 Mediterranean species A. ovalisporum could undergo massive population growth under future 35 36 393 climate conditions. Moreover, the simulation illustrates that the seasonal growth period of all 37 38 394 Nostocales will be prolonged in the future scenario.

³⁹₄₀395 Other factors, such as nutrient concentration must also be considered in regulating the growth and 41 3 9 6 competition of cyanobacteria. For example during eutrophication of Lake Balaton (Hungary) in the 42 43397 1970s, populations of A. gracile disappeared while first populations of C. raciborskii and 44 45 398 A. aphanizomenoides had been established. After re-eutrophication A. gracile reappeared and now 46 47</sub>399 co-occurs with the two invasive species (Padisák and Reynolds, 1998). In general, Nostocales are 48400 superior competitors under nitrogen shortage, because they can fix atmospheric nitrogen. However, 49 50401 it is unknown whether they differ in their ability to fix N₂ or to use dissolved nitrogen. Concerning 51 52 402 the efficiency of phosphate use, C. raciborskii is known to be a strong competitor under phosphate 53 54⁴⁰³ limitation (Isvánovics et al., 2000; Spröber et al., 2003; Posselt et al., 2009). However, to complete ⁵⁵404 the picture on the competitiveness of invasive and native cyanobacteria their growth under various 56 nutrient concentrations must be compared in further laboratory studies. 57405 58

⁵⁹406 Finally changes in the cyanobacterial community are of concern, because cyanobacteria can 60 produce different toxins. For example, a survey in German lakes showed that hepatotoxic 407 408 microcystins, which are manly produced by *Microcystis* or *Planktothrix* occur in high

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2 409 concentrations, while neurotoxic as saxitoxins or anatoxins, which are produced by Nostocales, 4 410 occur less frequent and in much lower concentrations (Fastner et al., 1999). More recently it was 411 shown that also the toxin cylindrospermopsin is widely distributed in German lakes (Fastner et al., 412 2007), where it is produced by A. flos-aquae and A. gracile (Preußel et al., 2006) and occurs in 9 413 concentrations that are in the same order of magnitude as those of microcystins (Rücker et al., 10 11414 2007). An increase in the abundance of Nostocales species could result in an increase of anatoxin, 12 13415 saxitoxin and cylindrospermopsin concentrations. Moreover, an introduction of the Mediterranean 14 15⁴¹⁶ A. ovalisporum could massively enhance cylindrospermopsin concentrations in temperate lakes, 16₄₁₇ 17 because all isolated strains of this species produce cylindrospermopsin (Banker et al., 1997; 18418 Quesada et al., 2006), whereas only a very small portion of A. flos-aquae and A. gracile isolated 19 20419 from German lakes can produce this toxin.

²³₂₄421 Conclusion

25422 In summary, we conclude that any further increase in water temperature would promote the 27423 development of all of the investigated Nostocales species in general, and that of the invasive species 29 29 424 in particular, and would enable a more northward expansion of A. ovalisporum. ³⁰₃₁425

A shift in the portion and abundance towards Nostocales in cyanobacterial communities would most ³²426 likely be accompanied by a shift in the predominating cyanotoxins.

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- 51 52 53 54
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- 56 57
- 58
- 59 60

1 2 /37					
3	Deferences				
4 438 5					
6 439 7	Baas Becking, L.G.M. (1934) <i>Geobiologie of inleiding tot de milieukunde</i> . Van Stockum & Zoon,				
8 440 9	The Hague.				
10 ⁴⁴¹	Banker, R., Carmeli, S., Hadas, O., Teltsch, B., Porat, R., and Sukenik, A. (1997) Identification of				
11 442 12	cylindrospermopsin in Aphanizomenon ovalisporum (Cyanophyceae) isolated from Lake Kinneret,				
13443 14	Israel. J Phycol 33 , 613-616.				
15444 16	Becker, S., Fahrbach, M., Boger, P., and Ernst, A. (2002) Quantitative tracing, by Taq nuclease				
17 ⁴⁴⁵	assays, of a Synechococcus ecotype in a highly diversified natural population. Appl Environ				
¹⁸ 446 19	Microbiol 68 , 4486-4494.				
20447 21	Briand, J.F., Leboulanger, C., Humbert, J.F., Bernard, C., and Dufour, P. (2004)				
22448 23	Cylindrospermopsis raciborskii (Cyanobacteria) invasion at mid-latitudes: Selection, wide				
24 ⁴⁴⁹	physiological tolerance, or global warming? J Phycol 40, 231-238.				
25 26 ⁴⁵⁰	Christen, T. (2006) Horizontale Unterschiede trophierelevanter Parameter in großen Seen - Ihre				
27 451 28	Ausprägung und Bedeutung für die Trophiebewertung. Diploma Thesis, BTU Cottbus, Bad Saarow,				
29452	Chair of Freshwater Conservation.				
31 453	Dokulil, M.T., and Mayer, J. (1996) Population dynamics and photosynthetic rates of a				
$32 \\ 33 454$	Cylindrospermopsis-Limnothrix association in a highly eutrophic urban lake, Alte Donau, Vienna,				
³⁴ 455 35	Austria. Algological Studies 83, 179-195.				
36456 37	Fastner, J., Neumann, U., Wirsing, B., Weckesser, J., Wiedner, C., Nixdorf, B., and Chorus, I.				
38457	(1999) Microcystins (hepatotoxic heptapeptides) in German fresh water bodies. Environ Toxicol 14,				
39 40 ⁴⁵⁸	13-22.				
41 42459	Fastner, J., Rucker, J., Stuken, A., Preussel, K., Nixdorf, B., Chorus, I. et al. (2007) Occurrence of				
43 460	the cyanobacterial toxin Cylindrospermopsin in northeast Germany. <i>Environ Toxicol</i> 22, 26-32.				
45461	Fogg, G.E., Stewart, W.D.P., Fay, P., and Walsby, A.E. (1973) The blue-green algae. Academic				
46 47 462	Press, London.				
48 49463	Foy, R.H., Gibson, C.E., and Smith, R.V. (1976) The influence of daylength, light intensity and				
⁵⁰ 464	temperature on the growth rates of planktonic blue-green algae. Br Phycol J 11, 151-163.				
52465	Gentile, J.H., and Maloney, T.E. (1969) Toxicity and Environmental Requirements of a Strain of				
53 54 466	Aphanizomenon Flos-Aquae (L) Ralfs. Can J Microbiol 15, 165-173.				
55 56 ⁴⁶⁷	Gkelis, S., Moustaka-Gouni, M., Sivonen, K., and Lanaras, T. (2005) First report of the				
57 58468	cyanobacterium Aphanizomenon ovalisporum Forti in two Greek lakes and cyanotoxin occurrence.				
59469	J Plankton Res 27, 1295-1300.				
470	Haande, S., Rohrlack, T., Ballot, A., Roberg, K., Skulberg, R., Beck, M. and Wiedner, C. (2008)				
471	Genetic characterisation of Cylindrospermopsis raciborskii (Nostocales, Cyanobacteria) isolates				

- ² 472 from Africa and Europe. *Harmful Algae* 7, 692-701.
- 4 473 Hadas, O., Pinkas, R., Malinsky-Rushansky, N., Shalev-Alon, G., Delphine, E., Berner, T. et al.
- ${}^{5}_{6}$ 474 (2002) Physiological variables determined under laboratory conditions may explain the bloom of
- ⁷₈ 475 *Aphanizomenon ovalisporum* in Lake Kinneret. *Eur J Phycol* **37**, 259-267.
- ⁹ 476 Hindak, F. (2000) Morphological variation of four planktic nostocalean cyanophytes members of
 11 477 the genus Aphanizomenon or Anabaena? *Hydrobiologia* 438, 107-116.
- Hoffmann, L. (1996) Geographic distribution of freshwater blue-green algae. *Hydrobiologia* 336,
 33-40.
- ¹⁶₁₇480 IPCC (2007) Summary for Policymakers. In Solomon, S., D. Qin, M. Manning, Z. Chen, M.
- 18481 Marquis, K.B. Averyt, M.Tignor and H.L. Miller (eds.), *Climate Change 2007: The Physical*
- 20482 Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the
- ²¹₂₂483 *Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, United
- Kingdom and New York, NY, USA.
- Istvanovics, V., Shafik, H.M., Presing, M., and Juhos, S. (2000) Growth and phosphate uptake
 kinetics of the cyanobacterium, *Cylindrospermopsis raciborskii* (Cyanophyceae) in throughflow
 cultures. *Freshwater Biol* 43, 257-275.
- ³⁰₃₁488 Jöhnk, K.D., Huisman, J., Sharples, J., Sommeijer, B., Visser, P.M., and Stroom, J.M. (2008)
- Summer heatwaves promote blooms of harmful cyanobacteria. *Global Change Biol* **14**, 495-512.
- 34490 Jöhnk, K.D., Brüggemann, R., Rücker, J., Luther, B., Simon, U., Nixdorf, B., and Wiedner, C. 35
- 36 491 (2010) Modelling life cycle and population dynamics of Nostocales (cyanobacteria). Unpublished
 37 38 492 data.
- Johnson, Z.I., Zinser, E.R., Coe, A., McNulty, N.P., Woodward, E.M.S., and Chisholm, S.W.
- 41 494 (2006) Niche partitioning among Prochlorococcus ecotypes along ocean-scale environmental
 42 gradients. *Science* 311, 1737-1740.
- Kim, B.H., Lee, W.S., Kim, Y.O., Lee, H.O., and Han, M.S. (2005) Relationship between akinete
 germination and vegetative population of *Anabaena flos-aquae* (Nostocales, Cyanobacteria) in
 Seokchon reservoir (Seoul, Korea). *Arch Hydrobiol* 163, 49-64.
- 49 50499 Komárek, J. (1994) Current trends and species delimitation in cyanoprokaryote taxonomy.
- ⁵¹ 52 500 *Algological Studies* **75**, 11-29.
- Lonsdale, W.M. (1999) Global patterns of plant invasions and the concept of invasibility. *Ecology*55 502 80, 1522-1536.
- 57 503 Mischke, U. (2003) Cyanobacteria associations in shallow polytrophic lakes: influence of
 58 environmental factors. *Acta Oecol Int J Ecol* 24, S11-S23.
- ⁶⁰505 Mischke, U., and Nixdorf, B. (2003) Equilibrium phase conditions in shallow German lakes: How
 - 506 Cyanoprokaryota species establish a steady state phase in late summer. *Hydrobiologia* **502**, 123-

2	507	132.
3		

- 4 508 Mitscherlich, E.A. (1909) Das Gesetz vom Minimum und das Gesetz des abnehmenden
- ⁵₆ 509 Bodenertrags. *Landw. Jhrb.* **38**, 537-552.
- Moisander, P.H., McClinton, E., and Paerl, H.W. (2002) Salinity effects on growth, photosynthetic
 parameters, and nitrogenase activity in estuarine planktonic cyanobacteria. *Microb Ecol* 43, 432 442.
- Nicklisch, A. (1992) The interaction of irradiance and temperature on the growth rate of Limnothrix
- redekei and its mathematical description. *Arch Hydrobiol Suppl* **91** (Algological Studies 63), 1-18.
- ¹⁶515 Nixdorf, B., Mischke, U., and Rücker, J. (2003) Phytoplankton assemblages and steady state in
- 18516 deep and shallow eutrophic lakes an approach to differentiate the habitat properties of
- 20517 Oscillatoriales. *Hydrobiologia* **502**, 111-121.
- Paasche, E. (1975) Growth Of The Plankton Diatom *Thalassiosira Nordenskioeldii* Cleve At Low
 Silicate Concentrations. *J Exp Mar Biol Ecol* 18, 173-183
- Padisák, J. (1997) Cylindrospermopsis raciborskii (Wolozynska) Seenayya et Subba Raju, an
 26
- expanding, highly adaptive cyanobacterium: worldwide distribution and review of its ecology. *Arch Hydrobiol Suppl* 107, 563-593.
- Padisak, J., and Reynolds, C.S. (1998) Selection of phytoplankton associations in Lake Balaton,
- Hungary, in response to eutrophication and restoration measures, with special reference to the cyanoprokaryotes. *Hydrobiologia* **384**, 41-53.
- Paerl, H.W., and Huisman, J. (2009) Climate change: a catalyst for global expansion of harmful
 cyanobacterial blooms. *Environ Microbiol Rep* 1, 27-37.
- Parmesan, C. (2006) Ecological and evolutionary responses to recent climate change. *Annu Rev Ecol Evol Syst* 37, 637-669.
- 43 530 Posselt, A.J., Burford, M.A., and Shaw, G. (2009) Pulses of Phosphate Promote Dominance of the
- Toxic Cyanophyte Cylindrospermopsis Raciborskii in a Subtropical Water Reservoir. J Phycol 45,
 540-546.
- ⁴⁸533 Preussel, K., Stüken, A., Wiedner, C., Chorus, I., and Fastner, J. (2006) First report on
- 50534 cylindrospermopsin producing Aphanizomenon flos-aquae (Cyanobacteria) isolated from two
- ⁵¹ 52535 German lakes. *Toxicon* **47**, 156-162.
- ⁵³₅₄536 Quesada, A., Moreno, E., Carrasco, D., Paniagua, T., Wormer, L., De Hoyos, C., and Sukenik, A.
- 55 537 (2006) Toxicity of Aphanizomenon ovalisporum (Cyanobacteria) in a Spanish water reservoir. *Eur* 57 538 *J Phycol* 41, 39-45.
- 58 59 539 Reynolds, C.S., and Walsby, A.E. (1975) Water-Blooms. *Biol Rev* **50**, 437-481.
- ⁶⁰540 Reynolds, C.S. (1984) The ecology of freshwater phytoplankton. In Beck, E., Birks, H.J.B., and
 - 541 Connor, E.F. (eds), *Cambridge Studies in Ecology*. Cambridge University Press, Cambridge.

- ² 542 Rohrlack, T., Edvardsen, B., Skulberg, R., Halstvedt, C.B., Utkilen, H.C., Ptacnik, R., and
- 4 543 Skulberg, O.M. (2008) Oligopeptide chemotypes of the toxic freshwater cyanobacterium
- ⁵₆ 544 *Planktothrix* can form subpopulations with dissimilar ecological traits. *Limnol Oceanogr* 53, 1279⁷₈ 545 1293.
- ⁹ 546 Rücker, J., Stüken, A., Nixdorf, B., Fastner, J., Chorus, I., and Wiedner, C. (2007) Concentrations
- of particulate and dissolved cylindrospermopsin in 21 *Aphanizomenon*-dominated temperate lakes.
 Toxicon 50, 800-809.
- ¹⁴₁₅549 Rücker, J., Tingwey, E.I., Wiedner, C., Anu, C.M., and Nixdorf, B. (2009) Impact of the inoculum
- size on the population of Nostocales cyanobacteria in a temperate lake. *J Plankton Res* 31, 1151 1159.
- 19 20552 Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R. et al. (2000)
- ²¹₂₂553 Biodiversity Global biodiversity scenarios for the year 2100. *Science* **287**, 1770-1774.
- ²³₂₄554 Scheffer, M. (1998) Ecology in shallow lakes. In Usher, M.B., DeAngelis, D.L., and Manly, B.F.J.
- 25 555 (eds), *Population and Community Biology Series*. Chapmann & Hall, London.
 26
- 27 556 Shafik, H.M., Herodek, S., Presing, M., and Vörös, L. (2001) Factors effecting growth and cell
- ²⁸
 ²⁹557 composition of cyanoprocaryote *Cylindrospermopsis raciborskii* (Woloszynska) Seenayya et Subba
 ³⁰31558 Raju. Arch Hydrobiol Suppl 140, 75-93.
- Spröber, P., Shafik, H.M., Presing, M., Kovacs, A.W., and Herodek, S. (2003) Nitrogen uptake and
 fixation in the cyanobacterium *Cylindrospermopsis raciborskii* under different nitrogen conditions.
- ³⁵ 36 561 *Hydrobiologia* **506**, 169-174.
- Stefaniak, K., Kokocinski, M. (2005) Occurrence Of Invasive *Cyanobacteria* Species In Polimictic
 Lakes Of The Wielkopolska Region (Western Poland). *Oceanol Hydrobiol Stud* 34 (Suppl. 3), 137 148.
- 42
 43565 Strayer, D.L., Eviner, V.T., Jeschke, J.M., and Pace, M.L. (2006) Understanding the long-term
 44
 45566 effects of species invasions. *Trends Ecol Evol* 21, 645-651.
- Stüken, A., Rücker, J., Endrulat, T., Preussel, K., Hemm, M., Nixdorf, B. et al. (2006) Distribution
 of three alien cyanobacterial species (Nostocales) in northeast Germany: *Cylindrospermopsis*
- 49
 50 569 raciborskii, Anabaena bergii and Aphanizomenon aphanizomenoides. Phycologia 45, 696-703.
- ⁵¹ ₅₂570 Tang, E.P.Y., Tremblay, R., and Vincent, W.F. (1997) Cyanobacterial dominance of polar
- ⁵³₅₄571 freshwater ecosystems: Are high-latitude mat-formers adapted to low temperature? *J Phycol* **33**, 55, 572
- ⁵⁵₅₆572 171-181.
- 57 573 Uehlinger, U. (1981) Experimental studies on the autecology of *Aphanizomenon flos-aquae* 58
- 59574 (Experimentelle Untersuchungen zur Autökologie von Aphanizomenon flos-aquae). Arch Hydrobiol
- ⁶⁰575 *Suppl* **60**, 260-288.
 - 576 Utermöhl, H. (1958) Zur Vervollkommnung der quantitativen Phytoplankton-Methodik. Mitt Int

- 2 577 *Ver Theor Angew Limnol* **9**, 1-38.
- 4 578 Wiedner, C., Nixdorf, B., Heinz, R., Wirsing, B., Neumann, U., and Weckesser, J. (2002)
- ⁵₆ 579 Regulation of cyanobacteria and microcystin dynamics in polymictic shallow lakes. *Arch Hydrobiol*⁷₈ 580 **155**, 383-400.
- ⁹ 581 Wiedner, C., Rücker, J., Brüggemann, R., and Nixdorf, B. (2007) Climate change affects timing and
- 11582 size of populations of an invasive cyanobacterium in temperate regions. *Oecologia* **152**, 473-484.
- ¹² 13583 Wiedner, C., Rücker, J., Fastner, J., Chorus, I., and Nixdorf, B. (2008) Seasonal dynamics of
- ¹⁴₁₅584 cylindrospermopsin and cyanobacteria in two German lakes. *Toxicon* **52**, 677-686.
- ¹⁶585 Wormer, L., Cires, S., Carrasco, D., and Quesada, A. (2008) Cylindrospermopsin is not degraded
- 18586 by co-occurring natural bacterial communities during a 40-day study. *Harmful Algae* 7, 206-213.
- 20587 Zevenboom, W. (1982) N2-Fixing Cyanobacteria: Why They Do Not Become Dominant In
- ²¹₂₂588 Shallow Hypertrophic Lakes. *Aquat Ecol* **16**, 289-290.

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2 589 3	Table and Figure legends
4 590 5	Table I: Studied strains: their origin (poly = polymictic; di = dimictic) and the experiments in which
6 591	they were used (T = temperature-dependent growth, $L = light-dependent$ growth, M = microcosm
8 592	experiment).
9 10 ⁵⁹³	(a) Isolated as described by Preußel (2007). (b) Isolated as A. flos-aquae but designated here
11 594 12	A. gracile as its morphology in culture is similar to that of 16D11 and ZIE23AFA. (c) Maximum
13 595	depth. (d) Northern Bay of Scharmützelsee, which can be considered a separated water body
14 15 <i>5</i> 96	(Christen 2006)
16 17 ⁵⁹⁷	
18 19 598	Table II: Parameters of temperature-dependent growth calculated using Equation (4), where R^2 is
20 599	the coefficient of determination, μ_{max} the maximum growth rate, T_{opt} the optimum growth
22600	temperature, α the slope at 10°C [d ⁻¹ µmol photons ⁻¹ m ² s], and Q10 the temperature coefficient
23 24 601	between 15 to 25°C and 20 to 30°C, respectively.
25 26 ⁶⁰²	
²⁷ ₂₈ 603	
29604	
30 31 605	Fig. 1 Temperature-dependent growth rates and growth curves at 80 μ mol photons m ⁻² s ⁻¹ . The
32 33 606	growth rate of A. aphanizomenoides at 40°C was not included in curve fitting. Error bars represent
$^{34}_{35}607$	standard deviation of the mean growth rate. Each symbol represents one strain.
36 ₆₀₈	
37 38 609	Fig. 2 Light-dependent growth rates and growth curves at 15°C (A) and 20°C (B). Error bars
39 40 610	represent standard deviation of the mean growth rate. Each symbol represents one strain.
41 42611	
⁴³ ₄₄ 612	Fig. 3 Maximum growth rate (μ_{max}), initial slope (α) and light saturation parameter (I_K) for
44 45613	individual strains of each species from light-dependent growth curves at 15°C (left) and 20°C
46 47 614	(right).
48 49615	
50 51 616	Fig. 4 (A) Microcosm experiment: Growth rates and growth curves (dashed lines) along a natural
⁵² 617	light gradient. In the case of A. macrospora, growth rates without curve fitting are shown. (B)
53 54618	Comparison of light-dependent growth curves derived from microcosm (dashed lines) versus
55 56619	laboratory experiment at 20°C (solid lines).
57 58 620	· · · · · ·
⁵⁹ 621	Fig. 5 Simulated population dynamics. Upper panel: Historical scenario with seasonal water
бU 622	temperature 2°C below current mean values. Middle panel: Presence scenario using seasonal mean

1 2 623	water temperatures. Lower panel: Future scenario with water temperature 4° C above current
3 4 624	temperatures
⁴ 02 ⁴ 5 625	temperatures.
6 7 8 9 10 11 12 13 14 15 6 7 8 9 10 11 12 13 14 15 6 7 8 9 10 11 23 24 5 6 27 28 9 0 11 22 34 55 6 27 28 9 0 31 23 34 53 6 37 38 9 0 41 42 34 45 6 7 8 9 0 11 12 23 45 6 27 28 9 0 31 23 34 5 36 7 8 9 0 41 42 33 45 6 27 28 9 0 31 23 34 5 6 37 8 9 0 41 42 33 45 6 27 28 9 0 31 23 34 5 6 27 28 9 0 31 23 34 5 6 37 38 9 0 41 42 33 45 56 57 8 9 0 11 22 34 56 57 8 9 0 31 23 34 56 57 8 9 0 11 22 34 56 57 8 9 0 31 23 34 56 57 8 9 0 41 42 33 45 56 57 8 9 0 15 23 45 56 57 8 9 0 12 23 24 5 6 57 55 56 57 55 56 57 58 9 60 51 23 34 55 67 58 9 60 51 23 34 55 67 58 9 0 41 42 34 55 56 57 55 56 57 55 56 57 58 9 60 51 23 34 55 56 57 58 9 60 51 23 45 56 57 58 9 60 51 23 34 55 56 57 58 9 60 51 23 34 55 56 57 58 9 60 51 23 34 55 56 57 58 9 60 57 57 57 57 57 57 56 57 57 57 57 57 57 57 57 57 57 57 57 57	

626 Tables

Table I: Studied strains: their origin (poly = polymictic; di = dimictic) and the experiments in

628 which they were used (T = temperature-dependent growth, L = light-dependent growth, M =

629 microcosm experiment).

Species Strain Lake of origin		Lake of origin	Mean lake depth [m]	Mixis type	Exp. per- formed	
Invasive species						
C. raciborskii	19F6 ^a	Melangsee (13°59'18" E, 52°09'40" N)	1.7	Poly	L	
C. raciborskii	ZIE11CR	Zierker See (13°02'12" E, 53°21'44" N)	1.6	Poly	L	
C. raciborskii	24G7 ^a	Werbellinsee (12°56'37" E, 52°55'27" N)	3.5°	Poly	L, T, M	
C. raciborskii	26D9 ^a	Rangsdorfer See (13°24'14" E, 52°17'19" N)	1.5	Poly	L	
A. bergii	LIE02AB	Lieps (13°09'30" E, 53°27'07" N)	2.3	Poly	L, T, M	
A. bergii	ZIE26AB	Zierker See	1.6	Poly	L	
A. aphanizomenoides	22C4-9 ^a	Heiliger See (13°04'18" E,	6.6	Di/	L, T, M	
A. aphanizomenoides	22F6-1 ^a	Heiliger See	6.6	Poly Di/ Poly	L	
Native species				2		
A. gracile	ZIE23AFA	Zierker See	1.6	Poly	L	
A. gracile	30D11 ^{a, b}	Petersdorfer See (14°04'27" E, 52°18'52" N)	1.9	Poly	L	
A. gracile	16D11 ^a	Scharmützelsee, Northern Bay ^d (14°02'46" E, 52°14'22" N)	7.9 ^c	Di/ Polv	L, T, M	
A. flos-aquae	ST115AF	Stechlin (13°01'40" E, 53°09'08" N)	22.8	Di	L, T, M	
A. flos-aquae	ST86AF	Stechlin	22.8	Di	L	
A. macrospora	ST195AS	Stechlin	22.8	Di	L, T, M	
Potentially invasive species						
A. ovalisporum	UAM290	Juan Carlos First Park, Spain (3°36'59" W, 40°27'42" N)	1.5	Poly	Т	

3 630

631 (a) Isolated as described by Preußel (2007). (b) Isolated as A. *flos-aquae* but designated here

A. gracile as its morphology in culture is similar to that of 16D11 and ZIE23AFA. (c)

633 Maximum depth. (d) Northern Bay of Scharmützelsee, which can be considered a separated

634 water body (Christen 2006)

2 3	635							
4 5	636	Table II: Parameters of temperature-dependent growth calculated using Equation (4), where						
6 7	637	R^2 is the coefficient of determination, μ_{max} the maximum growth rate, T_{ant} the optimum						
8 9	638	growth temperature	photons ⁻¹ m ² s], and $Q10$ the temperature					
10	639	coefficient between 15 to 25° C and 20 to 30° C, respectively.						
12		Encoing	\mathbf{p}^2				010 (15.25°C)	$(20.20^{\circ}C)$
13		Species C. raciborskii	<u> </u>	$\mu_{max} [d^{-}]$	$\frac{I_{opt}[^{\circ}C]}{27.8\pm0.9}$	$\frac{\alpha(10^{\circ}C)}{0.024}$	$\frac{Q10(15:25^{\circ}C)}{3.2}$	$\frac{Q10(20:30^{\circ}C)}{1.1}$
14		A heroii	0.99	0.34 ± 0.01 0.25 ± 0.01	27.8 ± 0.9 26 5 + 1 3	0.024	2.8	1.1
15		A. aphanizomenoides	0.98	0.25 ± 0.01 0.36 ± 0.01	28.8 ± 2.0	0.035	2.0	1.2
16		A. gracile	0.99	0.29 ± 0.02	27.1 ± 1.2	0.010	1.6	1.0
17		A. flos-aquae	0.96	0.27 ± 0.01	24.7 ± 0.8	0.011	1.4	0.2
18		A. macrospora	0.99	0.19 ± 0.01	25.5 ± 0.5	0.011	1.7	0.9
20	<i></i>	A. ovalisporum	0.99	0.36 ± 0.02	32.8 ± 0.9	0.014	3.6	2.1
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150x195mm (300 x 300 DPI)





237x270mm (300 x 300 DPI)



149x194mm (300 x 300 DPI)



187x275mm (300 x 300 DPI)