Check for updates

Received: 2 February 2021 | Revised: 22 August 2021 | Accepted: 23 August 2021

DOI: 10.1111/fwb.13822

ORIGINAL ARTICLE

Community shifts from eukaryote to cyanobacteria dominated phytoplankton: The role of mixing depth and light quality

Maria Stockenreiter[1] | Jana Isanta Navarro[2] | Felicitas Buchberger[1] | Herwig Stibor[1]

[1]Aquatic Ecology, Department Biology II, Ludwig-Maximilians-University Munich, Planegg-Martinsried, Germany

[2]Limnological Institute, University of Konstanz, Konstanz, Germany

Correspondence
Maria Stockenreiter, Aquatic Ecology, Department Biology II, Ludwig-Maximilians-University Munich, Grosshaderner Str. 2 82152, Planegg-Martinsried, Germany.
Email: stockenreiter@bio.lmu.de

Present address
Jana Isanta Navarro, Flathead Lake Bio Station, University of Montana, Polson, MT, USA

Funding information
Deutsche Forschungsgemeinschaft; EU H2020-INFRAIA AQUACOSM

Abstract

1. Lake stratification strengthens with increasing surface water temperatures, thereby reducing the depth of the mixed layer. Phytoplankton communities are not only exposed to different nutrient availability within a mixed water column, but also to different light quality. We conducted controled laboratory and mesocosm experiments to investigate phytoplankton, especially cyanobacteria, responses to different light quality and mixing depths.
2. Our mesocosm experiment allowed the manipulation of mixing depth in situ by a mesocosm approach and to follow the effects of changing mixing depth on the phytoplankton community composition. Our laboratory experiment allowed the control of temperature and light quantity. To investigate the effect of light quality on phytoplankton, we created a light gradient from full photosynthetic active radiation to a reduced blue spectrum.
3. In both experiments, shifts in phytoplankton community composition from eukaryote to cyanobacteria occurred at shallow mixing depth with higher availability of photosynthetic active radiation. Our results from the mesocosm experiment support the idea that reduced mixing depth can promote cyanobacterial abundance. With our laboratory experiment, we were able to manipulate light quality independent of temperature, available nutrients and light intensity influencing phytoplankton abundance. Results from the laboratory experiments support our hypothesis that a shift in light spectrum alone is a driver, strong enough to enhance cyanobacteria occurrence.
4. Most of the previous studies dealing with cyanobacterial blooms have investigated temperature and eutrophication effects. Certainly, these are major factors for the growth of phytoplankton, but our experiments show that other aspects, such as the quality of light, must be also taken into account to explain cyanobacterial blooms. Such shifts in the phytoplankton community from eukaryote to cyanobacteria dominated communities will have strong consequences for food web dynamics. Several cyanobacteria specific traits, (e.g., toxin production, lack of essential fatty acids, and inedibility through production of large colonies) reduce

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.
© 2021 The Authors. *Freshwater Biology* published by John Wiley & Sons Ltd.

transfer efficiencies of energy and matter between phyto- and zooplankton and therefore can influence higher trophic levels such as fish.

KEYWORDS
blooms, freshwater, mesocosms, phytoplankton, wavelengths

1 | INTRODUCTION

Lakes in the temperate zone of the northern hemisphere are dominantly dimictic and characterised mainly by their seasonal physical and biological patterns and processes (Winder & Schindler, 2004; Woolway & Merchant, 2019). Global warming has the potential to alter many of those patterns and processes. For example, increasing surface-water temperatures can lead to reduced or even no ice cover during winter (Benson et al., 2012; Magee et al., 2016), earlier onset of phytoplankton spring blooms (Berger et al., 2007), preferences of thermophilic species (Blenckner et al., 2007; Gerten & Adrian, 2002; Lürling et al., 2013), alterations in plankton body size (Rasconi et al., 2015), and stronger stratification events (Woolway et al., 2019). In particular, stronger stratification and the reduced depth of the mixed layer can cause high nutrient depletion in the upper water layers due to increased sedimentation of primary producers and reduced upward transport of recycled nutrients from deeper water layers (Winder & Sommer, 2012). At the same time warmer surface water can increase the activity of planktivorous fish and can thereby reduce zooplankton (Jeppesen et al., 2014; Mehner, 2000), which will in turn result in higher phytoplankton biomass (symptoms of eutrophication; Moss et al., 2011; Winder, 2012). Additionally, lower parts of the water column become anoxic when stratification is strong; this limits the availability of a deep water refuges for zooplankton avoiding predation (Doubek et al., 2018).

The composition of the phytoplankton community in terms of eukaryotes and prokaryote cyanobacteria depends strongly on abiotic parameters (Bock et al., 2018; Verbeek et al., 2018). Cyanobacteria possess a variety of key traits related to growth, resource use, sedimentation, and temperature optima (see Mantzouki et al., 2016), which may be beneficial when water temperatures increase, and stratification intensifies. Pelagic cyanobacteria have comparable high temperature optima for growth (Thomas & Litchman, 2016) and can outcompete eukaryotic phytoplankton groups such as bacillariophyta, cryptophyta and dinoflagellates with lower temperature optima (Senerpont Domis et al., 2007; Litchman et al., 2010) However, also chlorophyta can show high growth rates at high temperatures, but see Lürling et al. (2013). Another well investigated trait are gas vesicles formed by some cyanobacteria species, allowing them to control their position within the water column, thereby reducing high mortality by sedimentation (Visser et al., 1996; Zohary & Robarts, 1990). Regarding resource use, certain cyanobacteria possess traits related to atmospheric nitrogen fixation, offering access to nitrogen sources not available to eukaryotic primary producers (Mantzouki et al., 2016; Paerl & Huisman, 2009). Additionally, cyanobacteria have the ability to concentrate bicarbonate, especially when CO_2 becomes scarce at high levels of primary production and high pH values (Morales-Williams et al., 2017).

However, mixing patterns also have consequences for phytoplankton light availability in terms of quantity and quality. With a reduced mixing depth, available light quantity (Kunz & Diehl, 2003) and quality increase (Båmstedt, 2019). While the effects of altered light quantity resulting from different mixing depths of natural plankton communities are experimentally well studied (Berger et al., 2006; Diehl et al., 2002; Kunz & Diehl, 2003), there is a lack of experimental analyses of the effects of altered light quality. In the water column longer wavelengths are rapidly absorbed; therefore, phytoplankton in deeper water layers are less exposed to red, yellow and orange but more to blue light. Complementary to chlorophyll-*a*, cyanobacteria have accessory pigments (phycobilins) allowing them efficiently to use light within the green gap of chlorophyll-*a* and -*b* (Britton, 1983). Luimstra et al. (2020) showed in their laboratory study that cyanobacteria growth under blue light decreases because of low photosynthetic efficiency, when phycobilins are present. Growth increases otherwise under red and orange light. Huisman et al. (2004) have shown in a theoretical model that this is the case in shallow lakes, especially when vertical mixing depth is low. Predictions from theoretical work by Gray et al. (2019, 2020) demonstrated how shallower mixing and increasing temperatures shift the phytoplankton community towards a cyanobacteria-dominated one. A combination of altered physical and biological processes and patterns might even lead to cyanobacterial mass developments (blooms; Kosten et al., 2012; Paerl & Paul, 2012; Pick, 2016; Urrutia-Cordero et al., 2016).

Phytoplankton community shifts towards a cyanobacteria-dominated one may result in long-term community and food-web changes. Cyanobacteria are of poor food quality for zooplankton grazers because of morphological properties, the production of toxic secondary metabolites (DeMott et al., 2001; Witt et al., 2019), inadequate stoichiometry (Gulati & DeMott, 1997), and the lack of essential sterols and long-chain polyunsaturated fatty acids (Martin-Creuzburg et al., 2008; Müller-Navarra et al., 2004).

It is questionable which of the various effects that may be associated with higher surface water temperatures cause potential shifts towards a cyanobacterial dominance. For example, it is difficult to disentangle the two effects of temperature and mixing depth on phytoplankton communities using only observational field data, as both environmental parameters are strongly autocorrelated. The same applies to the effects of light quantity and quality, as higher light availability is usually correlated with a wider spectrum of photosynthetically active radiation (PAR). Therefore, controlled experimentation is needed.

Here, we present data from a mesocosm experiment in a eutrophic lake and from a controlled laboratory experiment with natural phytoplankton communities to investigate cyanobacterial responses to manipulations of maximum mixing depth of the upper water layer and related light-quality shifts. Our mesocosm experiment allowed manipulation of mixing depth in situ by a mesocosm approach and to follow the effects of changing possible mixing depth in a eutrophic, shallow lake. In addition, our laboratory experiments (communities from an oligotrophic and eutrophic lake) allowed for control of temperature and light quantity, thereby allowing us to disentangle the effects of depth-related shifts in light quality independent of shifts in light quantity.

Using such a comprehensive experimental approach we tested whether: (H1) reducing mixing depth of the upper water layer in a eutrophic lake promotes cyanobacterial abundance; and (H2) shifts towards more red light alone result in a favourable light climate for cyanobacteria, which are able to enhance their contribution to a natural phytoplankton community.

2 | MATERIAL AND METHODS

2.1 | Mesocosm experiment

The mesocosm experiment was carried out in Lake Bansee (NS47°5 7′52.788″EW12°26′25.527″, Southern Bavaria, Germany), which is a natural and shallow lake (area 3.3 ha, volume 79.900 m^3, maximum depth 4.5 m). Even though Lake Bansee is eutrophic (total phosphorus, TP >30 μg/L at spring circulation), the amount of phosphorus available for phytoplankton (soluble reactive phosphorus, SRP) varies from 3 to 6 μg/L. A nutrient limitation bioassay (Andersen et al., 2007) revealed a strong P limitation.

Mesocosms of varying length created experimental gradients of mixing depth. Mesocosms were made of clear plastic (LDPE Poly-Verpackung, Trappenkamp, Germany), heat-sealed at the bottom, open to the atmosphere, with an inner diameter of 0.95 m, and attached to an inflatable rubber ring as a swimming device. Five different depths (0.5, 1, 2, 3 and 4 m) were replicated three times. All 15 mesocosms were positioned vertically in the middle of Lake Bansee where the water column was 4.5 m deep. As the mesocosms were of different depths, the volume varied from 360 L (0.5 m) to 2,850 L (4 m). The mesocosms were filled with lake water filtered through 250-μm mesh (nylon mesh, VWR collection, Ismaning, Germany) to exclude meso-zooplankton but ensuring a complete and diverse phytoplankton community. Air pumps (compressor PM 50 63B-12Volt; up to 6 bar) were installed to ensure an air supply and allow for mixing to prevent steady sinking of nutrients and plankton within the mesocosm. For this, a tube (4 mm) with a weight was installed at the bottom of each mesocosm to ensure that the whole water column was mixed twice a week for 20 min. Mesocosms showed in the middle of the experiment no stratification, however, there were slight stratifications at the beginning and the end of the experiment (see Figure S1). Therefore, maximum mixing depth was guaranteed in the mesocosm experiment during the main phase of the experiment. Mesocosms were not fertilised at any time during the experiment, which lasted from end-March to mid-May (42 days).

2.2 | Laboratory experiment

We established phytoplankton communities originating from two different pond/lakes in Southern Bavaria in semi-continuous batch conditions (5% exchange rate of total experimental volume of each bottle per day). One community was taken from a shallow eutrophic (TP >30 μg/L) pond (MPI pond) close to the Max Planck Institute, Martinsried, Germany (N48°6′25.304″ E11°27′27.6″) and the other from the oligotrophic Lake Brunnensee (TP <3 μg/L), Germany (N47°59′3.3682″ E12°26′10.403″) in early spring (25 March). We took a 1-L water sample from the well-mixed epilimnion and filtered samples through a 250-μm mesh to remove meso-zooplankton. We acclimated samples in a climate chamber at 20°C and 100 μmol photons m^{-2} s^{-1} (12 hr/day) for 1 day prior to the start of the experiment.

To obtain an equal initial total algal biovolume of 1 mg carbon/L, the total volume of each phytoplankton community was determined with a cell counter (CASY®1 Cell Counter combined with Analyzer System TTC, Schärfe System GmbH, Germany), and based on these measurements each community was set to the same initial total phytoplankton volume. We used 250-ml translucent cell culture flasks (CELLSTAR®, Greiner Bio-one, Frickenhausen, Germany) filled with 200 ml of each lake community. To ensure semi-batch conditions, 5% of the existing volume was removed and replaced (under a laminar flow hood) with filtered lake water (Gf/F Whatman, GE Healthcare, U.S.A.) for each corresponding lake every day. This approach ensured constant nutrient supply during the experiment. Bottles were shaken gently every day before exchange of medium. During the experiment, we exposed cultures to 65 μmol photons m^{-2} s^{-1} for 24 hr day^{-1} at 20°C. We chose 24-hr light exposure for fast and direct responses of experimental manipulations of the phytoplankton. Laboratory experiments usually run on small volumes; an extended experimental duration may result in undesired strong bottle effects (wall growth etc.). We altered the light quality experienced by communities by varying the number of hours of exposure of the communities to blue and white light, thereby increasing the availability of red light. Five treatments were established, the blue (h)/white (h) light ratio ranging from 0:24 to 6:18, 12:12, 18:6, and 24:0; these ratios being chosen to mimic different deep-water layers. At deep mixing events, phytoplankton will be exposed mainly to blue light during the day, whereas at shallow mixing events they will be confronted with mainly the full PAR spectrum (white light). Consequently, to get a better resolution of the effects of such spectral shifts, we chose a gradient design with discrete steps between the two extreme conditions. We installed white light using cool-white-light lamps to provide the full PAR spectrum. For blue light, experimental units were covered with blue-light filter screens (transmission: 430–470 nm; LEE filters, Hampshire, U.K.; see Figures S2 and S3). We established two replicates for each light treatment × community type (n = 10 $lake^{-1}$). The experimental duration was 22 days.

2.3 | Sampling and measurements

Before each sampling every mesocosm was mixed for 5 min with compressed air from pumps; thus, we could ensure a homogeneous phytoplankton sample by taking 1.5 L of water from each mesocosm (250-μm filtered to exclude macro- and meso-zooplankton).

At start and final sampling dates, 100-ml water samples of each mesocosm and 50 ml per bottle in the laboratory experiment were added to brown glass bottles and preserved with Lugol's solution (following J.G.A Lugol 1786–1851). To estimate the initial and final phytoplankton species/genera composition in both experiments, we counted samples fixed with Lugol's iodine using the standard Utermöhl technique (Utermöhl, 1958). For filamentous and colonial species/genera we counted individual cells. For final phytoplankton biovolume, counts were calculated by genus-cell-specific biovolume. Specific biovolume data used were from Kremer et al. (2014).

For phytoplankton biomass in the mesocosms we measured particulate organic carbon (POC). We filtered 100 ml of mesocosm (250-μm filtered) water through glassfibre filters at the start and end of the experiment (GF/F, 0.7 μm, precombusted for 4 hr at 500°C and washed in 8% hydrochloric acid prior to use). Filters were incubated with phosphoric acid (0.5 M) for 30 s to evaporate the calcite. All filters were dried for 24 hr at 60°C, placed in tin foil and measured with an elemental analyser (vario MicroCube, Elementar, Germany).

Nitrate concentrations in the mesocosms were determined by ion chromatography (Dionex ICS-1100 basic integrated IC system with Dionex IonPac AS22; Thermo Scientific, U.S.A.). Samples were filtered (0.45 μm, CS 400 Syringe Filters Cellulose Acetate Nalgene, U.S.A.) prior to measurements. For SRP in the mesocosms, we calculated the difference between TP and particulate organic phosphorus (PP). The TP of 12 ml of mesocosm water (250 μm filtered) was measured using the molybdenum blue reaction following digestion with 0.7 ml of sulfuric acid. Subsequently, 0.7 ml of ascorbic acid and 0.7 ml of a reagent mixture (sulfuric acid, antimony potassium tartrate and ammonium molybdate solution) were added. The PP was analysed by filtering 100 ml of mesocosm water through glassfibre filters (GF/F, 0.7 μm, precombusted for 4 hr at 500°C and washed in 8% hydrochloric acid prior to use) and measuring PP using the molybdenum blue reaction after the filter was digested in 10 ml of distilled water and 0.7 ml of sulfuric acid (Wetzel & Likens, 1991). The blue-coloured complex was measured with a spectrophotometer at 880 nm after 30 min (Shimadzu UV-1700, Shimadzu GmbH, Germany). Chlorophyll-*a* in the laboratory experiment was measured in vivo fluorometrically with a AlgaeLabAnalyser (bbe moldaenke, Schentinental, Germany).

We took zooplankton samples 14 days after filling the mesocosm and at the end of the experiment. For this we used a 100-μm net (20-cm diameter; Hydrobios, Kiel, Germany) and sampled the whole water column in each mesocosm according to their individual depths. Zooplankton was fixed with sugar formol (4% final solution, Haney & Hall, 1973) and then identified with a stereo microscope (Leica, MZ8, Wetzlar, Germany) to genus/species level.

Temperature in the mesocosms was measured with a multi probe (YSI Professional, Xylem, Weilheim, Germany) in 0.5-m steps according to the depth of each mesocosm (1 day after sampling) weekly. For differences in temperature, we calculated and compared the mean temperature of every mesocosm. A detailed overview of temperature development in the different depth treatments can be found in the supporting information (Figure S1). The light attenuation coefficient *k* for PAR was calculated according to Lambert-Beer's law. For that we measured light transmission (SpectraPen SP 110-UVIS; PSInstruments, Czech Republic) through filtered lake water in 0.5- and 1-m water columns.

2.4 | Data analysis

Experimental data were analysed by univariate and multivariate analyses with PRIMER (Plymouth Routines in Multivariate Ecological Research, U.K.) version 7 and SigmaPlot 14 (Systat Software GmbH, Erkrath, Germany). Differences in phytoplankton community composition between mesocosm treatments of different depths were analysed using cluster analyses on a Bray–Curtis similarity matrix on abundance data (square-root transformed). Using exponential linear regression models, we were able to analyse the change in plankton community composition as a function of mesocosm depth in the mesocosm experiment or light quality exposure in the laboratory experiment. A non-metric multidimensional scaling analysis (*nMDS*) was carried out to examine groupings and similarity of mesocosms based on the phytoplankton group composition; *nMDS* stress value was 0.03. Stress values indicate how well data in a reduced two-dimensional space correspond with the actual multivariate distance. Stress values of <0.05 give an excellent two-dimensional representation, ensuring no misinterpretation (Clarke, 1993). A similarity percentage analysis (*SIMPER*; Clarke, 1993) was performed to understand the relative contribution of each algal group to community similarities between treatments. To test significant differences between zooplankton groupings a one-way analysis of similarity (*ANOSIM*) was performed. Phytoplankton diversity (Shannon Index H′; Krebs, 1989) in the mesocosm experiment was calculated based on phytoplankton microscopic counts transferred into biovolume (see 2.3). Statistical analyses of differences in diversity with changing mesocosm depth, as well as zooplankton, carbon, water chemistry, and temperature data were analysed by ANOVAs. Changes in diversity with decreasing red light availability were analysed using an exponential decay regression model.

3 | RESULTS

3.1 | Abiotic factors in the mesocosm experiment

Shallow mesocosms (0.5 m, 1 m, 2 m) were on average 3°C warmer (temperature averaged over the whole water column) than deeper mesocosms (3 and 4 m; one-way ANOVA, $F_{(1,15)} = 77.61$, $p < 0.001$)

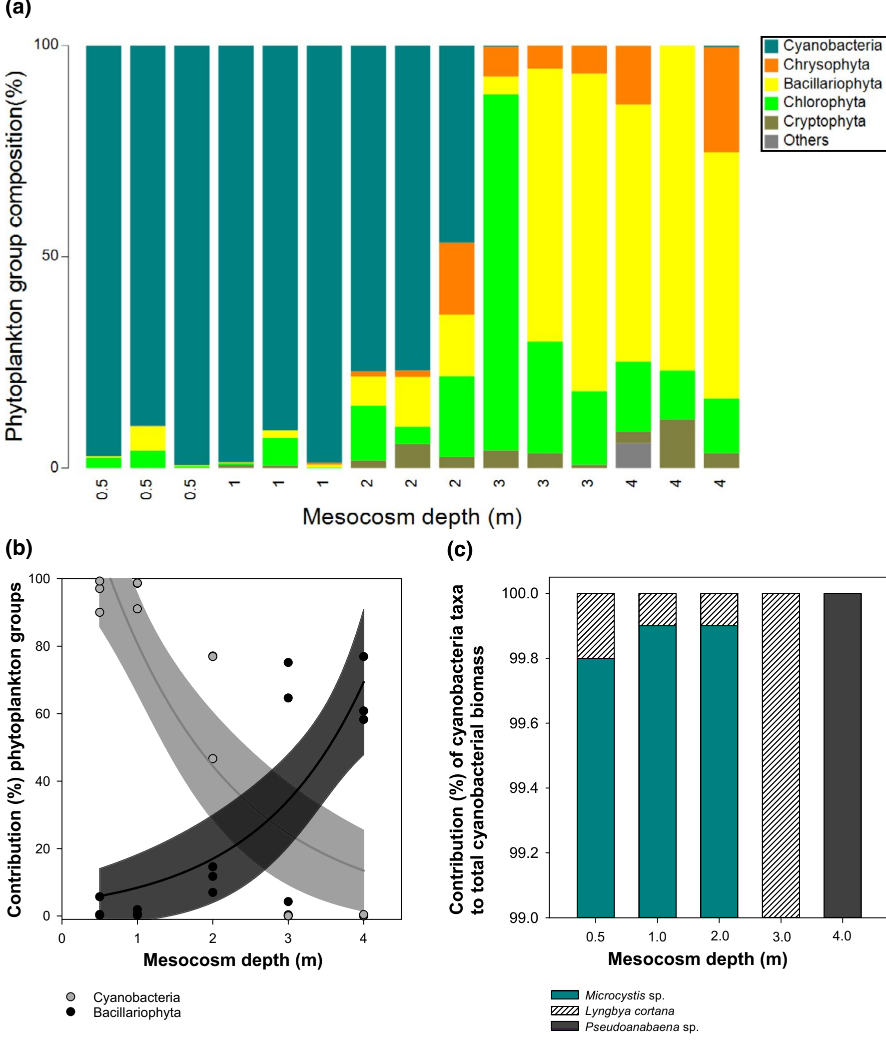


FIGURE 1 Final phytoplankton community composition (%) in the mesocosm experiment: (a) Phytoplankton group community composition (%) in each mesocosm. (b) Shifts from bacillariophyta to cyanobacteria dominance in different mesocosms. Black dots: bacillariophyta: non-linear regression: $y = 4.16 * \exp^{0.7x}$; $r^2 = 0.7$; $p = 0.0001$. Grey dots: cyanobacteria: non linear regression: $y = 146.8 * \exp^{-0.6x}$; $r^2 = 0.8$; $p < 0.0001$. Grey area and black lines represent fitted model and 95% confidence intervals. (c) Cyanobacteria taxon composition within the group of cyanobacteria at different mixing depths

in the end of the experiment. All mesocosms showed similar temperature at 0.5 and 2 m, and at no time was temperature higher than 16°C (see Figure S1). In the middle and towards the end there was no stratification in the mesocosms (see Figure S1c) and mesocosms were fully mixed over the whole water column.

Soluble reactive phosphorus and nitrate concentration in all mesocosms were significantly higher at the beginning compared to the end of the experiment (SRP: Holm–Sidak one-way ANOVA: $t = 9.74$; $p < 0.001$; nitrate: Kruskal–Wallis one-way ANOVA on ranks: $H = 6.818$; $p = 0.009$). However, SRP and nitrate availability decreased in a similar way in all treatments and there were no significant differences between mesocosms (SRP: one-way ANOVA: $F_{(10,14)} = 0.81$; $p = 0.54$; nitrate: one-way ANOVA: $F_{(3,4)} = 0.007$; $p = 0.9$).

3.2 | Phytoplankton community composition in the mesocosm experiment

At the beginning of the experiment the total phytoplankton biovolume in all mesocosms was dominated by chlorophyta (80%) and bacillariophyta (16%) and to a lower percentage by cyanobacteria, chrysophyta, and cryptophyta (based on microscopic counting). However, at the end of the experiment the phytoplankton composition varied between treatments. POC decreased significantly from the start to the end of the experiment (Holm–Sidak one-way ANOVA: $t = 2.46$; $p = 0.02$). However, POC decreased in a similar way in all treatments and there were no significant differences in POC amongst mesocosms (one-way ANOVA: $F_{(10,14)} = 0.55$; $p = 0.7$). Cyanobacteria dominated especially in shallow mesocosms (0.5, 1. and 2 m) with up to 97% contribution to phytoplankton biovolume compared to only 0.24% contribution in deeper mesocosms (Figure 1a,b). The decrease in cyanobacteria in shallow and deep mesocosms was statistically significant and best described by an exponential decay function with depth ($y = 146.8 * \exp^{-0.6x}$; $r^2 = 0.8$; $p < 0.0001$; Figure 1b). The contribution of bacillariophyta to total phytoplankton was also a function of mesocosm depth and best described by an exponential increase with depth ($y = 4.16 * \exp^{0.7x}$; $r^2 = 0.7$; $p = 0.0001$; Figure 1b). The presence of all other phytoplankton groups was low in shallow mesocosms (Figure 1a).

Only shallow enclosures (0.5 and 1 m) revealed more than one genus of cyanobacteria (Figure 1c). Both *Microcystis* and *Lyngbya*

FIGURE 2 Non-metric multidimensional scaling (MDS) plot representing phytoplankton community of each mesocosm in the end of the experiment with a stress value: 0.03 indicating a good fit. Shallower mesocosms are grouped together (grey triangles) showing more than 80% similarity. Deeper and shallower mesocosms show only max. 20% similarity. Similarity calculation is based on a Bray–Curtis matrix. Numbers at symbols represent depth of mesocosms

TABLE 1 SIMPER analyses showing the intragroup similarity (%) and dissimilarities among phytoplankton communities of mesocosms (%) along contribution of different phytoplankton groups analysed on a Bray–Curtis matrix

Factor depth (m)	Group	Average similarity (%)	Average dissimilarity (%)
0.5	a	88.29	*a & b:* 29.89
0.5	a		
0.5	a		
1	a		
1	a		
1	a		
2	b	83.73	*b & c:* 44.59
2	b		
2	b		
3	c	68.77	*a & c:* 78.87
3	c		
3	c		
4	c		
4	c		
4	c		

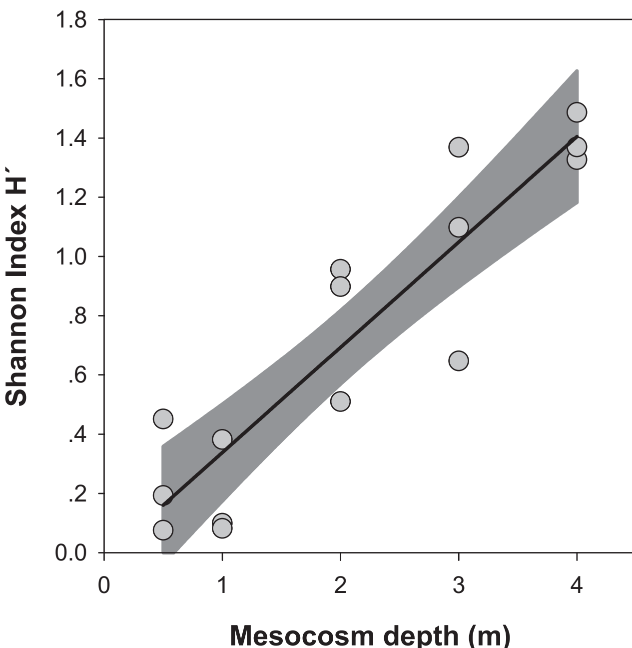
(0.1%–0.2%) were present in shallow mesocosms; however, *Microcystis* strongly dominated the cyanobacterial communities. In contrast to *Microcystis*, *Lyngbya* and *Pseudoanabaena* sp. were present in deeper mesocosms (Figure 1c); however, cyanobacterial abundances were <1% in deep mesocosms (Figure 1b).

The *nMDS* plot (Figure 2) shows three distinct groups of mesocosms in terms of phytoplankton similarity, and *SIMPER* analyses of phytoplankton group contribution showed a similarity within mesocosm groups of 68.77%–88.29%. Our analysis found the highest dissimilarity (78.87%) between shallow mesocosms of 0.5 and 1 m (group a) and 3- and 4-m deep mesocosms (group c; Table 1). *ANOSIM* revealed a significant difference occurred between 0.5- and 1-m mesocosms (group a) and 3- and 4-m mesocosms (group c; $r^2 = 0.88$; $p = 0.01$). However, there were no other significant differences between other clusters, such as between groups a and b or between groups b and c.

The dominance of cyanobacteria in the shallow mesocosms was also reflected in the diversity (Shannon H′): the deeper the mesocosm the higher the phytoplankton diversity (Shannon H′; one-way ANOVA: $F_{(10,14)} = 14.14$, $p < 0.001$, Figure 3), which varied from 0.1 in shallow mesocosms to 1.5 in deep mesocosms. Shallow mesocosms (0.5–2 m) showed significantly lower Shannon H′ than mesocosms of 3 or 4 m (Holm–Sidak: $t = 3.0$; $p = 0.009$).

3.3 | Red light availability in the mesocosm experiment

Whereas in the laboratory experiment the light quality was experimentally manipulated, in the mesocosm experiments light quality was



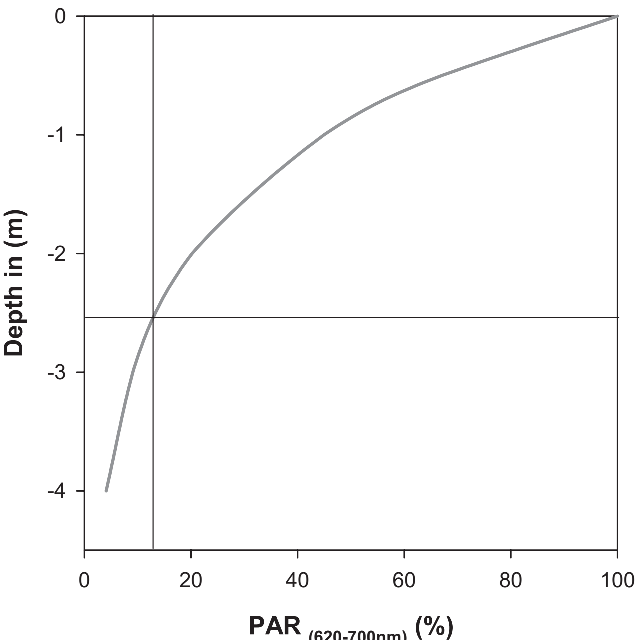


FIGURE 3 Shannon index (H′) of phytoplankton communities in mesocosms from 0.5 m to 4 m depth after 42 days of the experiment. Linear regression: $y = 0.35x + (-0.017)$; $r^2 = 0.82$; $p < 0.0001$. Grey area and black line represent fitted model and 95% confidence intervals

FIGURE 4 (a) Red light availability in percentage of photosynthetically active radiation from 620 to 700 nm ($PAR_{(620–700nm)}$) at different depths (m). Crossed lines indicate shifts in phytoplankton composition from a dominance of eukaryote to cyanobacteria in shallower mesocosms. (b) Shannon index (H′) of phytoplankton communities depending on $PAR_{(620–700nm)}$ after 42 days of the experiment. Exponential decay: $y = 1.5^{exp(-0.04x)}$; $r^2 = 0.83$; $p < 0.0001$. Grey area and black line represent fitted model and 95% confidence intervals

a function of mixing depth. Figure 4a shows the exponential decrease in red light availability relative to surface levels with increasing depth of experimental treatments. At 3- and 4-m depths, less than 10% of red light at surface was available. Shifts in mesocosm community composition are seen between 2 and 3 m, where less than 15% of red light at surface was still available (Figure 4). Phytoplankton diversity decreased exponentially (exponential decay: $y = 1.5^{exp(-0.04x)}$; $r^2 = 0.83$; $p < 0.0001$) with more red light availability in the mesocosm (Figure 4b) and therefore increased linearly with depth (linear regression: $y = 0.35x + (-0.017)$; $r^2 = 0.82$; $p < 0.0001$ Figure 3).

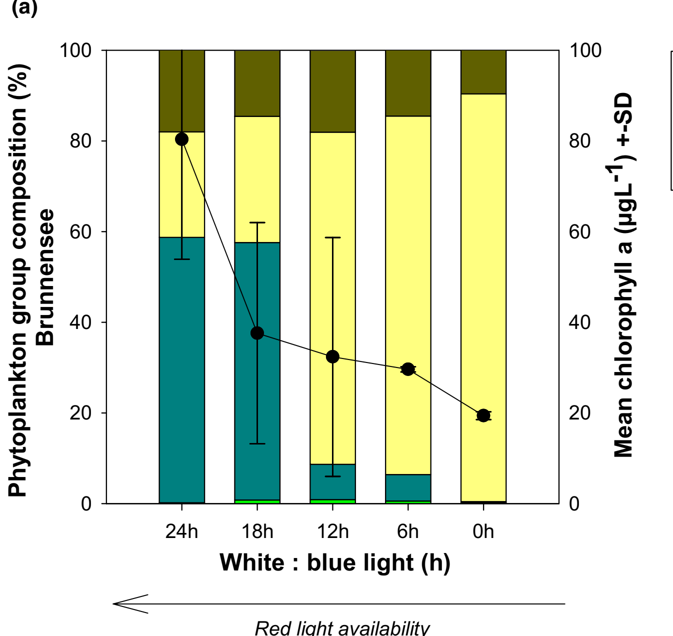
3.4 | Zooplankton in the mesocosm experiment

Although water was filtered through 250 μm when mesocosms were filled, zooplankton developed in the mesocosms over time through introduced eggs and nauplii. However, zooplankton in all mesocosms (on average <10 individuals/L) was rather low after 14 days compared to the zooplankton abundance in Lake Bansee (on average ~110 individuals/L). Up to the end of the experiment, zooplankton increased in the 0.5-m deep mesocosms significantly differently from all other mesocosms (Kruskal–Wallis one-way ANOVA on ranks: $H = 8.74$; $p = 0.03$; see Figure S4a). The increase in 0.5-m deep mesocosms was due to an increase in *Bosmina* sp. (see Figure S3b). In all other mesocosms the number of zooplankton (*Bosmina* sp. excluded) did not differ significantly between each (Kruskal–Wallis one-way ANOVA on ranks: $H = 2.08$; $p = 0.15$).

3.5 | Phytoplankton community composition in laboratory experiments

The community of oligotrophic Lake Brunnensee was dominated by bacillariophyta (99.79%), whereas the community of the eutrophic MPI pond was dominated by chlorophyta (52.12%; see Figure S5a,b). During the experiment the composition of both communities changed drastically in relation to experimental treatments simulating different spectral light regimes. Both natural communities exposed to the full PAR spectrum were finally dominated by cyanobacteria (57.98% Lake Brunnensee, 94.78% MPI pond). In contrast, when communities were exposed to blue light initially dominant algal groups (bacillariophyta in Lake Brunnensee, chlorophyta in MPI pond; Figure 5a,b) were also dominant at the end of experiments.

However, when communities were exposed to longer periods of full PAR spectrum including long wavelength (red) a shift to a cyanobacterial dominance was seen in the phytoplankton (biomass) composition. In Lake Brunnensee, the community shifted to cyanobacterial dominance when exposed to 18 and 24 hr white light (exponential rise to maximum: $r^2 = 0.79$; $p = 0.04$). Proportion of bacillariophyta decreased significantly with decreasing blue light availability (exponential decay: $r^2 = 0.82$; $p = 0.03$). A very similar pattern was seen in the phytoplankton communities originating from the MPI pond. Proportion of chlorophyta decreased significantly



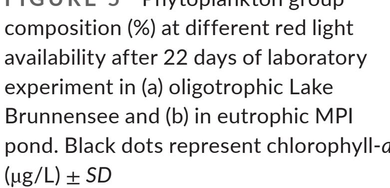
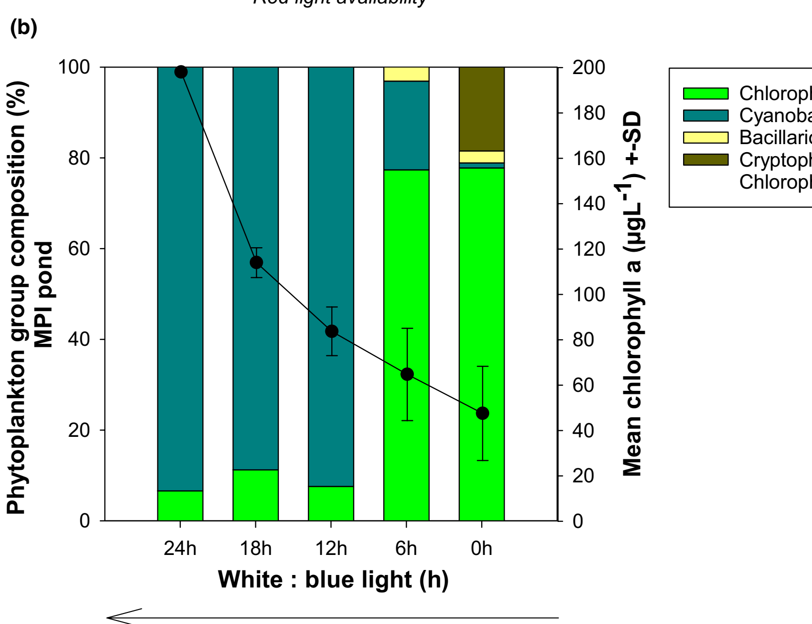


FIGURE 5 Phytoplankton group composition (%) at different red light availability after 22 days of laboratory experiment in (a) oligotrophic Lake Brunnensee and (b) in eutrophic MPI pond. Black dots represent chlorophyll-*a* (µg/L) ± *SD*



with decreasing blue light availability (exponential decay: $r^2 = 0.86$; $p = 0.02$) and proportion of Cyanobacteria increased with increasing full PAR availability (exponential rise to maximum: $r^2 = 0.77$; $p = 0.05$). At the same time total chlorophyll-*a* increased with increasing blue light availability in the MPI pond (linear regression: $y = 5.83x + 31.54$; $r^2 = 0.87$; $p = 0.004$) and in Lake Brunnensee (linear regression: $y = 2.16x + 13.86$; $r^2 = 0.76$; $p = 0.05$).

4 | DISCUSSION

Our results from the mesocosm experiment support the hypothesis that reduced mixing depth can promote cyanobacterial abundance (H1). The mesocosm experiment clearly showed that reducing a possible mixing depth from 4 to 2 m had a large effect on the phytoplankton community composition. Shallower vertical mixing introduces the possibility of phytoplankton being exposed to a broader light spectrum per se. The full PAR spectrum allows a larger number of functional groups to coexist, probably due to niche differentiation corresponding to different accessory pigments present in different phytoplankton species (Behl et al., 2011; Stockenreiter et al., 2013; Stomp et al., 2004; Striebel et al., 2009). In contrast, theoretical studies (e.g., Gray et al., 2019; Huisman et al., 1999, 2004) revealed that there are only few opportunities for species coexistence in the epilimnion when mixing depth is shallow because of a shift in the competitive balance of sinking and motile/buoyant phytoplankton. In our mesocosm experiment, phytoplankton communities in shallow mesocosms showed lower diversity (Shannon Index) than those

in deeper mesocosms. Reduced mixing depth due to increasing water surface temperatures could therefore result in undesired reduced phytoplankton community composition or even toxic blooms by favouring single phytoplankton groups. Our results from a eutrophic water body and a bloom-forming cyanobacterial genus (*Microcystis*) are in accordance with other studies: such species are well known to be able to dominate phytoplankton communities (Huisman et al., 2004; Visser et al., 1996; Zohary & Robarts, 1990). However, one could imagine cases where cyanobacteria would have opposite effects: for example, by maintaining high diversity through facilitation by nitrogen fixation. One experimental example of cyanobacteria acting as a *stabilising force* was described by Carey et al. (2017), where the genus *Gloetrichia* had positive effects on phytoplankton community dynamics in an oligotrophic lake.

In our mesocosm experiment the potentially toxic cyanobacterial genus *Microcystis* strongly dominated (up to 97% of total phytoplankton biovolume) the phytoplankton communities of shallow mesocosms, even if it was initially scarce. The rapid increase of *Microcystis* can be explained by two mechanisms. Firstly, the different light quality accompanying decreasing mixing depths could have favoured cyanobacteria. Previous studies into the effects of global climate change on phytoplankton communities typically manipulated temperature, nutrients, and light as quantitative resources (Berger et al., 2010; Blomqvist et al., 1994; Scheffer et al.,1997; Smith, 1986). However, the quality of light had rarely been considered in these studies. In their survey of 143 lakes, Kosten et al. (2012) showed that lakes with higher light absorbance had a higher cyanobacterial contribution to total phytoplankton biomass in very shallow lakes and speculated that this could be due to differences in the underwater light conditions; however, they did not specify further which light conditions were stimulating which phytoplankton groups. Interestingly, not all mesocosms in our experiment were dominated by *Microcystis*, which is one of the main bloom forming cyanobacteria genera. Its various abilities that enable it to have superiority over other species include a very dynamic genome and the ability to produce numerous biochemical metabolites influencing phytoplankton population dynamics (Harke et al., 2016; Wilhelm et al., 2020). For example, phytoplankton at shallower mixing depths is exposed to more UV radiation, which has negative effects on photosynthesis; *Microcystis* is known to produce extracellular metabolites that protect them from UV radiation (Xu et al., 2013).

As mixing depth increased, the contribution of cyanobacteria in general and *Microcystis* in particular declined. Instead, the cyanobacterial genera *Lyngbya* and *Pseudoanabaena* were found in small amounts in deeper mesocosms. Both genera are known to contribute substantially to phytoplankton growth in deeper water layers (Overmann & Tilzer, 1989). *Lyngbya*, for example, contains phycobilins that have absorption peaks at red light wavelengths (Suda et al., 1998); however, it can also grow in very low light intensities (as can *Pseudoanabaena*) (Overmann & Tilzer, 1989; Romo, 1994), such as in the deeper mesocosms. However, in our experiment, the overall contribution of cyanobacteria to total phytoplankton biovolume was less than 5% in the deeper mesocosms (3 and 4 m), which were dominated mainly by bacillariophyta. Together with the decreasing red light availability (less than 10% of the surface value) in deeper mesocosms, cyanobacteria decreased and bacillariophyta, together with chlorophyta and crysophyta, dominated the deeper mesocosms. It has also been shown theoretically (Gray et al., 2019) and experimentally (Selmeczy et al., 2018) that a deepening of the mixed layer can cause blooms of low-light adapted cyanobacterial species of the genus *Planktothrix*. However, *Planktothrix* is mostly found in large deep lakes and was not found in our experimental systems. Secondly, the temperature differences between shallow and deep mesocosms may also contribute to the observed cyanobacterial bloom, because cyanobacteria prefer warm temperatures (Huisman et al., 2018; Paerl & Huisman, 2008). A reduction in mixing depth resulted in an increase in average temperature by up to 4°C in our mesocosm experiment. However, full mixing of the water column of each mesocosm was achieved via artificial mixing using a pressure lift twice a week. Temperatures at 0.5 m were equal in all mesocosms and in the middle of the experiment there was no measurable stratification. Usually, cyanobacterial growth rates reach their optima when growth rates of eukaryotic taxa decline (Huisman et al., 2018; Paerl & Huisman, 2009). In our mesocosm experiment, cyanobacteria occurred mainly at water temperatures above 15°C, and this threshold was not passed in deep mesocosms (maximum temperature at the end of the experiment 12–13°C). Even though temperatures in our mesocosm experiment were not likely to represent the optimal temperatures for the growth of most cyanobacteria (above 20°C, see also Huisman et al., 2018), cyanobacteria were still able to outcompete eukaryotic phytoplankton. These direct effects of temperature on cyanobacteria might be amplified due to global warming as the surface water warms more rapidly (Paerl & Huisman, 2009). Additionally, the temperature profile showed slight stratification in the mesocosms and upper layers where equally warm in the end of the experiment. However, all mesocosms were artificially mixed twice a week for 20 min, preventing deeper mixing in longer mesocosms. This prevented stratification conditions in the middle of the experiment. Hence, our results show that increasing water temperatures might not only increase cyanobacterial abundances directly, but also indirectly through associated declines in water column mixing depth that increase exposure to the full PAR spectrum, which includes substantial amounts of favourable red wavelengths. While in the mesocosm experiment, the two mixing-depth-related factors discussed above, temperature and light availability, cannot be disentangled easily, the laboratory experiment provided more clarity, as it allowed greater experimental control.

4.1 | Disentangling co-varying abiotic factors enhancing cyanobacterial abundance

By keeping temperature and light quantity controlled we were able to manipulate light quality independently of the two other naturally co-occurring and confounding environmental parameters influencing phytoplankton growth. Our laboratory experiments supported

our hypothesis that shifts in light spectrum alone are a strong enough driver to result in a favourable light climate for cyanobacteria and enhance cyanobacterial abundance (H2).

In both natural phytoplankton communities, the dominant phytoplankton groups, chlorophyta and bacillariophyta, benefited from a reduced PAR spectrum towards shorter wavelengths (blue). In contrast, cyanobacteria showed increasing abundance with an increased exposure to a full PAR spectrum including longer wavelengths (red). Hence, consistent with the observations from the mesocosm experiment, cyanobacteria prevailed under simulated future light conditions. Cyanobacteria rapidly increase under a more full PAR spectrum and therefore more available red light. Increasing the daily exposure to a full PAR spectrum in the laboratory experiments is functionally similar to reducing mixing depths, as performed in the mesocosm experiments. In both cases, phytoplankton are more exposed to light of longer wavelength in the PAR spectrum. If cultures were exposed to more than 12 hr of white light, cyanobacteria dominated in both natural communities. Interestingly, this pattern was completely independent of which functional group dominated the community initially and whether the phytoplankton originated from an oligotrophic (bacillariophyta-dominated) or a eutrophic (chlorophyta-dominated) system.

4.2 | Drastic shift in natural phytoplankton communities

A surprising outcome of our mesocosm and laboratory experiments was the sudden shift from bacillariophyta/chlorophyta- to cyanobacteria-dominated communities. The rate of change towards cyanobacterial dominance from a eukaryote-dominated phytoplankton community related to mesocosm depth was much faster than expected. Our mesocosm experiment was conducted at temperatures (below 20°C) that are not known to strongly stimulate cyanobacterial abundances (Paerl, 2008; Zohary & Robarts, 1990). Furthermore, in the laboratory experiment, 20°C represented early summer temperatures rather than the very warm late summer surface temperatures often related to cyanobacterial blooms.

The abrupt change in the composition of the phytoplankton community at different mixing depths and the associated shift from a eukaryote-dominated to a cyanobacteria-dominated community can indeed have its mechanistic root in the effects of light quality and the physiological properties of the corresponding photosystems. For example, photosynthesis in cyanobacteria can be negatively influenced by blue light. Luimstra et al. (2018, 2020) showed that there is a major imbalance in electron transport between photo system (PS)I and PSII in the cyanobacterial genus *Synechocystis*. Cyanobacteria have more chlorophyll in PSI than in PSII. This imbalance, however, is compensated by the presence of phycobilins absorbing at red/orange wavelengths leading to a linear electron transport between the two PSs (Joshua et al., 2005; Mullineaux, 2008; Van Thor et al., 1998). In blue light, these phycobilins cannot absorb enough light, and a linear electron transport is no longer guaranteed (De Marsac, 2003; Luimstra et al., 2018; Six et al., 2007). Luimstra et al. (2018) showed that growth rates of *Synechocystis* were significantly lower than those of chlorophyta when cultivated under a mixture of blue and red light and when the ratio of red to blue light was below 20%. However, the observed shift in the phytoplankton community was additionally reinforced by a second possible mechanism. Under conditions where cyanobacteria show high photosynthetic performance, bacillariophyta, in contrast, decrease their efficiency. Valle et al. (2014) showed that the photosynthetic efficiency of PSII in the diatom *Phaeodactylum* decreased at high red light levels in comparison to white or blue light. This is mainly due to a lack of mechanisms to prevent and repair photodamage under red light conditions and, at the same time, genes important for encoding proteins for PSII repair are highly dependent on the signal of a blue-light receptor (Schellenberger Costa et al., 2013). That light quality is also important for the benthic community in streams was shown by DeNicola et al. (1992). In areas heavily shaded by dense tree canopy, less red light was measured under water. This had a strong influence on the composition of the bacillariophyta-dominated benthic communities. In both our mesocosm and laboratory experiments, cyanobacteria increased with the share of red wavelengths in the available PAR, and chlorophyta and bacillariophyta replaced cyanobacteria at high blue light availability. This in turn leads to alterations in the electron transfer efficiency under red light conditions.

In the laboratory experiment we could show that biomass dominated by bacillariophyta was even higher in treatments when exposed to more blue light.

5 | SUMMARY AND CONCLUSION

Our results show that shifts in the available light spectrum that accompany changes in mixing depth may affect the phototrophic base (phytoplankton communities) of food webs. These phytoplankton community shifts are likely to influence dynamics at higher trophic levels and thereby affect entire pelagic food-web processes. This will have far-reaching consequences at higher trophic levels, such as the match-mismatch scenarios described by Sommer et al. (2012). For example, an altered phytoplankton community as described here can then cause strong changes in the zooplankton community, which in turn can lead to a temporal mismatch between zooplankton and juvenile fish.

In our experiment, we could exclude nutrients as the driving force for this strong change within the phytoplankton community from eukaryotes to cyanobacteria. In the mesocosm experiment, nutrients decreased over time, but this was not significantly in all treatments. The laboratory semi-batch conditions ensured a constant nutrient supply. Hence, other resource-related parameters, such as light availability at certain wavelengths, needs to be taken into account when predicting possible changes in phytoplankton communities and cyanobacterial blooms (Pace et al., 2017) related to global change.

ACKNOWLEDGEMENTS

We thank Achim Weigert, Angelika Wild, and Sibylle Zavalla for technical support throughout the experiment. The experiment was funded by Deutsche Forschungsgemeinschaft (DFG) granted to MS (STO1075/1-1; 2-1) and EU H2020-INFRAIA AQUACOSM project No 731065. Open Access funding enabled and organized by Projekt DEAL.

CONFLICTS OF INTEREST

All authors declare that there is no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID

Maria Stockenreiter https://orcid.org/0000-0001-7380-071X
Jana Isanta Navarro https://orcid.org/0000-0002-6168-4499
Herwig Stibor https://orcid.org/0000-0001-5918-6020

REFERENCES

Andersen, T., Saloranta, T. M., & Tamminen, T. (2007). A statistical procedure for unsupervised classification of nutrient limitation bioassay experiments with natural phytoplankton communities. *Limnology and Oceanography: Methods*, *5*(4), 111–118. https://doi.org/10.4319/lom.2007.5.111

Båmstedt, U. (2019). Comparing static and dynamic incubations in primary production measurements under different euphotic and mixing depths. *Hydrobiologia*, *827*(1), 155–169. https://doi.org/10.1007/s10750-018-3762-1

Behl, S., Donval, A., & Stibor, H. (2011). The relative importance of species diversity and functional group diversity on carbon uptake in phytoplankton communities. *Limnology and Oceanography*, *56*(2), 683–694. https://doi.org/10.4319/lo.2011.56.2.0683

Benson, B. J., Magnuson, J. J., Jensen, O. P., Card, V. M., Hodgkins, G., Korhonen, J., … Granin, N. G. (2012). Extreme events, trends, and variability in Northern Hemisphere lake-ice phenology (1855–2005). *Climatic Change*, *112*(2), 299–323. https://doi.org/10.1007/s10584-011-0212-8

Berger, S. A., Diehl, S., Kunz, T. J., Albrecht, D., Oucible, A. M., & Ritzer, S. (2006). Light supply, plankton biomass, and seston stoichiometry in a gradient of lake mixing depths. *Limnology and Oceanography*, *51*(4), 1898–1905. https://doi.org/10.4319/lo.2006.51.4.1898

Berger, S. A., Diehl, S., Stibor, H., Trommer, G., & Ruhenstroth, M. (2010). Water temperature and stratification depth independently shift cardinal events during plankton spring succession. *Global Change Biology*, *16*(7), 1954–1965. https://doi.org/10.1111/j.1365-2486.2009.02134.x

Berger, S. A., Diehl, S., Stibor, H., Trommer, G., Ruhenstroth, M., Wild, A., … Striebel, M. (2007). Water temperature and mixing depth affect timing and magnitude of events during spring succession of the plankton. *Oecologia*, *150*, 643–654. https://doi.org/10.1007/s00442-006-0550-9

Blenckner, T., Adrian, R., Livingstone, D. M., Jennings, E., Weyhenmeyer, G. A., George, D. G., … Teubner, K. (2007). Large-scale climatic signatures in lakes across Europe: A meta-analysis. *Global Change Biology*, *13*(7), 1314–1326. https://doi.org/10.1111/j.1365-2486.2007.01364.x

Blomqvist, P., Pettersson, A., & Hyenstrand, P. (1994). Ammonium-nitrogen-A key regulatory factor causing dominance of non-nitrogen-fixing cyanobacteria in aquatic systems. *Archiv Für Hydrobiologie*, *132*(2), 141–164. https://doi.org/10.1127/archiv-hydrobiol/132/1994/141

Bock, C., Salcher, M., Jensen, M., Pandey, R. V., & Boenigk, J. (2018). Synchrony of eukaryotic and prokaryotic planktonic communities in three seasonally sampled Austrian lakes. *Frontiers in Microbiology*, *9*, 1290. https://doi.org/10.3389/fmicb.2018.01290

Britton, G. (1983). *The biochemistry of natural pigments*. Cambridge University Press.

Carey, C. C., Brown, B. L., & Cottingham, K. L. (2017). The cyanobacterium *Gloeotrichia echinulata* increases the stability and network complexity of phytoplankton communities. *Ecosphere*, *8*(7), e01830. https://doi.org/10.1002/ecs2.1830

Clarke, K. R. (1993). Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology*, *18*(1), 117–143. https://doi.org/10.1111/j.1442-9993.1993.tb00438.x

De Marsac, N. T. (2003). Phycobiliproteins and phycobilisomes: The early observations. *Photosynthesis Research*, *76*(1–3), 193–205. https://doi.org/10.1023/A:1024954911473

De Senerpont Domis, L. N., Mooij, W. M., & Huisman, J. (2007). Climate-induced shifts in an experimental phytoplankton community: A mechanistic approach. In *Shallow lakes in a changing world* (pp. 403–413). Springer.

DeMott, W. R., Gulati, R. D., & Van Donk, E. (2001). Daphnia food limitation in three hypereutrophic Dutch lakes: Evidence for exclusion of large-bodied species by interfering filaments of cyanobacteria. *Limnology and Oceanography*, *46*(8), 2054–2060. https://doi.org/10.4319/lo.2001.46.8.2054

DeNicola, M., Hoagland, K. D., & Roemer, S. C. (1992). Influences of canopy cover on spectral irradiance and periphyton assemblages in a prairie stream. *Journal of the North American Benthological Society*, *11*(4), 391–404. https://doi.org/10.2307/1467560

Diehl, S., Berger, S., Ptacnik, R., & Wild, A. (2002). Phytoplankton, light, and nutrients in a gradient of mixing depths: Field experiments. *Ecology*, *83*(2), 399–411. https://doi.org/10.2307/2680023

Doubek, J. P., Campbell, K. L., Doubek, K. M., Hamre, K. D., Lofton, M. E., McClure, R. P., … Carey, C. C. (2018). The effects of hypolimnetic anoxia on the diel vertical migration of freshwater crustacean zooplankton. *Ecosphere*, *9*(7), e02332. https://doi.org/10.1002/ecs2.2332

Gerten, D., & Adrian, R. (2002). Effects of climate warming, North Atlantic Oscillation, and El Nino-Southern Oscillation on thermal conditions and plankton dynamics in northern hemispheric lakes. *The Scientific World Journal*, *2*, 586–606. https://doi.org/10.1100/tsw.2002.141

Gray, E., Elliott, J. A., Mackay, E. B., Folkard, A. M., Keenan, P. O., & Jones, I. D. (2019). Modelling lake cyanobacterial blooms: Disentangling the climate-driven impacts of changing mixed depth and water temperature. *Freshwater Biology*, *64*(12), 2141–2155. https://doi.org/10.1111/fwb.13402

Gray, E., Mackay, E. B., Elliott, J. A., Folkard, A. M., & Jones, I. D. (2020). Wide-spread inconsistency in estimation of lake mixed depth impacts interpretation of limnological processes. *Water Research*, *168*, 115–136. https://doi.org/10.1016/j.watres.2019.115136

Gulati, R., & DeMott, W. (1997). The role of food quality for zooplankton: Remarks on the state-of-the-art, perspectives and priorities. *Freshwater Biology*, *38*(3), 753–768. https://doi.org/10.1046/j.1365-2427.1997.00275.x

Haney, J. F., & Hall, D. J. (1973). Sugar-coated *Daphnia*: A preservation technique for Cladocera 1. *Limnology and Oceanography*, *18*(2), 331–333. https://doi.org/10.4319/lo.1973.18.2.0331

Harke, M. J., Steffen, M. M., Gobler, C. J., Otten, T. G., Wilhelm, S. W., Wood, S. A., & Paerl, H. W. (2016). A review of the global ecology, genomics, and biogeography of the toxic cyanobacterium, Microcystis spp. *Harmful Algae*, *54*, 4–20. https://doi.org/10.1016/j.hal.2015.12.007

Huisman, J., Codd, G. A., Paerl, H. W., Ibelings, B. W., Verspagen, J. M., & Visser, P. M. (2018). Cyanobacterial blooms. *Nature Reviews Microbiology*, *16*, 471–483. https://doi.org/10.1038/s41579-018-0040-1

Huisman, J., Sharples, J., Stroom, J. M., Visser, P. M., Kardinaal, W. E. A., Verspagen, J. M., & Sommeijer, B. (2004). Changes in turbulent mixing shift competition for light between phytoplankton species. *Ecology*, *85*(11), 2960–2970. https://doi.org/10.1890/03-0763

Huisman, J., van Oostveen, P., & Weissing, F. J. (1999). Species dynamics in phytoplankton blooms: Incomplete mixing and competition for light. *The American Naturalist*, *154*(1), 46–68. https://doi.org/10.1086/303220

Jeppesen, E., Meerhoff, M., Davidson, T. A., Trolle, D., Søndergaard, M., Lauridsen, T. L., … Nielsen, A. (2014). Climate change impacts on lakes: An integrated ecological perspective based on a multifaceted approach, with special focus on shallow lakes. *Journal of Limnology*, *73*, 88–11. https://doi.org/10.4081/jlimnol.2014.844

Joshua, S., Bailey, S., Mann, N. H., & Mullineaux, C. W. (2005). Involvement of phycobilisome diffusion in energy quenching in cyanobacteria. *Plant Physiology*, *138*(3), 1577–1585. https://doi.org/10.1104/pp.105.061168

Kosten, S., Huszar, V. L. M., Bécares, E., Costa, L. S., Donk, E., Hansson, L.-A., … Scheffer, M. (2012). Warmer climates boost cyanobacterial dominance in shallow lakes. *Global Change Biology*, *18*(1), 118–126. https://doi.org/10.1111/j.1365-2486.2011.02488.x

Krebs, C. J. (1989). *Ecological methodology* (No. QH541. 15. S72. K74 1999.). Harper & Row.

Kremer, C. T., Gillette, J. P., Rudstam, L. G., Brettum, P., & Ptacnik, R. (2014). A compendium of cell and natural unit biovolumes for >1200 freshwater phytoplankton species: Ecological Archives E095–257. *Ecology*, *95*(10), 2984. https://doi.org/10.1890/14-0603.1

Kunz, T. J., & Diehl, S. (2003). Phytoplankton, light and nutrients along a gradient of mixing depth: A field test of producer-resource theory. *Freshwater Biology*, *48*(6), 1050–1063. https://doi.org/10.1046/j.1365-2427.2003.01065.x

Litchman, E., de Tezanos Pinto, P., Klausmeier, C. A., Thomas, M. K., & Yoshiyama, K. (2010). Linking traits to species diversity and community structure in phytoplankton. In L. Naselli-Flores & G. Rossetti (Eds.), *Fifty years after the "Homage to Santa Rosalia": Old and new paradigms on biodiversity in aquatic ecosystems* (pp. 15–28). Springer.

Luimstra, V. M., Schuurmans, J. M., Hellingwerf, K. J., Matthijs, H. C., & Huisman, J. (2020). Blue light induces major changes in the gene expression profile of the cyanobacterium *Synechocystis* sp. PCC 6803. *Physiologia Plantarum*, *170*(1), 10–26. https://doi.org/10.1111/ppl.13086

Luimstra, V. M., Schuurmans, J. M., Verschoor, A. M., Hellingwerf, K. J., Huisman, J., & Matthijs, H. C. (2018). Blue light reduces photosynthetic efficiency of cyanobacteria through an imbalance between photosystems I and II. *Photosynthesis Research*, *138*(2), 177–189. https://doi.org/10.1007/s11120-018-0561-5

Lürling, M., Eshetu, F., Faassen, E. J., Kosten, S., & Huszar, V. L. (2013). Comparison of cyanobacterial and green algal growth rates at different temperatures. *Freshwater Biology*, *58*(3), 552–559. https://doi.org/10.1111/j.1365-2427.2012.02866.x

Magee, M. R., Wu, C. H., Robertson, D. M., Lathrop, R. C., & Hamilton, D. P. (2016). Trends and abrupt changes in 104 years of ice cover and water temperature in a dimictic lake in response to air temperature, wind speed, and water clarity drivers. *Hydrology and Earth System Sciences*, *20*(5), 1681–1702. https://doi.org/10.5194/hess-20-1681-2016

Mantzouki, E., Visser, P. M., Bormans, M., & Ibelings, B. W. (2016). Understanding the key ecological traits of cyanobacteria as a basis for their management and control in changing lakes. *Aquatic Ecology*, *50*(3), 333–350. https://doi.org/10.1007/s10452-015-9526-3

Martin-Creuzburg, D., von Elert, E., & Hoffmann, K. H. (2008). Nutritional constraints at the cyanobacteria—*Daphnia magna* interface: The role of sterols. *Limnology and Oceanography*, *53*(2), 456–468. https://doi.org/10.4319/lo.2008.53.2.0456

Mehner, T. (2000). Influence of spring warming on the predation rate of underyearling fish on *Daphnia*–A deterministic simulation approach. *Freshwater Biology*, *45*(2), 253–263. https://doi.org/10.1046/j.1365-2427.2000.00551.x

Morales-Williams, A. M., Wanamaker, A. D., Jr., & Downing, J. A. (2017). Cyanobacterial carbon concentrating mechanisms facilitate sustained CO 2 depletion in eutrophic lakes. *Biogeosciences*, *14*(11), 2865–2875. https://doi.org/10.5194/bg-14-2865-2017

Moss, B., Kosten, S., Meerhoff, M., Battarbee, R. W., Jeppesen, E., Mazzeo, N., … Scheffer, M. (2011). Allied attack: Climate change and eutrophication. *Inland Waters*, *1*(2), 101–105. https://doi.org/10.5268/IW-1.2.359

Müller-Navarra, D. C., Brett, M. T., Park, S., Chandra, S., Ballantyne, A. P., Zorita, E., & Goldman, C. R. (2004). Unsaturated fatty acid content in seston and tropho-dynamic coupling in lakes. *Nature*, *427*(6969), 69–72. https://doi.org/10.1038/nature02210

Mullineaux, C. W. (2008). Phycobilisome-reaction centre interaction in cyanobacteria. *Photosynthesis Research*, *95*(2–3), 175. https://doi.org/10.1007/s11120-007-9249-y

Overmann, J., & Tilzer, M. M. (1989). Control of primary productivity and the significance of photosynthetic bacteria in a meromictic kettle lake. Mittlerer Buchensee, West-Germany. *Aquatic Sciences*, *51*(4), 261–278. https://doi.org/10.1007/BF00877171

Pace, M. L., Batt, R. D., Buelo, C. D., Carpenter, S. R., Cole, J. J., Kurtzweil, J. T., & Wilkinson, G. M. (2017). Reversal of a cyanobacterial bloom in response to early warnings. *Proceedings of the National Academy of Sciences of the United States of America*, *114*(2), 352–357. https://doi.org/10.1073/pnas.1612424114

Paerl, H. (2008). Nutrient and other environmental controls of harmful cyanobacterial blooms along the freshwater–marine continuum. In H. K. Hudnell (Ed.), *Cyanobacterial harmful algal blooms: State of the science and research needs* (pp. 217–237). Springer.

Paerl, H. W., & Huisman, J. (2008). Blooms like it hot. *Science*, *320*(5872), 57–58. https://doi.org/10.1126/science.1155398

Paerl, H. W., & Huisman, J. (2009). Climate change: A catalyst for global expansion of harmful cyanobacterial blooms. *Environmental Microbiology Reports*, *1*(1), 27–37. https://doi.org/10.1111/j.1758-2229.2008.00004.x

Paerl, H. W., & Paul, V. J. (2012). Climate change: Links to global expansion of harmful cyanobacteria. *Water Research*, *46*(5), 1349–1363. https://doi.org/10.1016/j.watres.2011.08.002

Pick, F. R. (2016). Blooming algae: A Canadian perspective on the rise of toxic cyanobacteria. *Canadian Journal of Fisheries and Aquatic Sciences*, *73*(7), 1149–1158. https://doi.org/10.1139/cjfas-2015-0470

Rasconi, S., Gall, A., Winter, K., & Kainz, M. J. (2015). Increasing water temperature triggers dominance of small freshwater plankton. *PLoS One*, *10*(10), e0140449. https://doi.org/10.1371/journal.pone.0140449

Romo, S. (1994). Growth parameters of *Pseudanabaena galeata* Böcher in culture under different light and temperature conditions. *Algological Studies/Archiv Für Hydrobiologie, Supplement Volumes*, *75*, 239–248. https://doi.org/10.1127/algol_stud/75/1995/239

Scheffer, M., Rinaldi, S., Gragnani, A., Mur, L. R., & van Nes, E. H. (1997). On the dominance of filamentous cyanobacteria in shallow, turbid lakes. *Ecology*, *78*(1), 272–282. https://doi.org/10.2307/2265995

Schellenberger Costa, B., Jungandreas, A., Jakob, T., Weisheit, W., Mittag, M., & Wilhelm, C. (2013). Blue light is essential for high light acclimation and photoprotection in the diatom *Phaeodactylum tricornutum*. *Journal of Experimental Botany*, *64*(2), 483–493. https://doi.org/10.1093/jxb/ers340

Selmeczy, G. B., Krienitz, L., Casper, P., & Padisák, J. (2018). Phytoplankton response to experimental thermocline deepening: A mesocosm experiment. *Hydrobiologia*, *805*(1), 259–271. https://doi.org/10.1007/s10750-017-3308-y

Six, C., Thomas, J.-C., Garczarek, L., Ostrowski, M., Dufresne, A., Blot, N., ... Partensky, F. (2007). Diversity and evolution of phycobilisomes in marine *Synechococcus* spp.: A comparative genomics study. *Genome Biology*, *8*(12), R259. https://doi.org/10.1186/gb-2007-8-12-r259

Smith, V. H. (1986). Light and nutrient effects on the relative biomass of blue-green algae in lake phytoplankton. *Canadian Journal of Fisheries and Aquatic Sciences*, *43*(1), 148–153. https://doi.org/10.1139/f86-016

Sommer, U., Adrian, R., Bauer, B., & Winder, M. (2012). The response of temperate aquatic ecosystems to global warming: Novel insights from a multidisciplinary project. *Marine Biology*, *159*(11), 2367–2377. https://doi.org/10.1007/s00227-012-2085-4

Stockenreiter, M., Haupt, F., Graber, A. K., Seppälä, J., Spilling, K., Tamminen, T., & Stibor, H. (2013). Functional group richness: Implications of biodiversity for light use and lipid yield in microalgae. *Journal of Phycology*, *49*(5), 838–847. https://doi.org/10.1111/jpy.12092

Stomp, M., Huisman, J., de Jongh, F., Veraart, A. J., Gerla, D., Rijkeboer, M., ... Stal, L. J. (2004). Adaptive divergence in pigment composition promotes phytoplankton biodiversity. *Nature*, *432*(7013), 104–107. https://doi.org/10.1038/nature03044

Striebel, M., Behl, S., Diehl, S., & Stibor, H. (2009). Spectral niche complementarity and carbon dynamics in pelagic ecosystems. *The American Naturalist*, *174*(1), 141–147. https://doi.org/10.1086/599294

Suda, S., Liu, Y., He, J., Hu, Z., Hiroki, M., & Watanabe, M. M. (1998). Morphological, biochemical and physiological characteristics of *Lyngbya hieronymusii* var. *hieronymusii* (Oscillatoriales, Cyanobacteria). *Phycological Research*, *46*, 51–55. https://doi.org/10.1046/j.1440-1835.1998.00125.x

Thomas, M. K., & Litchman, E. (2016). Effects of temperature and nitrogen availability on the growth of invasive and native cyanobacteria. *Hydrobiologia*, *763*(1), 357–369. https://doi.org/10.1007/s10750-015-2390-2

Urrutia-Cordero, P., Ekvall, M. K., & Hansson, L. A. (2016). Local food web management increases resilience and buffers against global change effects on freshwaters. *Scientific Reports*, *6*, 29542. https://doi.org/10.1038/srep29542

Utermöhl, H. (1958). Zur vervollkommnung der quantitativen phytoplankton-methodik: Mit 1 Tabelle und 15 abbildungen im Text und auf 1 Tafel. *Internationale Vereinigung Für Theoretische Und Angewandte Limnologie: Mitteilungen*, *9*(1), 1–38. https://doi.org/10.1080/05384680.1958.11904091

Valle, K. C., Nymark, M., Aamot, I., Hancke, K., Winge, P., Andresen, K., ... Bones, A. M. (2014). System responses to equal doses of photosynthetically usable radiation of blue, green, and red light in the marine diatom *Phaeodactylum tricornutum*. *PLoS One*, *9*(12), https://doi.org/10.1371/journal.pone.0114211

Van Thor, J. J., Mullineaux, C. W., Matthijs, H. C. P., & Hellingwerf, K. J. (1998). Light harvesting and state transitions in cyanobacteria. *Botanica Acta*, *111*(6), 430–443. https://doi.org/10.1111/j.1438-8677.1998.tb00731.x

Verbeek, L., Gall, A., Hillebrand, H., & Striebel, M. (2018). Warming and oligotrophication cause shifts in freshwater phytoplankton communities. *Global Change Biology*, *24*(10), 4532–4543. https://doi.org/10.1111/gcb.14337

Visser, P., Ibelings, B. A. S., Van Der Veer, B., Koedood, J. A. N., & Mur, R. (1996). Artificial mixing prevents nuisance blooms of the cyanobacterium Microcystis in Lake Nieuwe Meer, the Netherlands. *Freshwater Biology*, *36*(2), 435–450. https://doi.org/10.1007/s10452-015-9537-0

Wetzel, R. G., & Likens, G. (1991). *Limnological analysis* (2nd ed.). Springer-Verlag.

Wilhelm, S. W., Bullerjahn, G. S., & McKay, R. M. L. (2020). The complicated and confusing ecology of *Microcystis* blooms. *MBio*, *11*(3), https://doi.org/10.1128/mBio.00529-20

Winder, M. (2012). Limnology: Lake warming mimics fertilization. *Nature Climate Change*, *2*(11), 771–772. https://doi.org/10.1038/nclimate1728

Winder, M., & Schindler, D. E. (2004). Climatic effects on the phenology of lake processes. *Global Change Biology*, *10*(11), 1844–1856. https://doi.org/10.1111/j.1365-2486.2004.00849.x

Winder, M., & Sommer, U. (2012). Phytoplankton response to a changing climate. *Hydrobiologia*, *698*(1), 5–16. https://doi.org/10.1007/s10750-012-1149-2

Witt, B. A., Beyer, J. E., Hallidayschult, T. C., & Hambright, K. D. (2019). Short-term toxicity effects of *Prymnesium parvum* on zooplankton community composition. *Aquatic Sciences*, *81*(4), 55. https://doi.org/10.1007/s00027-019-0651-2

Woolway, R. I., & Merchant, C. J. (2019). Worldwide alteration of lake mixing regimes in response to climate change. *Nature Geoscience*, *12*(4), 271–327. https://doi.org/10.1038/s41561-019-0322-x

Woolway, R. I., Merchant, C. J., Van Den Hoek, J., Azorin-Molina, C., Nõges, P., Laas, A., ... Jones, I. D. (2019). Northern Hemisphere atmospheric stilling accelerates lake thermal responses to a warming world. *Geophysical Research Letters*, *46*(21), 11983–11992. https://doi.org/10.1029/2019GL082752

Xu, H., Cai, H., Yu, G., & Jiang, H. (2013). Insights into extracellular polymeric substances of cyanobacterium Microcystis aeruginosa using fractionation procedure and parallel factor analysis. *Water Research*, *47*(6), 2005–2014. https://doi.org/10.1016/j.watres.2013.01.019

Zohary, T., & Robarts, R. D. (1990). Hyperscums and the population dynamics of *Microcystis aeruginosa*. *Journal of Plankton Research*, *12*(2), 423–432. https://doi.org/10.1093/plankt/12.2.423

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Stockenreiter, M., Isanta Navarro, J., Buchberger, F., & Stibor, H. (2021). Community shifts from eukaryote to cyanobacteria dominated phytoplankton: The role of mixing depth and light quality. *Freshw Biol.*, 66, 2145–2157. https://doi.org/10.1111/fwb.13822