Variation in species light acquisition traits under fluctuating light regimes: implications for non-equilibrium coexistence

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Abstract

Resource distribution heterogeneity offers niche opportunities for species with different functional traits to develop and potentially coexist. Available light (photosynthetically active radiation or PAR) for suspended algae (phytoplankton) may fluctuate greatly over time and space. Species-specific light acquisition traits capture important aspects of the ecophysiology of phytoplankton and characterize species growth at either limiting or saturating daily PAR supply. Efforts have been made to explain phytoplankton coexistence using species-specific light acquisition traits under constant light conditions, but not under fluctuating light regimes that should facilitate non-equilibrium coexistence. In the well-mixed, hypertrophic Lake TaiHu (China), we incubated the phytoplankton community in bottles placed either at fixed depths or moved vertically through the water column to mimic vertical mixing. Incubations at constant depths received only the diurnal changes in light, while the moving bottles received rapidly fluctuating light. Species-specific light acquisition traits of dominant cyanobacteria (*Anabaena flos-aquae*, *Microcystis spp.*) and diatom (*Aulacoseira granulata, Cyclotella pseudostelligera*) species were characterized from their growth-light relationships that could explain relative biomasses along the daily PAR gradient under both constant and

fluctuating light. Our study demonstrates the importance of interspecific differences in affinities to limiting and saturating light for the coexistence of phytoplankton species in spatially heterogeneous light conditions. Furthermore, we observed strong intraspecific differences in light acquisition traits between incubation under constant and fluctuating light – leading to the reversal of light utilization strategies of species. This increased the niche space for acclimated species, precluding competitive exclusion. These observations could enhance our understanding of the mechanisms behind the Paradox of the Plankton.

Keywords: Fluctuating light; Light acquisition traits; Phytoplankton photoacclimation; Niche partitioning; Non-equilibrium coexistence.

Introduction

It is well recognized that spatial and temporal heterogeneity offer niche opportunities for species with different ecological strategies to develop and potentially coexist (Chesson and Case 1986, Chesson 2000). Spatial heterogeneity reduces niche overlap, enabling coexistence by favouring different species in different local environments through environmental filtering. Temporal heterogeneity can also promote species coexistence through differential nonlinear species-specific responses to a fluctuating limiting factor; different species dominating at times when they are able to most actively use the resource (Chesson 2000, Adler et al. 2013). Thus, the impact of environmental variability on organisms may lead to different species performances and community composition than those measured under constant conditions (Koussoroplis et al. 2017). Empirical work on the effects of resource heterogeneity on species diversity maintenance and competition has been done on animals and terrestrial plants (see Amarasekare 2003 and Silvertown 2004 for reviews). In aquatic ecology, the coexistence of several phytoplankton species in a seemingly homogeneous environment was originally characterized as the "Paradox of the Plankton" (Hutchinson 1961).

As the major primary producers on Earth, phytoplankton are responsible for about half of the global net production of photosynthetic organisms (Field et al. 1998). Their community composition may greatly affect food webs and biogeochemical cycles (Falkowski et al. 1998, Litchman et al. 2015). Consequently, it is important to understand

54 how environmental variation affects phytoplankton biodiversity. Phytoplankton have
55 very short generation times (≈ 1 day), are very easy to culture and have readily
56 measurable functional traits affecting fitness in a given environment. Thus, they provide
57 ideal models to test the effects of spatio-temporal environment variability on organisms.
58 Studies involving phytoplankton exposed to varying resource levels have focused
59 primarily on the effects of fluctuating nutrient supplies on species composition both in
60 the laboratory (Sommer 1984, 1985) and in nature (Beisner 2001). Light is another
61 essential resource for phytoplankton growth. Increasing efforts have been made to
62 better understand the effects of fluctuating intensities on phytoplankton physiology
63 under controlled (Nicklisch 1998, Havelková-Doušová et al. 2004, Shatwell et al. 2012)
64 and semi-natural conditions (Marra 1978, Köhler et al. 2018). Nevertheless, very few
65 studies have focused on the effects of fluctuating light levels on species competition and
66 coexistence (Litchman 1998, Flöder et al. 2002), solely investigating species diversity
67 and/or species-specific growth rates at either low or high light levels.

68 In nature, light availability for phytoplankton fluctuates on timescales ranging
69 from milliseconds to seasons (Falkowski 1984, Ferris and Christian 1991). Short-term
70 light fluctuations affect several physiological processes such as photosynthesis
71 (MacIntyre et al. 2000, Fietz and Nicklisch 2002), respiration (Avendaño-Coletta and
72 Schubert 2005) and consequently, growth (Shatwell et al. 2012, Köhler et al. 2018).

Phytoplankton growth is non-linearly related to light availability, with a proportional increase in the limiting range of light intensities, constant growth at saturating light intensities, and a transition region around the onset of growth saturation. From such growth-light relationships, one may extract demographic traits of a population that can be seen to represent light acquisition traits as they provide reliable indicators of the ability of one species to grow at certain light intensities (Litchman et al. 2012). Traits include: the initial slope of the growth-light curve (α) which reflects the growth efficiency at limiting light; the maximum growth rate at saturating light (μ_{max}); and the light intensity at zero growth (PAR_{comp}), the so-called compensation light intensity (Fig. 1).

These light acquisition traits calculated from traditional growth-constant light relationships measured in the laboratory have been used to explain phytoplankton distributions along environmental light gradients (Schwaderer et al. 2011). Assuming no co-limitation with other factors such as grazing or nutrient supply, a species with the higher α is expected to outcompete the others under limiting light levels. Conversely, a species with the highest μ_{max} is expected to outcompete the others under saturating light levels. However, it has been shown that the light acquisition traits are plastic and may have different values between incubations under constant and fluctuating light (Shatwell et al. 2012, Köhler et al. 2018). This trait plasticity reflects the timescale-dependent

92 ecophysiological acclimation processes of phytoplankton to changing light intensities
93 (Falkowski 1984, Ferris and Christian 1991). The acclimation mechanisms are species-
94 dependent (potentially even clonal-dependent, see Kardinaal et al. 2007) and should
95 thus alter interspecific competition, promote coexistence or exclude inefficient species in
96 diverse phytoplankton communities (Litchman 1998, Flöder et al. 2002). For instance, a
97 species that is the best competitor at a certain constant light supply could coexist or even
98 be displaced by a species with higher performance under fluctuating light of the same
99 mean intensity.

100 In general, it is still unknown how species light acquisition trait variation under
101 fluctuating light may alter niche partitioning and thus species coexistence in bulk
102 phytoplankton communities. We made the first attempt to fill this gap by investigating
103 the effects of fluctuating light on light acquisition traits and relative biomass of dominant
104 phytoplankton species from a diverse community under semi-natural conditions. We
105 deliberately measured the light acquisition traits in a community context, and not for
106 species cultured separately, because species generally diverge more in resource use to
107 reduce niche overlap in a multispecies context (Lawrence et al. 2012). We mimicked
108 vertical mixing and induced fluctuating light regimes by computer-controlled motion of
109 subsamples from a lake phytoplankton community in the frequently mixed, turbid,
110 hypertrophic Lake TaiHu (China). The investigated community was adapted to Lake

TaiHu's temperature and frequent mixing. It was incubated under nutrient-replete conditions and drastically reduced grazing pressure. Thus phytoplankton dynamics were expected to be mostly driven by rapid acclimation to light climate treatments within a couple of days. We evaluated variation in light acquisition traits of phytoplankton between stratified and mixed conditions and used these to describe realized light niches, thereby improving understanding of non-equilibrium species coexistence under semi-natural conditions. We hypothesized that in this natural phytoplankton community: (1) fluctuating light would modify species-specific growth-light relationships and, as a consequence, light acquisition traits (α, μ_{max} and PAR_{comp}). A set of species light acquisition traits was considered here as a light utilization strategy. Following support of this first hypothesis, we then expected (2) a relative change in species biomass over the light gradient (limiting vs. saturating light) and between subsamples incubated under fluctuating light conditions relative to those experiencing constant light. We further hypothesized that (3) niche partitioning of the dominant species was possible over gradients of light and mixing depth in the water column.

Material and Methods

Study site and experimental setup

129 Lake TaiHu (China, 31°14'N 120°8'E) is a very large (2340 km^2), shallow (1.9 m mean
130 depth), hypertrophic, turbid and wind-exposed lake. Due to the intensification of human
131 activities in the catchment area, total nitrogen and phosphorus concentrations in the lake
132 have been increasing since the 1980's and resulted in intensified blooms occurring more
133 frequently (Duan et al. 2009, Qin et al. 2010). Cyanobacteria blooms can reach 1000 km^2
134 and may occur from May to November (Duan et al. 2009). The field experiment was
135 conducted from September 7th to September 16th 2016, during the development of the
136 cyanobacteria bloom (mostly *Microcystis spp*.). Our experimental site was situated in the
137 Meiliang Bay of Lake TaiHu (northern part of the lake) on top of the Nanjing Institute of
138 Geography and Limnology (NIGLAS) landing, about 200 meters offshore.

139 Prior to sampling, we removed any surface scums containing dying cyanobacteria
140 cells and sampled lake water at 30 cm depth to recover the natural phytoplankton
141 community. We filtered the water through a 100 µm sized mesh to remove large
142 zooplankton, and then gently bubbled it with N_2 for five hours to kill any small remaining
143 zooplankton by anoxia. We added 12x concentrated MIII-KS fresh culture medium, to
144 obtain 1x final concentration (see Nicklisch et al. 2008 for detailed composition). After
145 re-aeration we distributed the lake water into 500 mL transparent incubation bottles
146 (Teflon Fluorinated Ethylene Propylene, Nalgene). These bottles provide the best trade-
147 off between robustness for incubation in the lake and Photosynthetically Active

148 Radiation (PAR [400-700nm]) and Ultra-Violet (UV-A [320-400nm]) transmittance
149 (mean transmittance to PAR = 72±6.6%; to UV-A = 51.4±3.5%).

150 We performed two identical experiments with regard to their design and
151 methods, starting at sunrise each time and lasting either 5 days (7^{th} – 11^{th} September)
152 and 4 days (13^{th} – 16^{th} September). No difference in species composition was noted
153 between inocula at the two experimental periods. The species composition of the inocula
154 was very diverse (n=57 species) (Appendix -Table 1).

155 Bottles were installed in triplicate in transparent holders placed at fixed depths
156 and vertically moved by a computer-controlled lift in the lake (method described in
157 Köhler et al. 2018). Phytoplankton incubated at constant depth received only the natural
158 sinusoidal diurnal course of sunlight, a treatment that we will refer to as constant light.
159 In contrast, communities incubated in bottles moved vertically through the water
160 column received fluctuating light, by superimposing the vertical light gradient on the
161 natural sinusoidal diurnal sunlight. The lifts simulated a circular movement with 20
162 minutes per revolution, replicating to some extent the full overturn of typical Langmuir
163 cells (Denman and Gargett 1983, Schubert and Forster 1997, Thorpe 2004). We fixed
164 incubation bottles in triplicates at 0, 0.2, 0.4 and 0.8 m depth (constant light treatment).
165 The moving bottles rotated between the water surface (0 m) and 0.5, 1.0 and 1.8 m depth

(fluctuating light treatment). The daily PAR values received in both treatments are given in the Appendix (Appendix - Table 2, Fig. 1).

Fully dark-adapted subsamples were taken each morning before sunrise. Sample volumes ranged from 80 to 100mL to ensure similar total biomass between the different incubation bottles. To avoid nutrient limitation, we refilled the bottles with a mix of filtered lake water (Whatman GF/F glass microfiber) and 12x concentrated MIII-KS fresh culture medium, to obtain 1x final concentration. The bottles were re-incubated in the lake within 20 minutes.

Abiotic conditions

Global radiation data were measured using a 2π light sensor type and were obtained from the NIGLAS monitoring station (TaiHu Laboratory for Lake Ecosystem Research TLLER) located near the experimental site. To obtain daily PAR intensities, we first corrected the global radiation for light attenuation in the lake following the Lambert-Beer's law:

$$I_z = I_o * e^{-kz}$$

where I_z is the light intensity at depth z (m), I_o is PAR at the water surface and k the light attenuation coefficient (m^{-1}). The latter was calculated from daily light measurements at 0.5m intervals from the surface to 1.5m depth with a spherical spectroradiometer (ASC-

185 VIS, TRIOS, Germany). Then, we corrected the light data for shade produced by the pier
186 (when applicable), for wavelength-specific transmittance of the incubation bottles and
187 the actual vertical position of the moved phytoplankton.

188 Vertical profiles of temperature were measured every 5 minutes using
189 temperature loggers (Tinytag, Aquatic 2 TG-4100) sealed to the bottles holders. The lake
190 was very well mixed with temperatures between the lake surface and the bottom
191 differing by less than 0.36°C on average during the experimental period.

192

193 ***Cell counts***

194 Species composition was monitored at the beginning, after 2 days and at the end of each
195 of the two experiments. Subsamples were fixed in Lugol's solution (Throndsen 1978).
196 Subsamples taken from each replicate were mixed together to reduce the number of
197 samples to count. Cell abundances of the dominant phytoplankton species were obtained
198 after counting at least 400 algal objects (cell, filament or colony) (Lund et al. 1958) per
199 sample by inverted microscopy (Nikon, Eclipse Ti-S) following the Utermöhl method
200 (Utermöhl 1958). Cell volumes were measured from at least 20 individuals of each
201 species from any sample under the same microscope using ImageJ software. Biovolumes
202 (proxy for phytoplankton biomass) were calculated by multiplying averaged cell
203 volumes by cell abundances. We measured biovolumes for 15 different species: 7

cyanobacteria, 5 diatoms and 3 chlorophyceae.

Data analysis

The biovolume of a species *i* relative to the biovolume of the group it belongs to was calculated after 2 days and at the end of both experiments as:

$$\text{relative biovolume}_{\text{species i}} = \frac{\text{biovolume}_{\text{species i}}}{\text{biovolume}_{\text{group}}}$$

Daily species-specific growth rates μ_i (day^{-1}) were calculated as follows, accounting for daily dilution:

$$\mu_i = \frac{\ln\left[\frac{\text{biovolume}_{t1} * \text{vol}}{\text{biovolume}_{t0} * (\text{vol} - \text{vol}_{\text{dilution}})}\right]}{t}$$

with *biovolume* $_{t0}$ and *biovolume* $_{t1}$ being the biovolumes of species *i* at times t0 and t1. *Vol* is the total volume of the incubation bottle and *vol* $_{dilution}$ is the volume sampled for analysis and replaced with fresh culture medium.

To build the growth-light relationships, we fit non-linear mixed effects models to the observed growth rates using the model of Webb et al. 1974:

$$\mu = \mu_{max}\left(1 - e^{\frac{-\alpha(PAR - PAR_{comp})}{\mu_{max}}}\right)$$

where μ_{max} is the growth rate at saturating light (d^{-1}), α is the growth efficiency at limiting light ($m^2 E^{-1}$), PAR_{comp} is the compensation light intensity (E m^{-2} d^{-1}) and *PAR* is the daily PAR exposure (E m^{-2} d^{-1}).

219 The daily PAR exposure was averaged over [day 0 - day 1] when plotting growth
220 rates measured at day 2 and averaged over [day 2 – end experiment] when plotting
221 growth rates measured at the end of the experiment. We obtained the estimates of the
222 light acquisition traits μ_{max}, α and PAR_{comp} (± standard error) for the best fitting model.
223 To obtain reliable trends along the light gradients and improve parameter
224 estimations of the effects of light fluctuations on non-equilibrium species coexistence
225 and phytoplankton physiology, we opted for counting more samples along the daily PAR
226 gradient over more replicates at fewer light intensities. This strategy is in line with the
227 recent call for "regression-based experimental designs" expressing the need to increase
228 the number of predictor levels while decreasing the number of replicates (Cottingham et
229 al. 2005, Beier et al. 2012, de Boeck et al. 2015, Schweiger et al. 2016). Schweiger et al.
230 (2016) recently provided methodological recommendations for such a protocol, arguing
231 that where greater systematic error is likely, such as in field studies, continuous
232 sampling without replication is preferable to sampling fewer but replicated predictor
233 levels along the same gradient.

234

235 ***Realized species niches to daily PAR and mixing depth gradients***

236 In addition to estimating the relative biovolumes of dominant species of cyanobacteria
237 and diatoms over a gradient of daily constant and fluctuating PAR, we also wanted to

238 describe the effects of the magnitude of light fluctuations on phytoplankton composition.
239 To this end, we examined species dominance or coexistence regions of diatoms and
240 cyanobacteria over gradients of mixing depths and daily PAR exposure. Traditionally,
241 one would examine the equilibrium phytoplankton growth. But stable growth over time
242 is usually only achievable in laboratory experiments. Given that our study monitored a
243 whole community under natural conditions with diurnal light variation, we cannot
244 expect phytoplankton species to be adapted to a given daily PAR. Thus, we defined
245 regions of "major contribution relative to other species". One species was declared the
246 "winner" over a second species if the difference between their relative biovolumes was >
247 10% (an arbitrary but useful threshold). Species "coexisted" when the variation around
248 their relative biovolumes was ≤ 10%. This approach does not describe steady-state
249 species composition but instead describes the short-term niche partitioning over the
250 daily light supply and mixing depth gradient.

251 We investigated how species within each group (diatoms or cyanobacteria) could
252 coexist *in situ* through their response to light conditions, because it is in these groups
253 that species are likely to compete more severely for light. Prokaryotes (cyanobacteria)
254 and eukaryotes (diatoms) differ in many aspects of their cellular components,
255 physiology, evolutionary history and acclimatization potential (Glover et al. 1987,

256 Gregory 2001, Yoon et al. 2004, Schwaderer et al. 2011) that should promote greater
257 differences in light use between than within groups (Schwaderer et al. 2011).

258

259 ***Statistical analyses***

260 Non-linear mixed effects models were implemented with the *nlme* R package (Pinheiro et
261 al. 2018 - library *nlme* R package version 3.1-137) with maximum log likelihood and
262 setting "incubation bottle" as random factor to account for temporal autocorrelation of
263 growth measurements and ensure independence of errors.

264 Differences in the light acquisition traits (μ_{max}, α and PAR_{comp}) between constant
265 and fluctuating light were assessed using the non-linear Webb model (Webb et al. 1974)
266 with "incubation bottle" as random factor. We tested the null hypothesis that the light
267 acquisition traits did not vary between constant and fluctuating light, against the
268 alternative hypothesis that one or more traits did vary between treatments. Conclusions
269 on treatment effects were based on model comparisons with F-tests following Bates and
270 Watts (1988, p. 105ff) and providing p-values. The models selected were also supported
271 by the lowest Akaike information criterion (AIC) (Akaike 1974; results not shown). We
272 used the same analytical approach to assess the interspecific differences in the light
273 acquisition traits (μ_{max}, α and PAR_{comp}) under constant and fluctuating light. Relative
274 species biovolumes along the daily PAR gradient were fit by a logarithmic function

(*coefficient * PAR + intercept*) using the *nls()* command. Interspecific differences after two days of experiment were assessed by the same method.

All analyses were performed with R version 3.3.2 (R core team 2016).

Data deposition

Data available from the Dryad Digital Repository: < http://dx.doi.org/10.5061/dryad.2rh61qk> (Guislain et al. 2018).

Results

Light affinities of dominant species

At all times and in all treatments four taxa, the cyanobacteria *Anabaena flos-aquae* and *Microcystis spp.* and the diatoms *Aulacoseira granulata* and *Cyclotella pseudostelligera,* dominated the assemblages (85.3±9.2% and 84.3±4.3% of the total biovolume under constant and fluctuating light respectively). For convenience we will refer to these phytoplankton taxa by their genus names. *Anabaena* and *Microcystis* combined accounted for 25.5±10.8% and 24.4±9.3% of the total biovolume during the entire experimental period under constant and fluctuating light respectively. *Aulacoseira* and *Cyclotella* combined accounted for 59.8±16.5% and 59.9±9.6% respectively under

293 constant and fluctuating light. The contributions of the main phytoplankton groups to the
294 total biovolume are given in the Appendix (Appendix - Table 3).

295 The contributions of diatoms to the total biovolume tended to slightly decrease
296 with increasing daily PAR supply for the benefit of cyanobacteria (PAR effect not
297 significant; $p>0.05$) (Appendix - Fig. 2). Chlorophyceae were always very sparse. We
298 noted no differences in the contribution of the main phytoplankton groups (diatoms,
299 cyanobacteria and chlorophyceae) between constant and fluctuating light exposure (all
300 p-values>0.05). Nevertheless, we observed a strong light dependency of the relative
301 contributions of species within diatoms and cyanobacteria.

302 Figure 2 depicts species-specific growth-light relationships of the 2 dominant
303 cyanobacteria (*Anabaena*, *Microcystis*) and the 2 diatoms (*Aulacoseira*, *Cyclotella*) under
304 constant and fluctuating light (see Appendix - Fig. 3 for intraspecific variation). The
305 growth-light relationships of *Anabaena* and *Microcystis* intersected under both constant
306 and fluctuating light because of different light affinities of each species to limiting and
307 saturating light. Under constant light (Fig. 2A), *Anabaena* had slightly higher growth
308 rates at saturating light than did *Microcystis*, but lower growth rates at limiting light.
309 Under fluctuating light (Fig. 2B) the strategies of both species were reversed with
310 *Microcystis* having higher growth rates at saturating light than *Anabaena*, but lower
311 growth rates at limiting light. Amongst the diatoms, *Cyclotella* always grew far better

than *Aulacoseira* at saturating light (Fig. 2C, D). At limiting light, drastic differences in growth rates between species occurred only under mixed conditions, as *Aulacoseira* grew better than *Cyclotella*.

Estimated values (± standard error) of α, μ_{max} and PAR_{comp} of species dominating the phytoplankton community are presented in Table 1.

For cyanobacteria, lower growth rates at limiting light were linked to higher values of PAR_{comp}. *Anabaena* had significantly higher PAR_{comp} than *Microcystis* under constant light ($p<0.01$). The opposite was true under fluctuating light ($p<0.01$). Under constant light, *Anabaena* attained slightly higher μ_{max} than *Microcystis*, but needed a higher PAR_{comp} than under fluctuating light. Conversely, under fluctuating light, *Microcystis* had higher μ_{max} than *Anabaena* but needed a significantly higher PAR_{comp} than under constant light ($p<0.001$). Growth efficiencies (α) did not drive the differences in growth rates between species as *Microcystis* always had higher α than *Anabaena* under both light exposures. Note that this trait increased slightly with positive intraspecific variation in μ_{max} and PAR_{comp}.

Amongst the diatoms, *Cyclotella* grew significantly faster at saturating light than *Aulacoseira* under both constant ($p<0.001$) and fluctuating ($p<0.001$) light (Table 1). In contrast to the cyanobacteria, higher μ_{max} of *Cyclotella* than of *Aulacoseira* was linked to higher PAR_{comp} under fluctuating light ($p<0.001$) but not under constant light ($p>0.05$).

To support the increase of its μ_{max} under fluctuating light, *Cyclotella* needed a significantly higher PAR_{comp} ($p<0.001$) than under constant light. The three light acquisition traits of *Aulacoseira* slightly increased under constant light ($p>0.05$).

As for the cyanobacteria, growth efficiencies (α) did not drive the differences in growth rates between species, as *Cyclotella* always had higher α than *Aulacoseira* under both light exposures. Note that this trait also increased with positive intraspecific variations of μ_{max} and PAR_{comp}. In addition, compensation light intensities of both diatoms were almost always lower and α and μ_{max} almost always higher than for the cyanobacteria species.

Relative biovolumes of dominant species over the daily PAR gradient

The relative biovolumes of the two dominant cyanobacteria depended greatly on the daily PAR (Fig. 3A, B) and were significantly different between species (all p-values<0.05). Similar to the growth-light relationships that were measured in the same species community context, the fits of relative biovolumes intersected (Fig. 3A). *Anabaena* contributed more at constant saturating light, following its higher μ_{max} under such conditions. On the other hand, a lower PAR_{comp} and higher α enabled *Microcystis* to dominate at constant limiting light.

The incubation of the same initial community under fluctuating light reversed, after 2 days only, the relative biovolumes observed under constant light, reflecting the

changes in light acquisition traits of both species between the two light exposures (Fig. 3B). *Microcystis* was the saturating light specialist under fluctuating light, increasing its contribution to the assemblage with fluctuating light intensities. *Anabaena* clearly dominated at fluctuating limiting light following its lower PAR_{comp} under such conditions.

PAR_{comp} values of the dominant cyanobacteria species clearly determined their relative contributions to the assemblage at limiting light. *Microcystis* always grew more efficiently (higher α) than did *Anabaena* under constant or fluctuating limiting light (Table 1). Yet, *Microcystis* dominated the assemblage only at constant limiting light (Fig. 3A). Nevertheless, at saturating light under both light treatments, the differences in relative biovolumes of the cyanobacteria were less pronounced (Fig. 3A, B). Note that the differences in light-dependent relative biovolumes were larger after 5 days (not shown because of the time dependence of biovolumes measured after 2 days and at the end of the experiments).

Unlike the cyanobacteria, the relative biovolumes of the diatoms along the gradient of daily PAR followed a similar pattern under both constant and fluctuating light (Fig. 3C, D) and were significantly different between species (all p-values<0.05). This result reflected the consistency of light affinities between constant and fluctuating light: *Cyclotella* always had higher μ_{max} than *Aulacoseira* under both constant and fluctuating light (Table 1). Therefore, the contribution of *Cyclotella* increased with increasing daily

PAR supply. Differences in relative biovolumes of diatoms were more pronounced under fluctuating light and were described by higher μ_{max} and PAR_{comp} of *Cyclotella* under fluctuating light than under constant light. As for the cyanobacteria, differences in light-dependent relative biovolumes were more pronounced after 5 days (data not shown).

Realized light niches over the daily PAR and mixing depth gradients

Realized light niches of cyanobacteria species were partitioned on both the daily PAR and mixing depth gradients (Fig. 4A). Under stagnant conditions, *Microcystis* dominated the cyanobacteria biovolume at limiting light whereas *Anabaena* dominated at saturating light levels above 5 E m^{-2} d^{-1}. Under mixing conditions, *Anabaena* dominated the cyanobacteria assemblage at all investigated daily light intensities when the mixing depth was higher than 0.5 m. Finally, *Anabaena* and *Microcystis* equally contributed to the cyanobacteria community roughly at a daily light supply ranging from 2 to 5 E m^{-2} d^{-1} under stagnant conditions. Under mixing conditions, both species contributed equally at shallow mixing (0.5 m mixing depth).

Unlike the cyanobacteria species, the diatoms maintained consistent light utilization strategies under constant and fluctuating light (Fig. 2C, D and Table 1). Realized niches were thus determined only by the daily PAR gradient (Fig. 4B). *Aulacoseira* dominated over *Cyclotella* under stagnant and mixed conditions at low daily

388 PAR. In contrast, when the daily PAR supply was greater than roughly 2 E m^{-2} d^{-1},
389 *Cyclotella* dominated over *Aulacoseira* regardless of mixing conditions.
390
391 **Discussion**
392 ***Mechanistic linkage between physiological processes and community dynamics***
393 Light acquisition traits capture important aspects of the ecophysiology of phytoplankton
394 (Litchman 2007), offering a promising mechanistic link between the environment and
395 community dynamics in both marine (Edwards et al. 2013a) and freshwater (Edwards et
396 al. 2013b) ecosystems. However, most studies to date used data obtained from
397 traditional growth-light experiments performed in the laboratory and under constant
398 light exposure, *de facto* underestimating the importance of light acquisition traits
399 variation towards fluctuating light in nature (Nicklisch 1998, Shatwell et al. 2012).
400 The light acquisition traits we focused on (light-saturated growth μ_{max}, growth
401 efficiency at limiting light α and compensation light intensity PAR_{comp}) integrate many
402 underlying physiological processes that are sensitive to light levels. μ_{max} and α are mainly
403 driven by the energy allocated to growth (e.g. ribosomes) and light-harvesting
404 machinery (e.g. chlorophyll complexes (Chla:C ratio) and accessory pigments)
405 respectively (Langdon 1988, Klausmeier et al. 2004, Litchman 2007, Talmy et al. 2013).
406 PAR_{comp}, the light intensity when $\mu = 0$, is driven by the balance between photosynthesis

(and thus, light-harvesting machinery) at limiting light and maintenance respiration (Langdon 1988). PAR_{comp} is primarily affected by maintenance respiratory costs (Langdon 1988). Respiration consumes oxygen in the production of ATP and NADPH to support biosynthesis and cell growth (see Ferris and Christian 1991 for review). As a consequence, the respiration maintenance to growth ratio is higher for high-light acclimated, fast-growing species (high μ_{max}) than for low-light acclimated species. Fast-growing species achieve compensation levels at higher light intensities and are thus less competitive at limiting light (Geider and Osborne 1989, Geider et al. 1996, Dubinsky and Stambler 2009). Also, excessive photosynthetic excitation may damage the photosystems that could result in additional respiratory costs (Richardson et al. 1983).

These light acquisition traits are inherently plastic and their values define the potential of species to grow at certain light supply. The light-saturated growth μ_{max} reflects the affinity for saturating light and a species with high μ_{max} is considered to be an opportunist, growing faster when light levels increase. On the other hand, a species with high growth efficiency at limiting light (α) and low compensation light intensity (PAR_{comp}) has low light requirements and is considered as gleaner (Grover 1990, Litchman and Klausmeier 2008).

Because of the limited energy that can be devoted to the acquisition of a particular resource, physiological trade-offs are expected between the light acquisition traits, such

426 as between maximum growth rate (at saturating light) and growth efficiency (at limiting
427 light) (Litchman and Klausmeier 2008). Therefore, one species may outcompete another
428 at saturating or limiting light if its trait value offers a better overall performance. In our
429 study, high μ_{max} always (under both constant and fluctuating light) described competitive
430 dominance at saturating light levels. In contrast, species with low PAR_{comp} were more
431 efficient at limiting light and almost always dominated their group biovolume under such
432 conditions. The growth efficiency (α) has been used to characterize the affinity of a
433 species when light is limiting (Schwaderer et al. 2011, Edwards et al. 2013a, 2013b,
434 2015). Our study demonstrates that PAR_{comp} was the most relevant trait related to the
435 ability of a species to outcompete others under constant and fluctuating limiting light
436 supply. According to our results, the dominant species at limiting light was almost
437 always the one with the lowest PAR_{comp} value, regardless of α. We expect that this may
438 result from the short duration of our experiment as maintenance costs, such as
439 photoprotection mechanisms (influencing PAR_{comp}) could act at shorter timescales than
440 growth (determined by α at limiting light) (Falkowski 1984, Ferris and Christian 1991,
441 MacIntyre et al. 2000). By measuring the species dominance patterns after only couple of
442 days, we increased the relative importance of short-term mechanisms and likely
443 favoured species with low PAR_{comp} rather than high α under limiting light. It is likely that
444 α values could have had greater impact on competitive outcomes at limiting light on

445 longer timescales. However, longer periods of constant conditions rarely occur in
446 dynamic systems.
447 Overall, the short-term gleaner-opportunist trade-off exhibited by species in our study
448 seemed to be driven by the enhancement of photosynthesis that increases slightly α, and
449 to a much larger extent μ_{max} – increasing *de facto* the maintenance respiratory costs
450 (PAR_{comp}). Nevertheless, under more stable conditions (such as in the laboratory) and at
451 longer time scale, it is likely that the gleaner-opportunist trade-off is mostly driven by
452 the balance between resource allocation to growth machinery (e.g. ribosomes) at
453 saturating light (affecting μ_{max}) and allocation to light-harvesting machinery (e.g.
454 chlorophyll complexes) at limiting light (affecting α).
455 Different light acquisition traits will cause big changes in species biovolumes only
456 in the long run. After very few days of new conditions, the now better acclimated species
457 will not necessarily already dominate the group/community. All the dominant species
458 were probably well adapted to the lake conditions prior to our sampling. This could be
459 explained by the assumption of variable conditions in such wind-exposed shallow lake,
460 covering both stagnant and mixing periods.
461
462 ***Effects of constant light intensities gradient***

There is a great deal of evidence that interspecific variation in light acquisition traits plays a role in maintaining species diversity through niche partitioning in communities (Litchman and Klausmeier 2001, Schwaderer et al. 2011, Adler et al. 2013). In a stratified eutrophic lake, phytoplankton must cope mostly with spatial heterogeneity in light intensity that declines exponentially with depth. Phytoplankton at the surface receives saturating light, but exclusively on days with little cloud cover. At deeper layers, light availability limits phytoplankton growth. Light availability is also limiting if scums of buoyant colonies / floating macrophytes shade lower depths or colonies self-shade the inner cells. In our study, we mimicked calm thermally stratified conditions by incubating phytoplankton at fixed depths in the lake.

The growth-light relationships of *Anabaena* and *Microcystis* under constant light intersected over the daily PAR gradient. The species displayed different light affinities to limiting and saturating light, thereby exhibiting a gleaner-opportunist trade-off (Grover 1990). As the gleaner (high α and low PAR_{comp}), *Microcystis* grew more efficiently at limiting light and dominated under constant limiting light. As the opportunist (high μ_{max}), *Anabaena* grew better under saturating light and contributed more to the cyanobacteria biovolume with increasing daily PAR. These alternative light utilization strategies exhibited after only couple of days allowed coexistence of these species on a gradient of constant PAR while avoiding competitive exclusion. Previous studies also identified the

482 importance of the gleaner-opportunist trade-off for species coexistence along the PAR
483 gradient (Litchman and Klausmeier 2001). Ultimately our results confirmed that
484 opportunist species (high μ_{max}) are more likely to thrive under saturating light, especially
485 when high losses (e.g. by predation) limit self-shading. In contrast, gleaner species (high
486 α, low PAR_{comp}) are more competitive in highly productive/turbid systems when light
487 levels are low.

488 The gleaner-opportunist trade-off was not evident amongst the dominant diatom
489 species. While *Cyclotella* had higher μ_{max} and α than *Aulacoseira*, their PAR_{comp} were
490 similar. Meta-analyses of growth-light experiments on marine diatoms species (Edwards
491 et al. 2015) indicate a positive correlation between μ_{max} and α. High values in both
492 maximal growth rates and growth efficiency at limiting light likely evolved by allowing
493 diatoms to survive in turbulent systems where they are usually present and where PAR
494 fluctuates between high and low intensities. This evolutionary hard-wiring in the growth
495 traits is apparently still expressed under constant light conditions in our experiment.
496 Interspecific differences in μ_{max} values between diatoms explained why *Cyclotella*
497 contributed more to the biovolume of diatoms with increasing daily PAR. In contrast, the
498 dominance of *Aulacoseira* at limiting light is not explainable by light traits (lower growth
499 efficiency and similar PAR_{comp}). Traits like affinity for nutrients or vulnerability for
500 grazing were excluded in our experiment but act under natural conditions. There, the

unicellular *Cyclotella* should suffer from higher grazing losses than the filamentous *Aulacoseira*. This might explain the higher biomass of *Aulacoseira* than of *Cyclotella* in the inocula, which were assembled from the natural system. Our experiment was likely too short to enable drastic changes in relative species biomass at low light where absolute growth rates of both species were low. In the long run, *Cyclotella* should outcompete *Aulacoseira* at all light intensities if our incubation conditions (replete nutrients, low grazing pressure, no sedimentation) are provided.

Our results confirm generally, that under semi-natural conditions, interspecific variation of light acquisition traits can reduce niche overlap within few days thereby precluding competitive exclusion in a spatially heterogeneous light climate. As a consequence, species diversity within the same phytoplankton group is maintained owing to the PAR gradient occurring in the lake. Nevertheless, such constant light conditions would rarely occur in well-mixed water layers.

Effects of fluctuating light under vertical mixing

Under semi-natural conditions, temporal light fluctuations may result in differences in light acquisition parameters of phytoplankton communities incubated either under constant or fluctuating light (Köhler et al. 2018). However, it is still unknown how the species-specific variation in light acquisition traits may affect the coexistence *in situ*.

520 Thus, it is critical to estimate light acquisition traits under fluctuating light conditions to
521 explain the development of phytoplankton at vertical mixing.

522 Under fluctuating light conditions, phytoplankton must cope with light
523 heterogeneity that is both spatial (in the water column) and temporal (in our study,
524 diurnal course of light + 20 minute fluctuations). Hence, phytoplankton must be
525 acclimated to both mean level and dynamics of light intensity as they have to cope with
526 the probability of the different light intensities and with the speed of changes. Forecasts
527 of phytoplankton development *in situ* are uncertain if based on growth-light
528 relationships measured under constant light because mean intensity as well as dynamic
529 of light availability may co-limit growth. Indeed, our results showed that strong
530 intraspecific variation in light acquisition traits under constant and fluctuating light
531 affected competitive outcomes.

532 As was the case for constant light exposure, the cyanobacteria displayed a
533 gleaner-opportunist trade-off also under fluctuating light. However, the dominant
534 species switched their strategies and dominance patterns: *Microcystis*, gleaner under
535 constant light became opportunist (high μ_{max}) under fluctuating light while *Anabaena*,
536 opportunist under constant light became a gleaner (low PAR_{comp}) under fluctuating light.
537 This intraspecific variation indicates a strong and fast plasticity of cyanobacteria light
538 acquisition traits, explaining the observed changes in relative biovolumes of dominant

539 species after only two days. The reduction of the minimal light requirements of
540 *Anabaena flos-aquae* under fluctuating light (4h high:4h low light) compared to constant
541 light has been hypothesized to be one of the reasons of the increased coexistence
542 potential with another cyanobacteria (the filamentous *Phormidium luridum var.*) in the
543 laboratory by Litchman (2003).

544 In contrast, light utilization strategies of diatoms were not reversed and the
545 competitive outcomes remained similar. Again, these results indicate the strong
546 adaptation of diatoms to vertical mixing (Reynolds 2006). It is also worth noting that
547 diatoms had overall higher growth rates than cyanobacteria. Nevertheless, because of
548 their relatively small size and high density, diatoms must cope with higher losses by
549 sedimentation and grazing. Therefore, in nature, diatoms may attain a lower biomass
550 than cyanobacteria despite faster gross growth.

551 With increasing μ_{max}, or higher affinity to saturating light, α of both diatoms and
552 cyanobacteria species increased slightly. Such phenomenon could be explained by
553 photosynthesis enhancement whereby opportunists benefit from intermittent saturating
554 light peaks at the water surface to optimize performance (Marra 1978, Kana and Glibert
555 1987), but which negatively influences their ability to grow at limiting light levels
556 because of increasing maintenance metabolic cost (Richardson et al. 1983).

557

Realized light niches over the daily PAR and mixing depth gradients

One of the main challenges in community ecology is to understand how environmental variability shapes the community composition and dynamics *in situ* (Chesson 2000, Adler et al. 2013). We observed that inter- and intraspecific variation in light acquisition traits toward both mean level and dynamics of light intensity enhanced species coexistence over the PAR gradient. Yet the daily PAR received by phytoplankton in lakes depends, amongst other factors, on the surface irradiance and the mixing depth, the latter being inversely related to the daily PAR.

Diatoms displayed the more straightforward scenario. As mixing specialists, diatoms did not modify their light utilization strategies between constant and fluctuating light regimes. The opportunist *Cyclotella* dominated the diatom biovolume along the whole mixing gradient at saturating light, while *Aulacoseira* did so along the whole mixing gradient at limiting light. Under mixing conditions, the dominance of *Aulacoseira* over *Cyclotella* was favoured by its lower compensation light intensity. Their relative contributions along the gradient of fluctuating light regimes were very distinct after 2 days (Fig. 3D) and amplified after 5 days of incubation under both light exposures (Fig 4B). Thus, no region of similar contribution appeared on the daily PAR x mixing depth gradients. However, these results are not fully transferable to natural conditions. Our incubations avoided losses by sedimentation and largely grazing. Under calm conditions,

577 sedimentation should affect the larger *Aulacoseira* more strongly than the single-celled
578 *Cyclotella*. In contrast, the latter is more vulnerable to grazing.

579 The niche partitioning between the cyanobacteria species was more complicated.
580 The gleaner *Microcystis* strongly dominated cyanobacteria biovolume under stagnant
581 conditions when light was limiting. Under constant saturating light conditions *Anabaena*
582 was dominant. Both species are buoyant and therefore their permanent occurrence in
583 dim layers of a non-mixed lake is unlikely. Instead, we assume that variation in available
584 light is driven solely by changing cloud cover and light distribution within the colonies.
585 Unlike the diatoms, the cyanobacteria species had similar relative biomasses across a
586 large range of light intensities (from 2 to 5 E m^{-2} d^{-1}) under both constant and fluctuating
587 light exposure (Fig. 4A). This phenomenon might be, at least partly, explained by self-
588 shading inside of colonies which is poorly understood so far. Nonetheless, it is
589 conceivable that the development of the colonial cyanobacterial opportunist allowed the
590 gleaner to develop because of the limiting effects of self-shading in the colony. On the
591 other hand, at limiting light levels, only the gleaner with very low light requirements
592 could thrive. This explains the observed higher differences in growth rates and relative
593 biovolumes of species at limiting than at saturating light. Thus, cyanobacteria species
594 may coexist under both stable and mixing conditions at sub-saturating irradiances, and a
595 drastic increase or decrease of the daily PAR may quickly favour the opportunist or

596 gleaner species respectively. Cyanobacteria were affected by vertical mixing with
597 *Anabaena* and *Microcystis* switching light utilization strategies, resulting in a niche
598 partitioning along gradients of daily PAR and mixing depth. The gleaner *Anabaena*
599 benefited from vertical mixing deeper than 0.5 m when the daily PAR was low, and from
600 its higher initial biovolume. *Microcystis* could not outcompete the latter because of its
601 high compensation light intensity under fluctuating light. However, at shallow mixing
602 depths (below 0.5 m deep) a region of similar contribution existed owing to lower
603 interspecific differences in absolute growth rates at saturating than at limiting light.

604 Our study points to the mechanistic linkages between more natural light
605 environment and phytoplankton dynamics in Lake TaiHu. That said, our goal was not to
606 forecast the development of phytoplankton communities in this particular lake under
607 mixed or stratified conditions. We investigated only one frequency of light fluctuation
608 (20 minutes) and the light dynamics within the lake itself will be more stochastic,
609 operating at different temporal scales. The observed light-dependency of growth is
610 caused by physiological mechanisms which act at different time scales. However, our
611 experiment resembled natural conditions much better than any approach that neglects
612 light dynamics or species interactions. We advocate approaches that target the variation
613 in light acquisition traits under constant and fluctuating light directly as these may
614 counter predictions made on a species-by-species basis.

615

616 ***Conclusions***

617 High biodiversity of natural phytoplankton communities has been attributed primarily to
618 eco-evolutionary responses of phytoplankton groups to different levels of constant light
619 exposure (i.e. variation across depth only). Our study demonstrates under semi-natural
620 conditions the existence of interspecific variation in light affinities allowing the
621 coexistence of species with different light utilization strategies in spatially
622 heterogeneous light conditions. In addition, the overlooked intraspecific variation in
623 light acquisition traits under fluctuating light impacted the community composition. We
624 demonstrated for the first time that vertical mixing may alter, or even reverse, light
625 utilization strategies of phytoplankton species. Non-equilibrium conditions increase the
626 amount of niches where acclimated species may thrive, allowing coexistence and
627 avoiding competitive exclusion even in seemingly homogeneous environments.

628

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Declarations

The authors declare no conflict of interest

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Table 1. Calculated light acquisition traits α, μ_{max} and PAR_{comp} (estimate±standard error) of the four dominant species under **A)** constant and **B)** fluctuating light. The goodness of fit is also presented for each trait in brackets. Units: μ_{max} in d^{-1}, α in $m^2\,E^{-1}$ and PAR_{comp} in $E\,m^{-2}\,d^{-1}$.

A	*Anabaena*	*Microcystis*	*Aulacoseira*	*Cyclotella*
μ_{max}	0.32 ± 0.18 (0.11)	0.25 ± 0.08 <0.05	0.48 ± 0.11 <0.01	1.16 ± 0.16 <0.001
α	0.31 ± 0.12 <0.05	0.52 ± 0.25 (0.08)	0.71 ± 0.43 (0.15)	0.88 ± 0.30 <0.05
PAR_{comp}	1.60 ± 0.39 <0.01	0.65 ± 0.23 <0.05	0.44 ± 0.20 (0.08)	0.16 ± 0.12 (0.25)
B				
μ_{max}	0.18 ± 0.08 (0.08)	0.32 ± 0.20 (0.19)	0.40 ±0.07 <0.05	1.69 ± 0.84 (0.09)
α	0.24 ± 0.27 (0.43)	0.60 ± 0.23 (0.06)	0.44 ± 0.17 (0.08)	0.94 ± 0.29 <0.05
PAR_{comp}	0.76 ± 0.87 (0.43)	1.54 ± 0.22 <0.01	Set to 0	1.27 ± 0.13 <0.001

Figure Legend

Figure 1. Graphical description of the light acquisition traits α, μ_{max} and PAR_{comp}

Figure 2. Species-specific growth-light relationships of the two dominant cyanobacteria (*Anabaena*, *Microcystis*) under **A)** constant and **B)** fluctuating light; and the two dominant diatoms (*Cyclotella*, *Aulacoseira*) under **C)** constant and **D)** fluctuating light.

Figure 3. Light-dependency of the relative biovolumes of *Anabaena* and *Microcystis* to the cyanobacteria biovolume **(A, B)** and of *Cyclotella* and *Aulacoseira* to the biovolume of diatoms **(C, D)** under constant **(A, C)** and fluctuating light **(B, D)**. Only relative biovolumes after 2 days of experiment are depicted.

Figure 4. Realized niches of the **A)** cyanobacteria and **B)** diatoms after 2 days and at the end of the experiments (crossed symbols) over gradients of daily PAR exposure (E m^{-2} d^{-1}) and mixing depth (m).

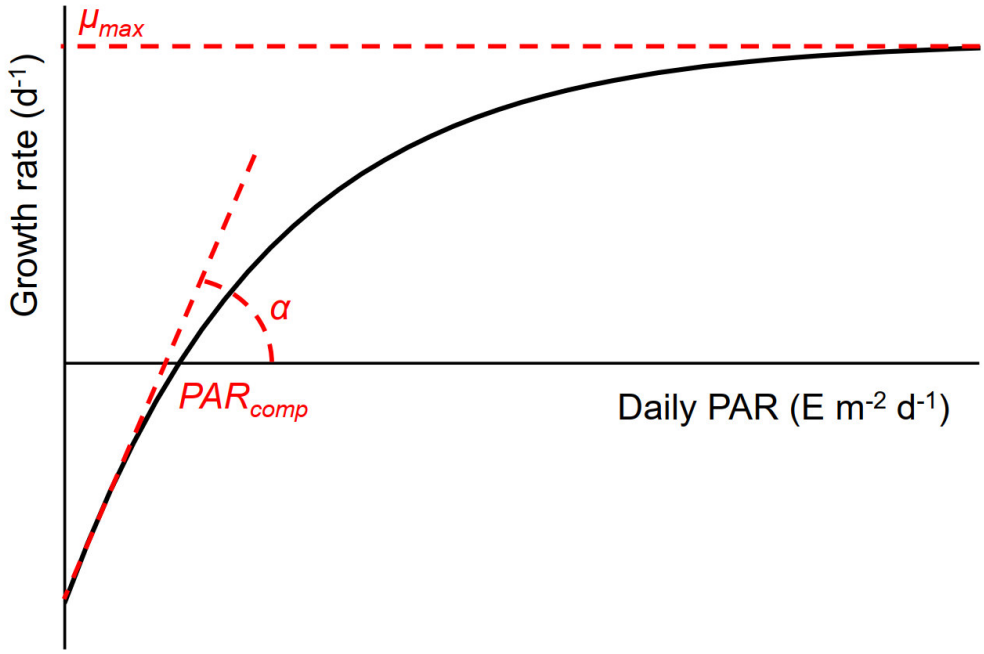


Figure 1

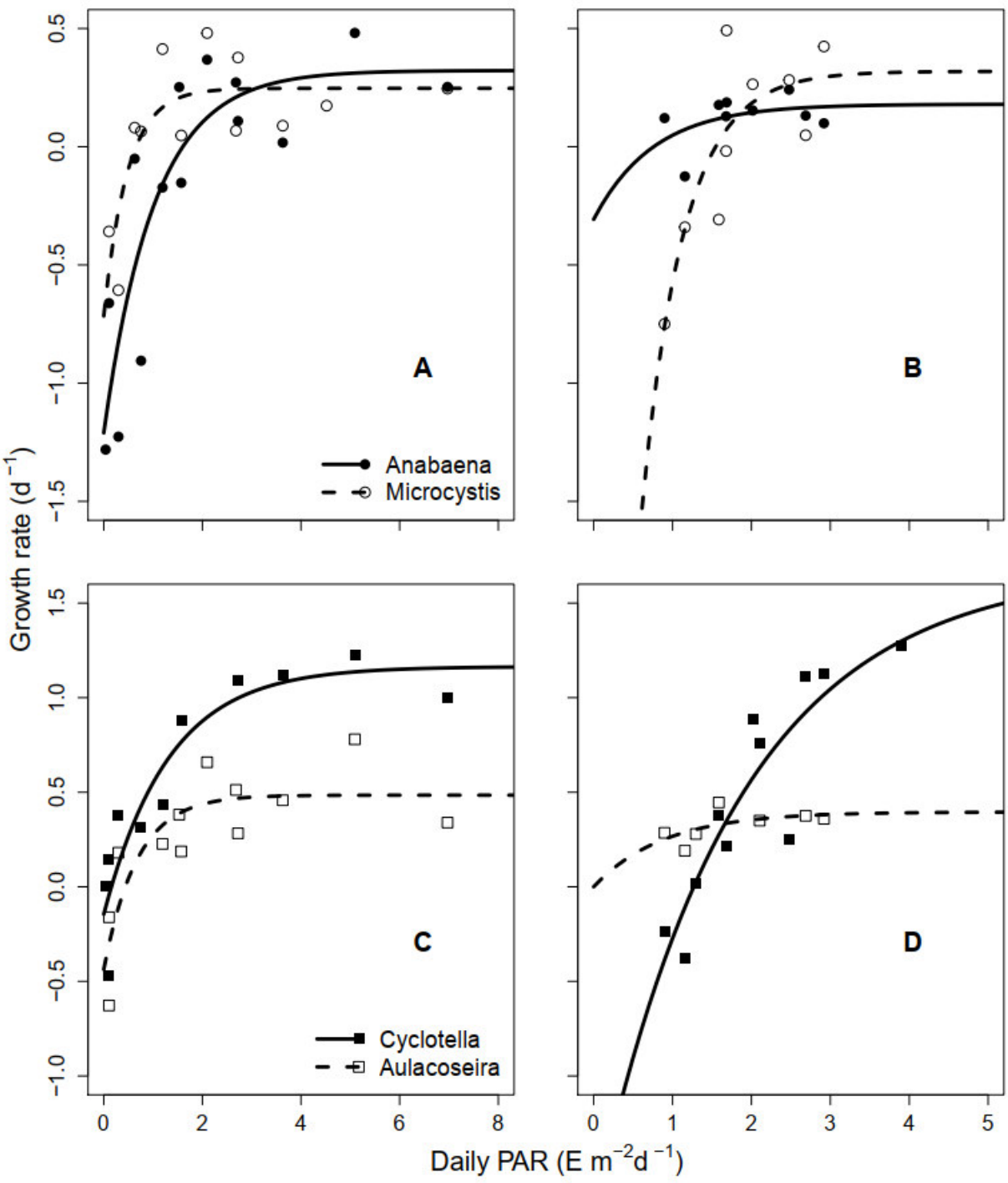

A
B
C
D
Anabaena
Microcystis
Cyclotella
Aulacoseira
Growth rate (d^{-1})
Daily PAR (E m^{-2}d^{-1})
0.5
0.0
−0.5
−1.0
−1.5
1.5
1.0
0
2
4
6
8
1
3
5

Figure 2

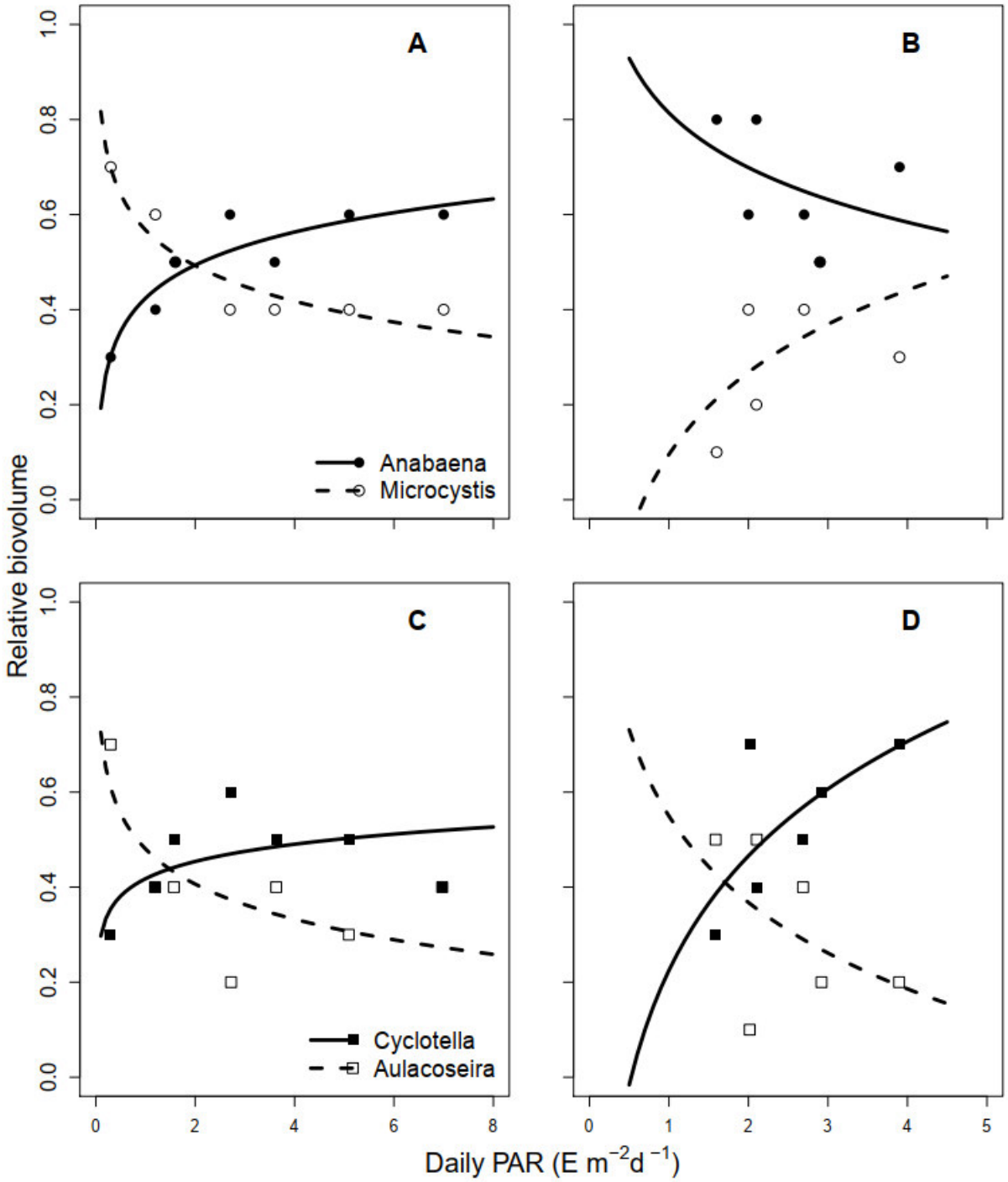

A
B
C
D
Anabaena
Microcystis
Cyclotella
Aulacoseira
Relative biovolume
Daily PAR (E m^{-2}d^{-1})
0.0
0.2
0.4
0.6
0.8
1.0
0
2
4
6
8
1
3
5

Figure 3

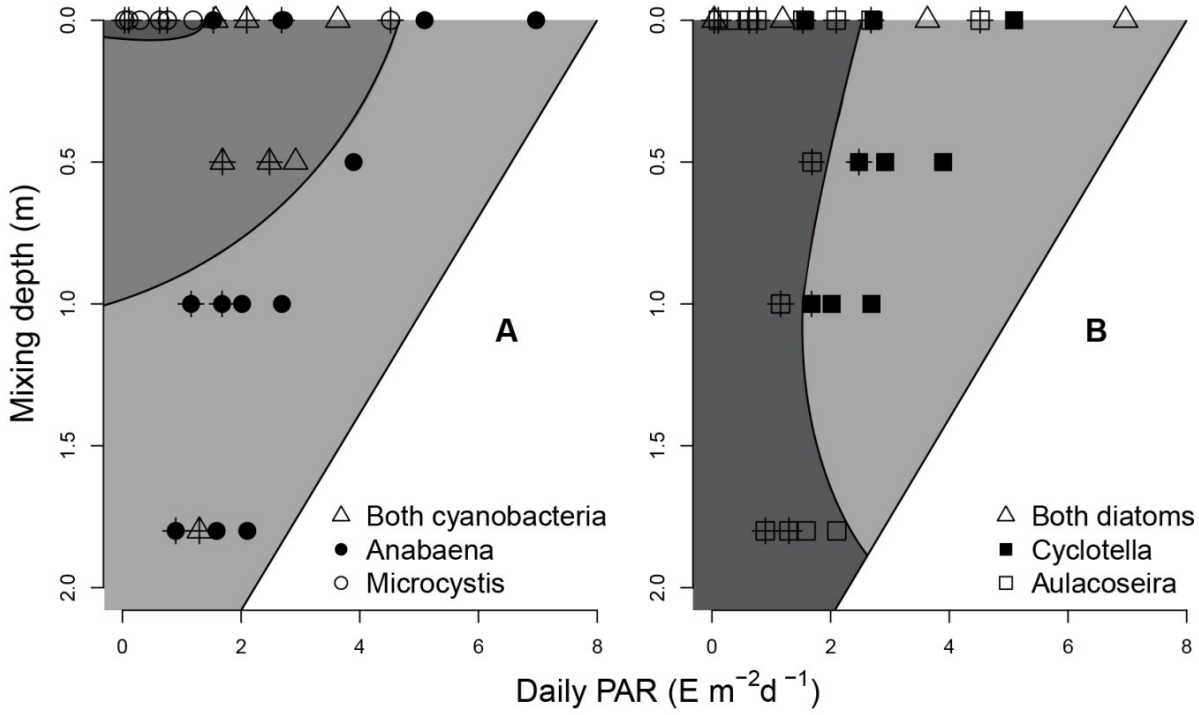

Mixing depth (m)
0.0
0.5
1.0
1.5
2.0
A
B
Both cyanobacteria
Anabaena
Microcystis
Both diatoms
Cyclotella
Aulacoseira
0
2
4
6
8
Daily PAR (E m^{-2}d^{-1})

Figure 4

Appendix-Table 1. Species composition of the isolated Lake TaiHu phytoplankton community during the experiment. *Chloro*: Chlorophyceae; *Bacill*: Bacillariophyceae; *Cyano*: Cyanophyceae; *Zygn*: Zygnematophyceae.

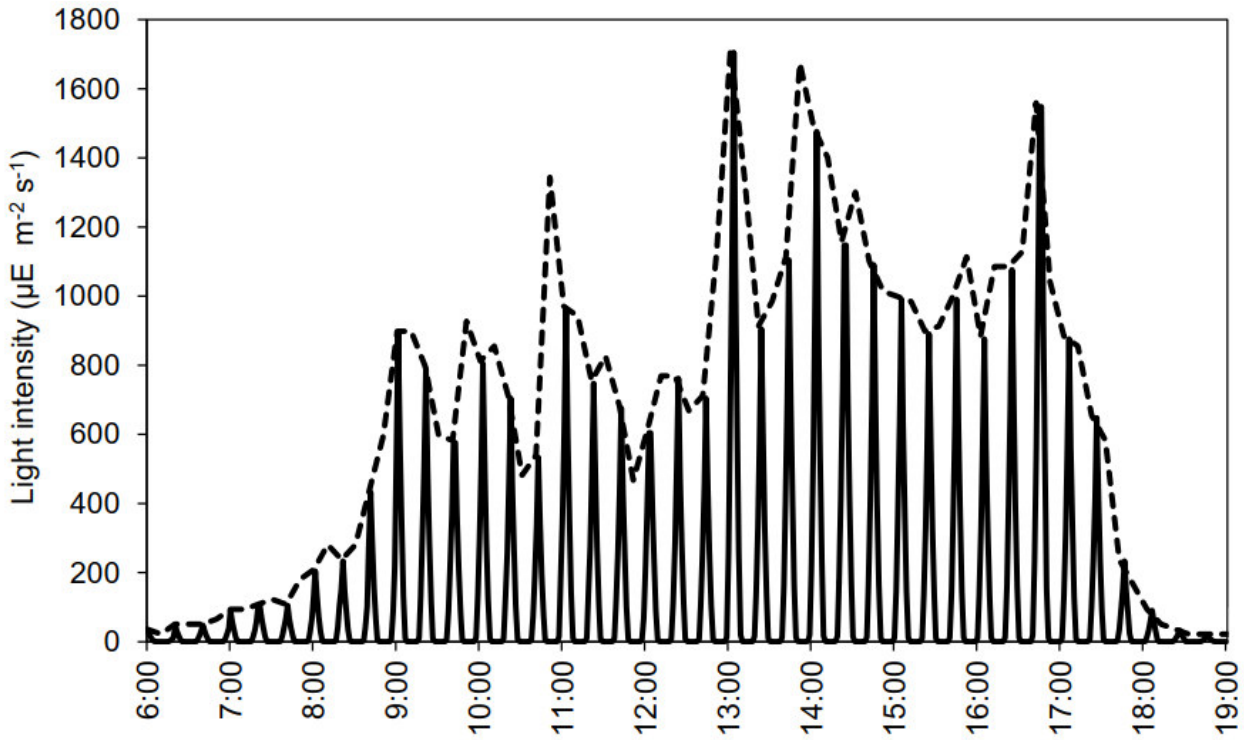
Class	Species
Chloro	*Actinastrum hantzschii*
-	*Coelastrum astroideum*
-	*Coelastrum microporum*
-	*Crucigenia fenestrata*
-	*Crucigenia quadrata*
-	*Crucigeniella apiculata*
-	*Didymocystis spec.*
-	*Elakatothrix spec.*
-	*Eudorina spec.*
-	*Lagerheimia ciliata*
-	*Lagerheimia wratislavensis*
-	*Micractinium pusillum*
-	*Monoraphidium arcuatum*
-	*Monoraphidium contortum*
-	*Monoraphidium griffithii*
-	*Oosystis spp.*
-	*Pediastrum boryanum*
-	*Pediastrum duplex*
-	*Pediastrum simplex*
-	*Pediastrum tetras*
-	*Planktonema (Binuk.) lauterbornii*
-	*Planktosphaeria gelatinosa*
-	*Raphidocelis spec.*
-	*Scenedesmus acuminatus*
-	*Scenedesmus bijuga*
-	*Scenedesmus communis*
-	*Scenedesmus falcatus*
-	*Scenedesmus intermedius*
-	*Scenedesmus maximus*
-	*Scenedesmus sempervirens*
-	*Scenedesmus serratus*
-	*Scenedesmus subspicatus*
-	*Scenedesnus spp*
-	*Schroederia indica*
-	*Schroederia setigera*
-	*Schroederia spec.*
-	*Tetraedron caudatum*
-	*Tetraedron minimum*
Bacill	*Aulacoseira granulata*
-	*Aulacoseira spp.*
-	*Cyclotella pseudostelligera*
-	*Nitzschia acicularis*
-	*Nitzschia fonticola*
-	*Nitzschia spp.*
Cyano	*Anabaena flos- aquae*
-	*Anabaena spec., gerade*
-	*Aphanizomenon issatschenkoi*
-	*Chroococcus turgidus*
-	*Geitlerinema unsure*
-	*Limnothrix spec.*
-	*Merismopedia spec*
-	*Microcystis spec.*
-	*Oscillatoria spp.*
-	*Planktothrix spp*
-	*Raphidiopsis curvata*
-	*Raphidiopsis spec.*
Zygn	*Closterium acutum v. variabile*

Appendix-Table 2. Daily photosynthetically active radiation (E m^{-2} d^{-1}) received by each treatment over the whole experiment period. Daily PAR exposure was corrected for shade, light attenuation of the lake, transmittance of the incubation bottles and vertical motion of moved algae.

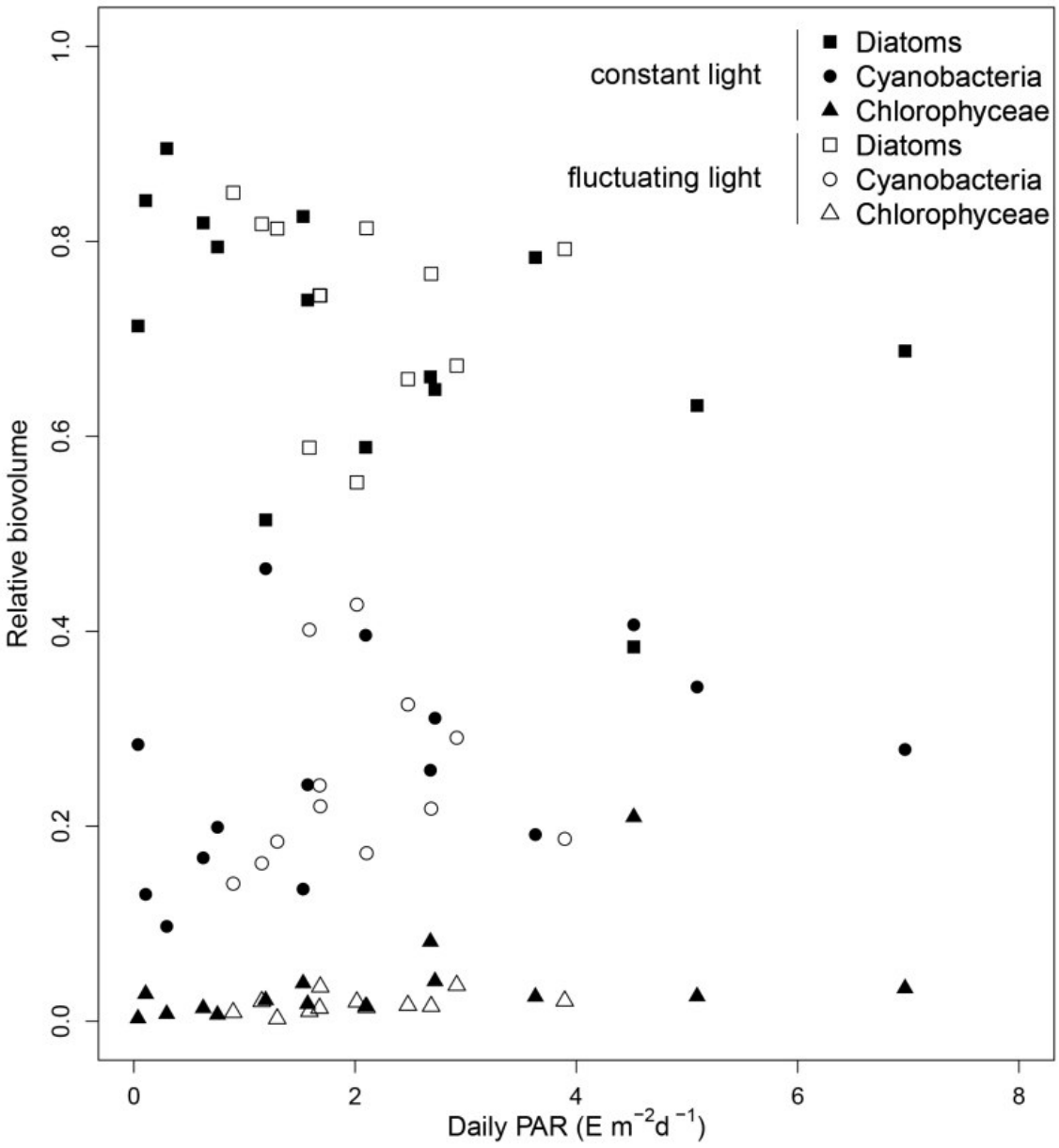
		0 - 0.5m		0 - 1m		0 - 1.8m	
	surface	Fixed	Moved	Fixed	Moved	Fixed	Moved
7 Sept	3.00	1.42	1.65	0.53	1.12	0.03	0.93
8 Sept	7.19	4.02	4.19	1.86	2.91	0.18	2.25
9 Sept	10.23	4.67	5.58	1.64	3.78	0.07	2.91
10 Sept	1.65	0.88	0.94	0.38	0.65	0.03	0.50
11 Sept	1.68	0.74	0.91	0.25	0.61	0.01	0.47
13 Sept	12.58	6.78	7.22	2.97	4.99	0.57	3.90
14 Sept	1.36	0.48	0.57	0.17	0.39	0.02	0.31
15 Sept	2.78	1.39	1.55	0.55	1.06	0.09	0.81
16 Sept	2.58	1.68	1.82	0.71	1.25	0.13	0.99
Average	4.78	2.45	2.71	1.01	1.86	0.13	1.45

Appendix-Table 3. Averaged relative contributions of the main phytoplankton groups to the total biovolume under constant and fluctuating light across the entire experimental period.

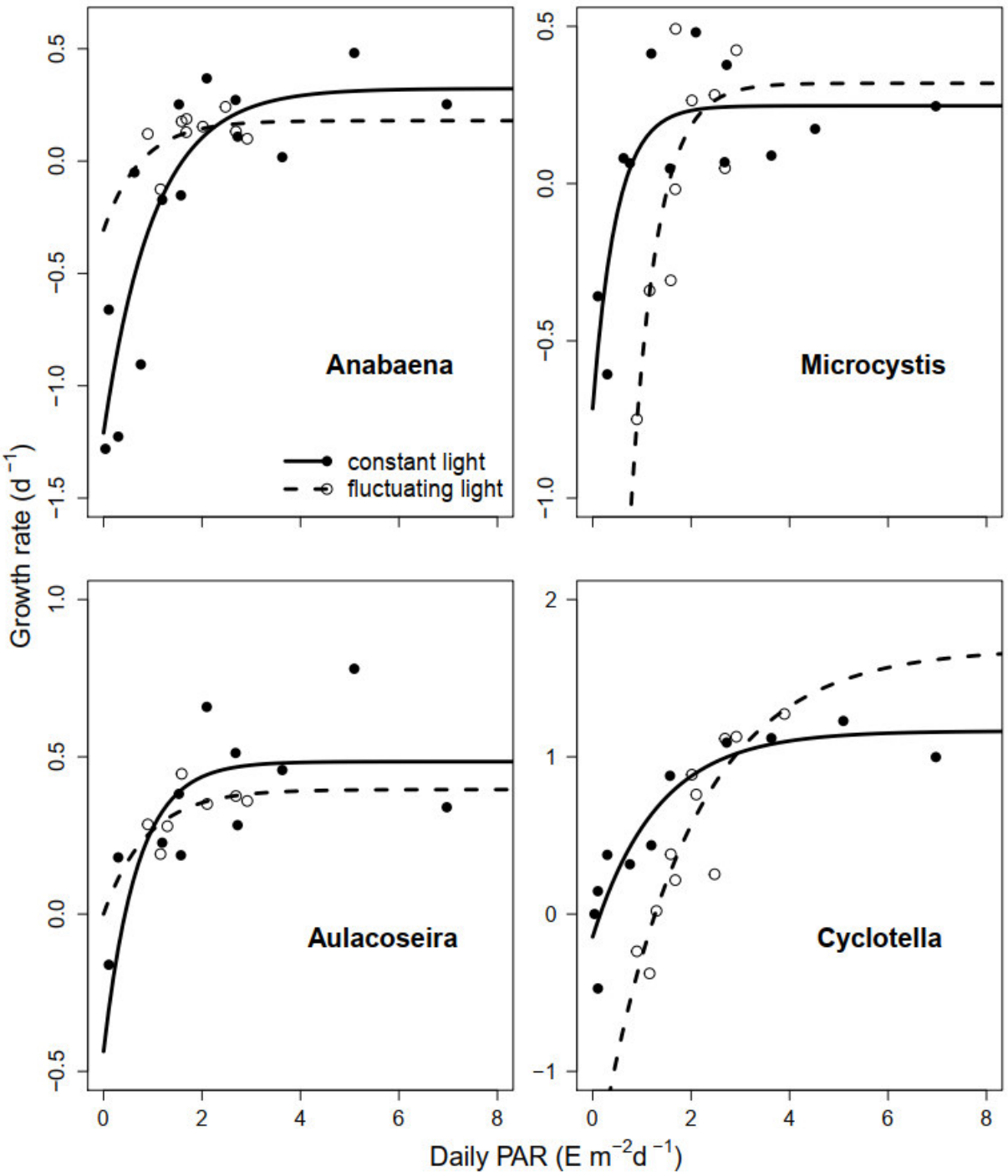
	Constant light			Fluctuating light		
	Cyanobacteria	Diatoms	Chlorophyceae	Cyanobacteria	Diatoms	Chlorophyceae
Minimal contribution	0.10	0.38	0	0.14	0.55	0
Maximal contribution	0.46	0.90	0.21	0.43	0.85	0.04
Mean ± Standard deviation	0.27 ± 0.11	0.69 ± 0.14	0.04 ± 0.05	0.25 ± 0.09	0.73 ± 0.1	0.02 ± 0.01



Appendix - Figure 1. Example of diurnal course of light intensity at the water surface (dotted line) and experienced by phytoplankton under complete water column mixing (0–1.8m) (full line) for the two extreme light supply treatments taken at the Lake station, 7th September 2016 (attenuation coefficient = 4.97m^{-1}). Phytoplankton received 3 E m^{-2} d^{-1} (100% PAR relative) at the surface versus 0.93 E m^{-2} d^{-1} (30.9% PAR relative) for the case of full over-turn.



Appendix - Figure 2. Light-dependency of the relative biovolumes of diatoms, cyanobacteria and chlorophyceae to the total biovolume, under fluctuating (open symbols) and constant light (closed symbols). Averages over [day 0 - day 1] and [day 2 – end experiment] represented the relative contributions at day 2 and at the end of the experiment respectively.



Appendix - Figure 3. Species-specific growth-light relationships of *Anabaena flos-aquae*, *Microcystis spp*., *Aulacoseira granulata* and *Cyclotella pseudostelligera* under fluctuating and constant light.