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Are laboratory growth rate experiments relevant to explaining bloom-forming cyanobacteria distributions at global scale?

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ABSTRACT

Predicting algal population dynamics using models informed by experimental data has been used as a strategy to inform the management and control of harmful cyanobacterial blooms. We selected toxic bloom-forming species *Microcystis* spp. and *Raphidiopsis raciborskii* (basionym *Cylindrospermopsis raciborskii*) for further examination as they dominate in 78 % and 17 %, respectively, of freshwater cyanobacterial blooms (cyanoHABs) reported globally over the past 30 years. Field measurements of cyanoHABs are typically based on biomass accumulation, but laboratory experiments typically measure growth rates, which are an important variable in cyanoHAB models. Our objective was to determine the usefulness of laboratory studies of these cyanoHAB growth rates for simulating the species dominance at a global scale. We synthesized growth responses of *M. aeruginosa* and *R. raciborskii* from 20 and 16 culture studies, respectively, to predict growth rates as a function of two environmental variables, light and temperature. Predicted growth rates of *R. raciborskii* exceeded those of *M. aeruginosa* at temperatures $\gtrsim$ 25 °C and light intensities $\gtrsim$ 150 µmol photons m^{-2} s^{-1}. Field observations of biomass accumulation, however, show that *M. aeruginosa* dominates over *R. raciborskii*, irrespective of climatic zones. The mismatch between biomass accumulation measured in the field, and what is predicted from growth rate measured in the laboratory, hinders effective use of culture studies to predict formation of cyanoHABs in the natural environment. The usefulness of growth rates measured may therefore be limited, and field experiments should instead be designed to examine key physiological attributes such as colony formation, buoyancy regulation and photoadaptation. Improving prediction of cyanoHABs in a changing climate requires a more effective integration of field and laboratory approaches, and an explicit consideration of strain-level variability.

1. Introduction

Cyanobacterial harmful algal blooms (cyanoHABs) are ubiquitous across lentic freshwater systems worldwide (Huisman et al., 2018). CyanoHABs, some of which are associated with cyanotoxin production, can be costly due to requirements for increased water treatment, loss of tourism and recreation revenue, and lower property values (Dodds et al., 2009; Hamilton et al., 2013). The frequency and intensity of cyanoHABs also appears to be increasing worldwide in response to rising ambient temperatures and CO_2 levels, as well as eutrophication (Kosten et al., 2012; O'Neil et al., 2012; Thomas et al., 2016; Visser et al., 2016). Understanding and predicting algal population dynamics and their key drivers are essential to manage and potentially control cyanoHABs (Burford et al., 2019).

The cyanobacteria *Microcystis* spp. and *Raphidiopsis raciborskii* (Wołoszyńska) Aguilera, Berrendero Gómez, Kastovsky, Echenique & Salerno (basionym *Cylindrospermopsis raciborskii* (Wołoszyńska) Seenayya & Subba Raju) (Aguilera et al., 2018) are of particular concern because they dominate cyanoHAB events in freshwater ecosystems globally, and have toxin-producing strains (Antunes et al., 2015; Harke et al., 2016). *Microcystis* forms blooms with buoyant colonies that accumulate at the water surface but exists as single cells in laboratory cultures (Xiao et al., 2017b). More than 50 *Microcystis* morphospecies have been recognised according to their morphological, biochemical

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and genetic differences. However, classification at species level is contentious and continually being refined (Otsuka et al., 2001; Xu et al., 2016), making it even more difficult to differentiate the morphospecies in cultures. In comparison, diazotrophic *R. raciborskii* forms subsurface blooms *in situ* with straight and coiled filamentous trichomes, and filaments in the laboratory (McGregor and Fabbro, 2000).

Microcystis spp. and *R. raciborskii* frequently dominate successively or simultaneously within the same waterbody (Soares et al., 2009; Yamamoto et al., 2011). *Microcystis* spp. are the dominant phytoplankton species in some of the world's largest lakes, such as Lake Erie in North America and Lake Taihu in China (Paerl and Huisman, 2009), while *R. raciborskii* is considered an invasive species and has expanded its dominance from tropical or subtropical lakes to temperate lakes within the past 30 years (Antunes et al., 2015; Padisák, 1997; Wood, 2004). *R. raciborskii* is also thought to have gradually replaced *Microcystis* spp. as the dominant or co-dominant species in some tropical reservoirs (Marinho and Huszar, 2002). Therefore, an updated global geographic distribution of these species is needed for a better understanding of their relative dominance, as a warming climate is hypothesized to increase the occurrence of cyanoHABs (Richardson et al., 2019).

Cyanobacterial growth and dominance is affected by a range of physical, chemical and biological factors of a waterbody (Burford et al., 2019). Excess nutrients are believed to be a key driver of recent increases in frequency and magnitude of cyanoHABs (Conley et al., 2009; Paerl et al., 2001), but uncertainty remains in the effects of physical factors on cell growth and species dominance, as well as the interactions amongst species and strains. Growth rate, as the most fundamental and direct indicator for cell growth, has been widely examined in the laboratory under a wide range of light and temperature conditions. Culture experiments have particularly focused on identifying the light (Briand et al., 2004; Dyble et al., 2006; Wiedner et al., 2003) and temperature conditions (Briand et al., 2004; Li et al., 2015; Thomas and Litchman, 2016) that yield optimal growth of *Microcystis* spp. and *R. raciborskii* strains.

In this study we aimed to examine the relevance of growth rates of multiple strains of *Microcystis* spp. and *R. raciborskii* measured in laboratory experiments for simulating the dominance of these species across the globe. We tested the suitability of laboratory data for use in ecological forecasting (Dietze et al., 2018) of cyanoHABs, by comparing the observed global distribution of these species and the simulated competition outcome under a range of light and temperature conditions derived from a growth model parameterized from laboratory-based studies.

2. Material and methods

2.1. Collation of global distributions of cyanoHABs

A literature review of field investigations of freshwater cyanoHABs from 1988 to 2017 was undertaken based on publications in *ISI Web of Science* using two searches: (1) 'freshwater', and (2) 'cyanobacterial bloom' or 'algal bloom' (Stage 1 in Fig. 1). The latitude and longitude of the freshwater systems, and the dominant bloom species were extracted from each reference (Table S1.1). Dominance of *Microcystis* spp., *R. raciborskii* or other cyanobacteria species was based on authors' descriptions of the dominant bloom species. Succession in algal communities that led to major shifts in phytoplankton community structure was also included when evaluating species dominance. *Microcystis* spp. were evaluated to morphospecies level which included *M. aeruginosa*, *M. wesenbergii* and *M. ichthyoblabe*, due to the considerable uncertainty remaining in the identification of these morphospecies. Global distributions of species dominance were then subdivided into the following climatic zones: tropical (23.08 °N to 23.08 °S), subtropical (23.08 °N to 40 °N and 23.08 °S to 40 °S) and temperate (40 °N to 66.5 °N and 40 °S to 66.5 °S).

For each field investigation, the light and temperature conditions in the summer period when cyanoHABs mostly occur were predicted across latitudes (Stage 2 in Fig. 1). The temperature was predicted from linear-regression of the summer surface water temperatures assembled from 291 lakes in 2009 (Sharma et al., 2015) to corresponding waterbody latitudes. The light intensity was predicted from linear-regression of the mid-month photosynthetically active radiation (PAR) of the northern hemisphere land surface from July to September to latitudes (Lewis, 2011), after correcting for albedo (8 % of the global irradiance) and converting to instantaneous light, assuming a 12 h photoperiod as per Reynolds (1997).

2.2. Collation of culture studies on growth

Another literature review of laboratory studies of growth rates of *M. aeruginosa* and *R. raciborskii* was undertaken based on publications in *ISI Web of Science* using two searches: (1) '*Microcystis aeruginosa*' and 'growth', and (2) '*Cylindrospermopsis raciborskii*' and 'growth' (Stage 3 in Fig. 1). A more general search term 'cyanobacteria' and 'growth' was also used to check if any related studies were missed. We manually selected studies of *M. aeruginosa* conducted using batch unicellular monocultures. Studies of colonial *M. aeruginosa* were rejected because: (1) *M. aeruginosa* exists as single cells in most cultures, and (2) colonies, in rare cases where they occur in cultures, are generally not morphologically or physiologically similar to those in the field (Xiao et al., 2018). Culture studies of both straight and coiled *R. raciborskii* were included. To isolate light and temperature effects, we removed studies of: nutrient limited growth (no dissolved nitrogen or phosphorus added to growth media); interactions with biological communities including with other cyanobacteria, bacteria, zooplankton and macrophytes, allelopathy; and trace metal impacts. After data filtering, 20 publications for *M. aeruginosa* and 16 publications for *R. raciborskii* were identified globally, including multiple strains (Fig. S2.1, Tables S1.2, S1.3). Growth rate, light intensity, light/dark cycle (photoperiod), temperature, light and temperature history, and strain origin (where the strain was originally isolated) were extracted from each study. Data were from tabulated material or otherwise extracted from the graphs in each paper using ScanIt (AmsterCHEM, Almería, Spain).

2.3. Standardization, parameterization and prediction of growth rates

We extrapolated growth rates of *M. aeruginosa* and *R. raciborskii* from the collated 20 and 16 publications, respectively, to predict relative dominance of the two species. The predictions included a three-stage process - standardization, parameterization and prediction of growth rates (Stages 4–6 in Fig. 1).

Firstly, we standardized the growth rates to a common photoperiod (Stage 4 in Fig. 1). The light/dark cycle used for culture experiments varied between studies: 24:0, 18:6, 16:8, 14:10, and 12:12 h, thus photoperiod varied between 24, 18, 16, 14 and 12 h, respectively. We used a linear relationship of growth rate to photoperiod (Geider et al., 1997; Reynolds and Irish, 1997) to place photoperiod of each study on a common time scale (12 h):

$$\mu_d = \frac{\mu_m}{T_{ex}} \times 12 \tag{1}$$

where μ_d (d^{-1}) is the photoperiod-corrected growth rate, μ_m (d^{-1}) is the measured growth rate, and T_{ex} (h) is the photoperiod used for the study.

Secondly, we performed non-linear regression of the photoperiod-corrected growth rates μ_d on light and temperature values for *M. aeruginosa* and *R. raciborskii*, at both species and strain levels (Stage 5A, 5B in Fig. 1). The calibrated parameters for the phytoplankton growth rate model were given by Eqs. (2) – (6). We assumed that the effects of light and temperature on growth rate were multiplicative (Nicklisch et al., 2007):

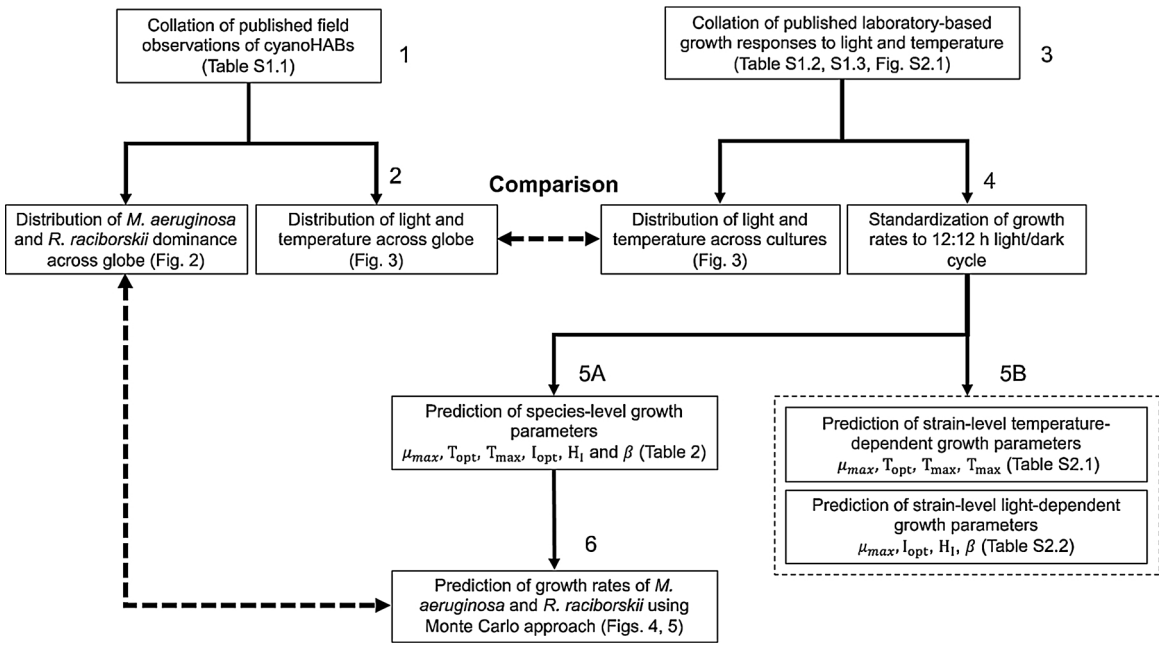

Fig. 1. Summary of the methods used in this study to extrapolate the growth rates of *M. aeruginosa* and *R. raciborskii* in culture studies to predict their relative dominance. μ_{max}, H_I, β, I_{opt}, T_{max} and T_{opt} are the growth parameters used in the phytoplankton growth model.

$$\mu = \mu_{max} f_I(I) f_T(T) - L \quad (2)$$

where μ_{max} (d^{-1}) is the maximum growth rate which occurs at the optimum light and temperature. L (d^{-1}) was maintenance (mostly respiratory) loss rate approximated as 10 % of the growth rate following Reynolds (2006):

$$L = 0.1\mu_{max} f_I(I) f_T(T) \quad (3)$$

$f_I(I)$ and $f_T(T)$ represent the effects of light and temperature on growth rate, respectively, and range between 0 and 1. $f_I(I)$ was expressed in the form of a photosynthesis-irradiance curve as per Xiao et al. (2017a):

$$f_I(I) = ((\sqrt{\mu_{max}} + \sqrt{H_I\beta})^2 \frac{I}{H_I + I} - \beta I)/\mu_{max} \quad (4)$$

where H_I (μmol photons m^{-2} s^{-1}) is the half-saturation irradiance constant, and β ((μmol photons m^{-2} $s^{-1})^{-1}$ d^{-1}) is the photoinhibition parameter. The optimal light intensity I_{opt} at which μ_{max} occurs is given by:

$$I_{opt} = \sqrt{\mu_{max} H_I/\beta} \quad (5)$$

The derivation of light limited growth $f_I(I)$ and the optimum light intensity I_{opt} are given in Appendix S3. $f_T(T)$ was based on an empirical formula from Adams et al. (2017) and Yan and Hunt (1999):

$$f_T(T) = (\frac{T_{max} - T}{T_{max} - T_{opt}})(\frac{T}{T_{opt}})^{T_{opt}/(T_{max} - T_{opt})} \quad (6)$$

where T_{max} (°C) is the maximum temperature above which growth rate ceases, and T_{opt} (°C) is the optimum temperature for growth.

For species-level parameterization (Stage 5A in Fig. 1), the mean growth rate of all replicates under each growth condition of each strain was used for each species. Equations (2) – (6) gave a mean and standard deviation of the specific growth parameters, i.e., μ_{max}, H_I, β, I_{opt}, T_{max} and T_{opt} based on the best fit, and an uncertainty of growth rate in the regression represented by the root mean square error (RMSE).

For strain-level parameterization (Stage 5B in Fig. 1), we performed similar non-linear regressions for individual strains of *M. aeruginosa* and *R. raciborskii*, to examine intraspecific variation in growth rates. Since most studies were undertaken at fixed light or temperature, or with one of these varying, dependence of growth rate on light and temperature was parameterized separately for each strain from each study. Note that only strains that were cultured under at least five light or temperature levels were selected, with all the replicates under a given light and temperature included. For each strain, response to temperature was determined by non-linear regression at the optimal light conditions $I = I_{opt}$, i.e., $f_I(I) = 1$. Hence, Eqs. (2) – (6) gave a mean and standard deviation of the specific growth parameters, i.e., μ_{max}, T_{max} and T_{opt} based on the best fit. Similarly, response to light was determined for each strain at the optimal temperature conditions $T = T_{opt}$, i.e., $f_T(T) = 1$. Hence, Eqs. (2) – (6) gave a mean and standard deviation of the specific growth parameters, i.e., μ_{max}, H_I and β, based on the best fit.

For both species and strain-level parameterization (Stage 5A, 5B in Fig. 1), the value of β was chosen to be > 0 or 0, depending on which was the best fit to the growth rate (highest R^2 value).

Thirdly, the growth rates of *M. aeruginosa* and *R. raciborskii* were predicted from Eq. (2) (Stage 6 in Fig. 1) across a range of light and temperature levels using the species-level parameters. Growth rates were predicted for temperatures ranging from 0 to 40 °C (resolved at 0.5 °C intervals), to cover the range of summer surface water temperatures assembled from 291 lakes in 2009 (Sharma et al., 2015), and for daily light intensities ranging from 0 to 55 mol m^{-2} d^{-1}, to cover the range of mid-month photosynthetically active radiation (PAR) values expected at the water surface across latitudes (Lewis, 2011). We converted the daily light dose range to instantaneous light intensity by assuming a 12 h photoperiod, yielding 0–1,300 μmol photons m^{-2} s^{-1}, which we resolved at 5 μmol photons m^{-2} s^{-1} interval for growth rate predictions. A Monte Carlo approach was applied to propagate the variability of all parameters in the growth model, i.e., μ_{max}, H_I, β, I_{opt}, T_{max} and T_{opt}, and develop an envelope of growth rate predictions. Equations (2) – (6) were run 10,000 times under each of the selected light and temperature conditions.

The predicted growth rates (from Stage 6 in Fig. 1) were then compared quantitatively between *M. aeruginosa* and *R. raciborskii*. If the growth rate of *M. aeruginosa* was higher than *R. raciborskii* in < 25 % or > 75 % of the 10,000 simulations under a given light and temperature condition, *M. aeruginosa* was defined to grow slower or faster, respectively, than *R. raciborskii*, otherwise (25–75%) the growth rates of

the two species were considered not distinguishable. Note that if both *M. aeruginosa* and *R. raciborskii* had negative growth rates in over 20 % of the simulations, we assumed no cell growth.

The strain-level variations in growth rate were also examined under a specific light intensity (100 μmol photon m^{-2} s^{-1}) and temperature (20 °C), respectively. For both species, the growth curve under variable temperatures at 100 μmol photon m^{-2} s^{-1} and under variable light intensities at 20 °C, respectively, were compared amongst strains.

2.4. Monte Carlo approach

The Monte Carlo approach refers to running the model equations multiple times using randomly sampled values from probability distributions for each parameter (Gardner and O'Neill, 1983), to assess the effect of parameter variability on simulated variables. In our study, a Monte Carlo approach was used to provide insights into how the variability of parameters, i.e., μ_{max}, H_I, β, I_{opt}, T_{max} and T_{opt}, between and within species affects the population dynamics. The probability distribution of each parameter was assumed to be log-normal, so that positive values were selected in the Monte Carlo process. The mean and standard deviation of the log-normal distributions were calculated following (Mood et al., 1974). The uncertainty in the predicted growth rate that we calculated for each species also included a root mean square error (RMSE), by selecting values from a normal distribution. Ten-thousand simulations per light and temperature value were sufficient to ensure that the results from each simulated condition were reproducible to < 2 %.

2.5. Comparison of model predictions and laboratory data

The light and temperature levels predicted from the freshwater ecosystems at Stage 2 were compared to those used in laboratory cultures at Stage 3 (Fig. 1). The relative growth rates of *M. aeruginosa* and *R. raciborskii* at a range of light and temperature levels at Stage 6 were also compared with the field observation of species dominance at Stage 1 (Fig. 1). All the environmental variables and growth parameters of cyanobacterial species used in this study are described in Table 1.

3. Results

3.1. Global distribution of cyanoHAB dominance

Reports of cyanoHABs have been published from at least 1,130 freshwater ecosystems, including lakes, rivers, reservoirs and ponds across all continents (except Antarctica) from 1988 to 2017 (Fig. 2, Table S1.1). Over 80 % of these systems were found to be dominated by *Microcystis* spp. or *R. raciborskii* on at least one occasion over that time period, with dominance varying throughout tropical, subtropical and temperate zones. *Microcystis* dominated in more systems than *R. raciborskii* (78 % vs. 17 %), irrespective of climatic zones. *Microcystis* and *R. raciborskii* were found to dominate successively or simultaneously in over 13 % of the systems, most of which were located in the tropics (60 %), followed by the subtropics (23 %) and temperate zone (17 %). About half of the systems dominated by *Microcystis* were in the temperate zone (49 %), followed by the subtropics (31 %) and tropics (20 %). In comparison, half of the systems dominated by *R. raciborskii* were located in the tropics (50 %), followed by the subtropics (31 %) and temperate zone (19 %).

3.2. Light and temperature environment

In the freshwater ecosystems dominated by *Microcystis* spp. or *R. raciborskii*, the incident light intensities were predicted to range mostly from 750 to 1200 μmol photons m^{-2} s^{-1} (Fig. 3A, C). The summer surface water temperatures were predicted to range from 18 to 30 °C (Fig. 3B, D). In comparison, in laboratory culture studies, the incident light intensities varied widely but were constant throughout the experiments and were usually < 250 μmol photons m^{-2} s^{-1} (Fig. 3A, C). The temperatures used were also constant, and mostly ranged from 20 to 30 °C (Fig. 3B, D).

3.3. Interspecific variation in growth parameters

The laboratory experiments collated in this study include data from strains originally isolated across all continents (except Antarctica) (Fig. 2). Many of the strains were isolated in Australia (51 strains in total, over 90 % of which were *R. raciborskii*), followed by North America (40 in total), Europe (15 in total) and Asia (13 strains in total, over 70 % of which were *M. aeruginosa*). There were nine strains isolated from South America, predominantly *R. raciborskii*. Only one *R. raciborskii* strain isolated from Africa was suitable to be used for study of growth responses to light and temperature (Fig. 2).

When standardized to a 12 h photoperiod for all culture studies, the growth rates of *M. aeruginosa* were < 0.87 d^{-1} (Fig. 4A) while for *R. raciborskii* they were < 1.23 d^{-1} (Fig. 4B). Variability in growth responses to light and temperature within and between species was high. The parameterized growth model showed a higher maximum growth rate at its optimal light and temperature for *R. raciborskii* (0.77 ± 0.47 d^{-1}) than *M. aeruginosa* (0.52 ± 0.32 d^{-1}) (Table 2, Fig. 4C, D). The half-saturation constant for irradiance and the optimal light for maximum growth of *R. raciborskii* (30.0 ± 18.6 and 133.4 ± 13.5 μmol photons m^{-2} s^{-1}) were nearly three-fold and two-fold higher, respectively, than values for *M. aeruginosa* (12.6 ± 8.3 and 77.3 ± 11.4 μmol photons m^{-2} s^{-1}) (Table 2, Fig. 4C, D). *M. aeruginosa* had a slightly lower mean value of optimal temperature, and there were no substantial intraspecific differences between the maximum

Table 1
Parameters and variables used in this study.

Descriptions		Symbol	Units
Parameters	Maximum growth rate at the optimal light and/or temperature	μ_{max}	d^{-1}
	Optimal light for maximum growth	I_{opt}	μmol photons m^{-2} s^{-1}
	Half-saturation irradiance constant	H_I	μmol photons m^{-2} s^{-1}
	Photoinhibition parameter	β	(μmol photons m^{-2} s^{-1})$^{-1}$ d^{-1}
	Optimal temperature for maximum growth	T_{opt}	°C
	Temperature at which cell growth stops	T_{max}	°C
	Mortality rate	L	d^{-1}
Variables	Temperature from culture studies	T	°C
	Incident light intensity from cultures	I	μmol photons m^{-2} s^{-1}
	Photoperiod from cultures	T_{ex}	h
	Measured growth rate from cultures	μ_m	d^{-1}
	Photoperiod-corrected growth rate	μ_d	d^{-1}
	Predicted growth rate	μ	d^{-1}

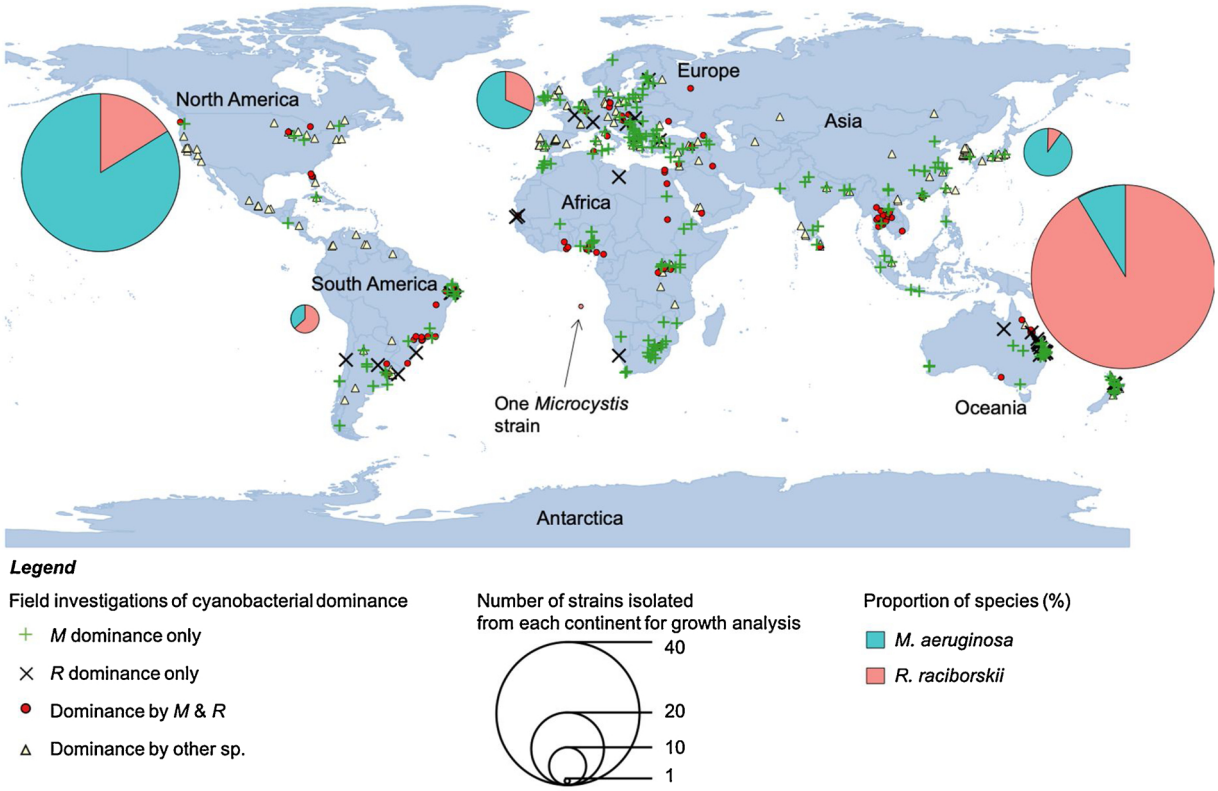

Fig. 2. Global map indicating observations of freshwater cyanobacterial dominance from 1988 to 2017, and the strains isolated from each continent for culture studies. Dominance by *Microcystis* spp. only and *R. raciborskii* only are shown in green and black crosses, dominance by both species is shown by red dots, and dominance by other species is shown in yellow triangles. The size of pie charts shows strain number, and the proportion shows *M. aeruginosa* (in pink) and *R. raciborskii* (in blue) strains that were isolated from each continent.

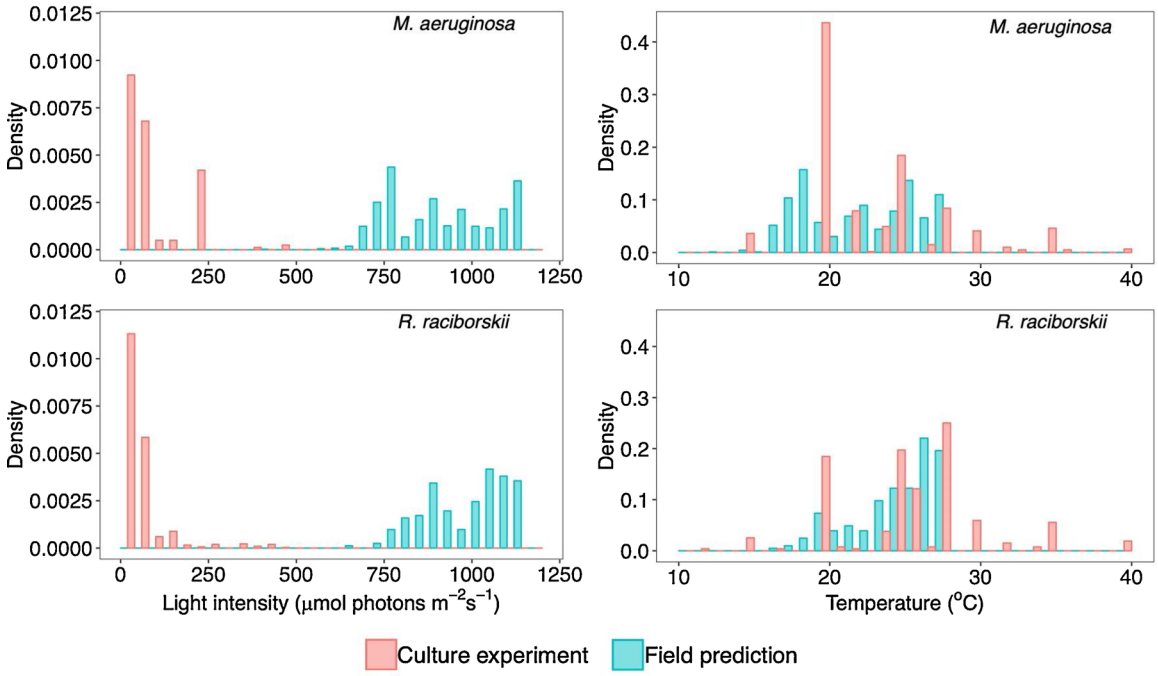

Fig. 3. Kernel density plots to compare the incident light intensity and temperatures collated from culture experiments and predicted from the freshwater systems dominated by *Microcystis* spp. and *R. raciborskii*, respectively, in summer periods. The pink bars indicated experiments and the blue bars indicated predictions.

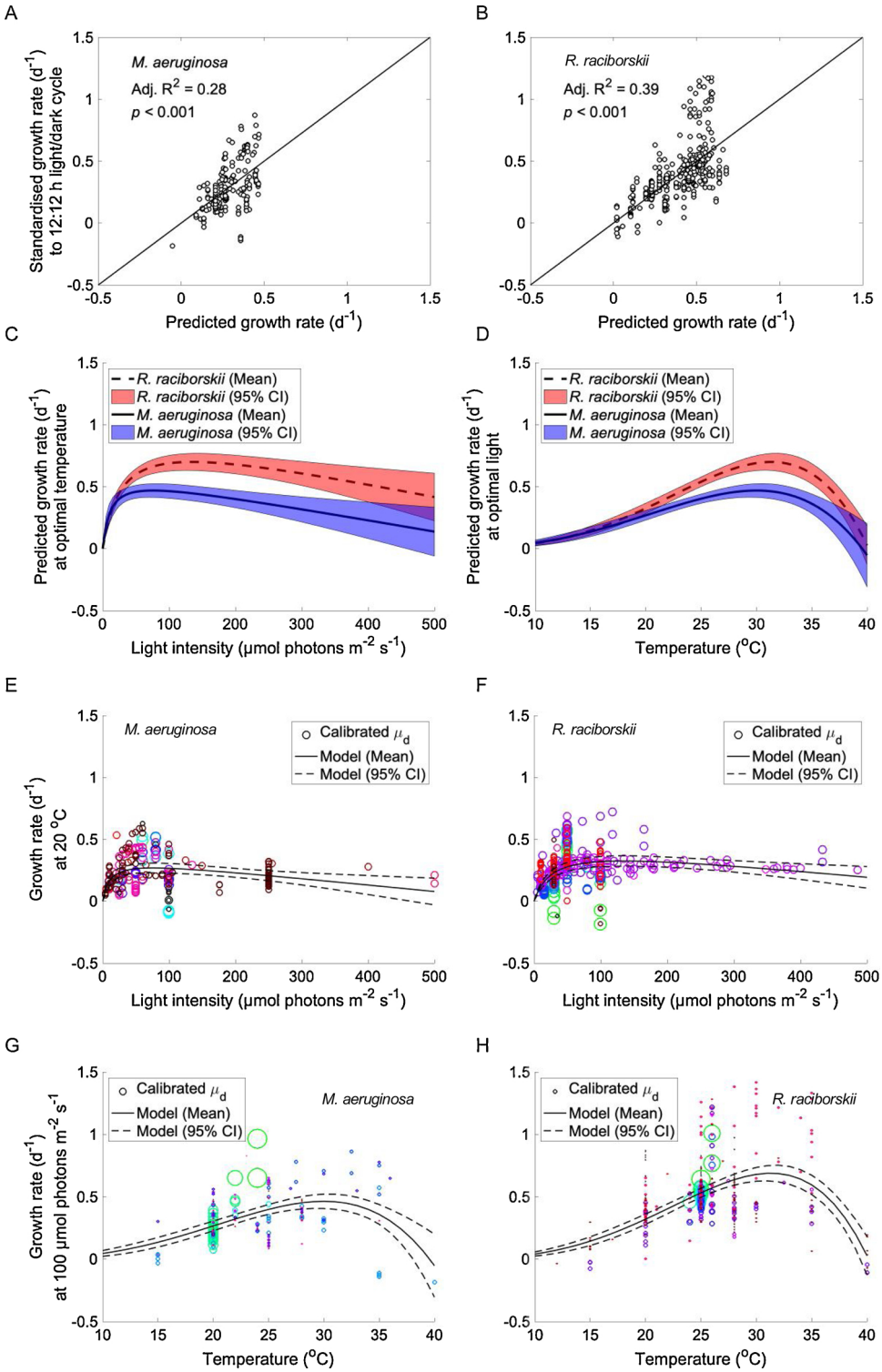

Fig. 4. Interspecific and intraspecific variations in growth rate predictions using parameterized growth model (Eqs. (2) – (6)). A – B: Comparison of predicted growth rates with the published growth rates standardized to 12 h photoperiod (μ_d): A. *M. aeruginosa* ($R^2 = 0.28$, $P < 0.001$, n = 197); B. *R. raciborskii* ($R^2 = 0.39$, $P < 0.001$, n = 349). The diagonal lines represent slope = 1:1. C: Predicted light curves at the optimal temperature for growth of both species, with associated variability (5th and 95th percentiles of predictions). D: Predicted growth curves at the optimal irradiance for growth of both species, with associated variability (5th and 95th percentiles of predictions). E – F: Predicted growth curves of both species at 20 °C, compared with calibrated growth rates at 20 °C of all strains in cultures. Colours indicated different light levels from culture data and size corresponds to temperature scaled from 10 to 40 °C. G – H: Predicted growth curves of both species at 100 μmol photons m^{-2} s^{-1}, compared with calibrated growth rates at this light (photoperiod-corrected) of all strains. Colours indicate temperature levels from cultures and size corresponds to light intensity scaled from 0 to 500 μmol photons m^{-2} s^{-1}. μ_d indicates the growth rates corrected to a photoperiod of 12 h.

Table 2
Species-level specific growth parameters with best fit (mean ± standard deviation) for *M. aeruginosa* and *R. raciborskii*: maximum growth rates at optimal light and temperature μ_{max} (d^{-1}); optimal light for maximum growth I_{opt} (μmol photons m^{-2} s^{-1}); half-saturation irradiance H_I (μmol photons m^{-2} s^{-1}); photoinhibition parameter β ((μmol photons m^{-2} $s^{-1})^{-1}$ d^{-1}); optimal temperature for maximum growth T_{opt} (°C); maximum temperature where growth rate ceases T_{max} (°C); and root mean square error of the predicted growth rate (RMSE, d^{-1}). Parameters were obtained from fitting Eq. (2) to the data collected from 20 and 16 studies for *M. aeruginosa* and *R. raciborskii*, respectively. Both model fits were significant ($P < 0.001$).

Estimated parameters	Species		Units
	M. aeruginosa	*R. raciborskii*	
μ_{max}	0.52 ± 0.32	0.77 ± 0.47	d^{-1}
I_{opt}	77.3 ± 11.4	133.4 ± 13.5	μmol photons m^{-2} s^{-1}
H_I	12.6 ± 8.3	30.0 ± 18.6	μmol photons m^{-2} s^{-1}
β	0.0011 ± 0.0007	0.0013 ± 0.0008	(μmol photons m^{-2} $s^{-1})^{-1}$ d^{-1}
T_{opt}	30.0 ± 18.2	31.3 ± 19.0	°C
T_{max}	39.6 ± 24.0	40.1 ± 24.3	°C
RMSE of predicted growth rate	0.16	0.19	d^{-1}
R^2	0.28	0.39	–

temperature, the optimal temperature and the photoinhibition parameter (Table 2, Fig. 4C, D).

3.4. Intraspecific variation in growth parameters

Variability in growth response to light and temperature was also high across strains (Fig. 4E – H, Tables S2.1, S2.2). For example, the mean value of maximum growth rate at optimal temperature and light varied among strains by a factor of ~5.5 (Table S2.1) and ~4 (Table S2.2), respectively. Even strains of each species isolated from the same waterbody differed in respect to growth parameters. For example, *M. aeruginosa* strains BearAC-02 and BearAG-02, originally isolated from Bear Lake, Michigan, North America (Thomas and Litchman, 2016), had a 2-fold difference in their maximum growth rates (Table S2.1). Wide variations also occurred for the same strain isolated from the same waterbody when grown under different conditions in different laboratories, i.e., *R. raciborskii* LETC CIRF-01 (Lürling et al., 2013; Soares et al., 2013).

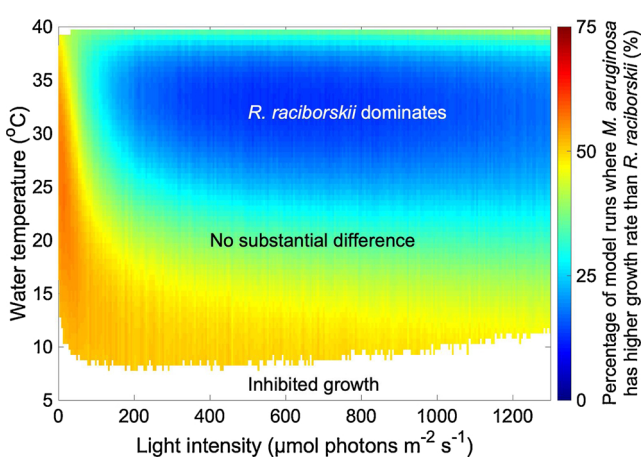

Fig. 5. Percentage of model runs (%) where predicted growth rate of *M. aeruginosa* was higher than *R. raciborskii* under a range of light and temperature conditions, based on Monte Carlo simulation of parameterized growth model (Eqs. (2) – (6)). The white area indicates conditions corresponding to zero net growth of either species. The blue area indicates where *R. raciborskii* had higher growth rate than *M. aeruginosa* at a frequency of 25 % over 10,000 simulations.

3.5. Dependence of growth rate on light and temperature

R. raciborskii was predicted to have higher growth rates than *M. aeruginosa* when the light intensity was ≳ 150 μmol photons m^{-2} s^{-1} (12 h light per day) and temperature was above ~25 °C (Fig. 5). Growth of both species was predicted to be negligible when the temperature was < ~8 °C across all light intensities, or < 12 °C when light intensity increased to ~1200 μmol photons m^{-2} s^{-1} due to the combined effects of photoinhibition and temperature exceeding the optimal value ($T > T_{opt}$) (Fig. 5). For temperatures of up to 25 °C or light intensities of up to 150 μmol photons m^{-2} s^{-1}, the predicted growth rates were not substantially different between *M. aeruginosa* and *R. raciborskii* (Fig. 5). *M. aeruginosa* was not predicted to have higher growth rates than *R. raciborskii* under any light or temperature conditions at a frequency of 25 % over 10,000 simulations (Fig. 5).

4. Discussion

4.1. Contrasting results - species dominance in model prediction vs. observations

Our collation of field observations of cyanoHABs showed that *Microcystis* spp. dominated more often than *R. raciborskii* in lentic waterbodies (78 % vs. 17 % dominance of cyanoHABs globally) irrespective of climatic zones. This observation suggests that knowledge of growth rates measured in the laboratory may not explain global dominance patterns of these two species. To specifically test this, we synthesized the growth rates of *M. aeruginosa* (representing *Microcystis* spp.) and *R. raciborskii* to light and temperature measured in laboratory studies. We predicted higher growth rates of *R. raciborskii* than *M. aeruginosa* at temperatures ≳ 25 °C and light intensities ≳ 150 μmol photons m^{-2} s^{-1}, which, as suspected, does not correspond to the field observations of the relative dominance of each species, indicated by biomass accumulation.

Our growth model, derived from laboratory culture studies, applied surface water temperature and depth-averaged irradiance in predicting growth rates. Summer surface water temperatures ≳ 25 °C occurred in over 32 % of the 291 lakes examined in 2009 in a global study (Sharma et al., 2015). The ambient summer light intensity is typically > 150 μmol photons m^{-2} s^{-1} (equivalent to 6.5 mol m^{-2} d^{-1} assuming a 12 h photoperiod with constant light intensity) across latitudes (Lewis, 2011). This irradiance represents a depth-averaged value of a deep surface mixed layer (SML; 7 m) in relatively clear waters (background light attenuation coefficient k_{bg} = 0.3 m^{-1}) with an incident light intensity of 1300 μmol photons m^{-2} s^{-1}. This irradiance is also much lower than light intensities corresponding to shallower SMLs. Therefore, *R. raciborskii* should be predicted to have higher growth rates than *M. aeruginosa* in a large proportion of lentic waters across different latitudes under nutrient-replete conditions. By contrast, field observations showed that *Microcystis* dominates more often, irrespective of climatic zones. Although growth rate is a fundamental parameter that is always measured in cultures and widely applied in phytoplankton growth models, the mismatch between field observations of laboratory experimental values obtained in this study suggest that higher growth rate is not equivalent to higher biomass, hence is a poor predictor for relative dominance of species *in situ*. Similarly, diatoms and green algae are reported to have much higher growth rates than cyanobacteria; however they lose their competitiveness to cyanobacteria when turbulent diffusivity of the water column is low (Huisman et al., 2004).

Pooling all available culture studies yielded substantially higher maximum growth rates, higher optimal light intensities I_{opt} and lower half-saturation irradiance constants for *R. raciborskii* than *M. aeruginosa*, but no substantial differences in their optimal temperatures T_{opt}. Hence, this prediction suggests that warmer temperatures may not be the only

driver of the relative dominance of *R. raciborskii* over *M. aeruginosa* and light may play a more important role than temperature in determining their relative dominance. However, in the case of *M. aeruginosa,* laboratory and field studies show contradictory responses to light, with field populations better adapted to higher light intensities. This prediction differs from a culture study of *R. raciborskii* (Pierangelini et al., 2015) which indicates that this species is better adapted to lower light intensities. It also differs from the field observations that *Microcystis* forms surface scums during blooms while *R. raciborskii* can develop subsurface blooms at water depths of 2–3 m (Saker and Griffiths, 2001) or that it tends to be evenly distributed in the surface mixed layer with a relatively low I_{opt} (O'Brien et al., 2009).

4.2. Intraspecific variation in growth parameters

The co-existence of strains (i.e., ecotypes within a species) leads to a wide intraspecific variation in growth responses of *M. aeruginosa* and *R. raciborskii* to environmental conditions (Sandrini et al., 2014; Willis et al., 2016; Xiao et al., 2017a). This intraspecific variation can be accounted for in dynamic models which aim to forecast cyanoHABs by using probabilistic approaches, such as the Monte Carlo method used in this study. It is acknowledged that the probability of dominance by *M. aeruginosa* over *R. raciborskii* (Fig. 5), was determined based on a statistical model that explicitly assumes log-normal distribution for their growth rate parameter values (Table 2). These parameter probability distributions were derived from uncertainty in the collated experimental data. In other words, the uncertainty in the input data is being used to provide information on the uncertainty in the outcome of the growth predictions.

Some of the variation in growth among strains in different studies may also be attributed to differences in photoperiod. We addressed this issue by standardizing growth rates to 12:12 h light/dark cycle in our analysis, however photoperiod may also interact nonlinearly with temperature and light to affect cyanobacterial growth rates (Nicklisch et al., 2007).

Strains of species can undergo major evolutionary changes over multiple generations as a result of adaptation to culture conditions (Lakeman et al., 2009). Hence, strain response to environmental variables depends on how long it has been in culture, i.e., longer time in culture means less retention of field traits (Lakeman et al., 2009). These physiological changes may help to explain the different growth rates of the same strain across studies, such as for *R. raciborskii* LETC CIRF-01 (Lürling et al., 2013; Soares et al., 2013). Therefore, the widely reported light or temperature optima for growth of different strains of the same species might not reflect their 'real' optima but rather a conditioning to the environmental conditions at which they were grown (Briand et al., 2004).

The strain concept for *Microcystis* spp. is further complicated by the description of 'morphospecies' or 'morphotypes'. Over 50 *Microcystis* morphospecies have been identified (Komárek and Komárková, 2002), however, there is inconsistency between the classical Linnaean taxonomy and modern molecular taxonomy in classifying these *Microcystis* species. Differentiating *Microcystis* strains from different morphospecies in laboratory cultures is even more difficult. *Microcystis* strains used across studies may not necessarily be from one morphospecies. We attempted a level of standardization by selecting laboratory studies based on *M. aeruginosa* only, to reduce the inconsistency of differentiating different *Microcystis* morphospecies. However, we acknowledge the successive dominance of different morphospecies (Li et al., 2013) and consider the physiology amongst and within these species in the process-based models for prediction of blooms and dominance of *Microcystis*.

4.3. Future considerations in cyanobacterial prediction

To better predict and model the global distribution and dominance of species *in situ*, there are several issues that need to be considered. A key factor that hinders a more robust prediction of species dominance is that culture studies fail to reflect several key physiological attributes of cyanobacteria. For example, *Microcystis* has a variety of mechanisms that allow it to better control its vertical position in the water column, and to therefore be subjected to specific light and temperature environments. Factors affecting water column position include colony formation (Yamamoto et al., 2011), buoyancy regulation (Brookes and Ganf, 2001; Ibelings et al., 1991), and changes in morphology and size in relation to turbulent mixing (Li et al., 2018). Large colony size of *Microcystis* spp. translates into higher flotation velocities ($\sim 10\ m\ h^{-1}$, Li et al. (2016)); the fastest recorded for freshwater cyanobacteria, with mean velocities almost four magnitudes higher than those of *R. raciborskii* (Xiao et al., 2018). This rapid flotation velocity enables *Microcystis* spp. to optimize light capture (Ganf and Oliver, 1982), and to disentrain from the predominant water motions under low to moderate turbulence (Humphries and Lyne, 1988). *Microcystis* colonies are also less susceptible to high irradiance compared to single cells, due to a higher quota of photosynthetic pigments (Wu et al., 2011; Wu and Song, 2008; Zhang et al., 2011) and the ability to protect cells within the colony by self-shading (Reynolds, 2006). Hence, culture studies of *Microcystis,* which typically used or formed single cells instead of colonies, are likely to underestimate the growth of *Microcystis* under high light or light-saturated conditions.

In nutrient-enriched systems, the large biomass of *Microcystis* spp. could protect sub-surface colonies from high irradiance by shading them, whilst potentially limiting the growth of other species, including *R. raciborskii* in deeper waters. This is consistent with the dominance of *Microcystis* over *R. raciborskii*, as demonstrated in our collation of field data. In laboratory experiments, however, where cultures are typically grown under constant temperature, light and other physico-chemical conditions, *Microcystis* exists mostly as single cells or sometimes as colonies that are usually morphologically or physiologically different to those observed in the field, with little capacity for buoyancy regulation (Marinho et al., 2013; Xiao et al., 2018; Yang et al., 2008). In an ideal world, colonial studies of *Microcystis* would be used to inform predictions in the field, however, there is currently no effective way of forming colonies in the laboratory comparable to those of the field.

Photoadaptation is also likely to affect the physiological responses of each species (O'Brien et al., 2009; Zevenboom and Mur, 1984). Litchman (2000) found that phytoplankton growth may be depressed or accelerated under fluctuating light conditions and, as a result of differences among species, light fluctuations may structure phytoplankton communities and alter their diversity (Litchman and Klausmeier, 2001). Since *Microcystis* spp. and *R. raciborskii* may be distributed heterogeneously through the water column, with varying levels of instantaneous light exposure (Huisman et al., 2004), adaptation to antecedent light may play an important role in shaping populations but is not able to be addressed in culture studies under constant light intensity. Moreover, the timescale for the regulation of velocity under changing light could in turn affect the species' light exposure, hence altering competitiveness. A particular strain that responds faster in a changing environment could potentially establish a dominance earlier than the strains constituting the rest of the population, which may promote dominance of the species.

Of note in our synthesis of culture studies of *M. aeruginosa* and *R. raciborskii* was that few experiments were conducted at light intensities > 250 μmol photons $m^{-2}\ s^{-1}$. Most culture studies investigate a light regime representative of the bottom of a reasonably deep surface mixed layer in relatively clear waters. However, the light regimes corresponding to shallower SMLs are much higher than those used in the vast majority of culture studies. The reason why low light intensities are used is because the artificial light, e.g., fluorescence tubes or LEDs, has a relatively low maximum light intensity. The low light intensities lead to an under-representation of photoinhibition, a critical physiological response which affects phytoplankton population

dynamics, including growth rates (Whitelam and Cold, 1983). Culture studies could usefully increase light intensity to better mimic a high-light case often seen in the field.

It is acknowledged that environmental factors, such as nutrient availability, interactions with other biological factors, including those affecting the mortality of cyanobacteria, such as zooplankton grazing and viruses, allelopathic substances produced by species and strains, also interact with light and temperature to affect cell growth, and hence species dominance. The current knowledge base of these responses is limited, and uncertainty is therefore considered to be too high to quantify and model these responses.

5. Conclusions

Improving predictions of the growth and dominance of cyanoHABs under a changing climate is a high priority for water authorities around the world. Growth rate of cells, as a fundamental parameter that has been widely studied under controlled culture studies in the laboratory, has been widely used in current phytoplankton models. This study used a competition model with synthesized growth rates of *Microcystis* and *R. raciborskii* from laboratory-based culture studies from across the globe. The model predictions demonstrated that laboratory-derived light- and temperature-dependent growth rates do not yield the observed field dominance of *Microcystis* over *R. raciborskii* indicated by biomass accumulation. Therefore, the use of growth rate measurements from laboratory studies in modelling or synthesis studies should be reconsidered, and experiments should instead be designed to examine measures such as biomass accumulation. Moreover, consideration of additional key physiological processes is required to develop greater confidence in field predictions that are based culture studies. Studies in the laboratory oversimplify the complex environmental conditions in the field, hence the applicability of laboratory studies in a synthesis or for forecasts of cyanoHABs in a changing climate will continue to be limited without detailed consideration of these processes.

Declaration of Competing Interest

The authors declare no conflict of interest.

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Appendix A. Supplementary data

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