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Responses of phytoplankton community dynamics to reduced underwater light in spring

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Abstract Air pollution and lake eutrophication have led to a reduction in incident total radiation and water transparency in many lakes, resulting in a decrease in available underwater light. This reduction in available light depends significantly on the dynamics of spring phytoplankton communities. However, the process and mechanisms behind these effects are not yet well understood. In this study, we conducted a field mesocosm experiment to observe the responses of the phytoplankton community to varying levels of light intensity (100%, 85%, and 65% photosynthetically active radiation, PAR). Our study revealed that reducing PAR resulted in an earlier peak of cyanobacterial biomass in spring, while the biomass of chlorophytes and bacillariophytes declined with decreasing light intensity. The weakening of light intensity promoted the recovery of photosynthetic activity in cyanobacteria but reduced the photosynthetic activity in chlorophytes and bacillariophytes. Additionally, the decrease in light intensity reduced the diversity of phytoplankton communities, accelerating the rate of species turnover. However, the rate of species turnover slowed down as the dominance of cyanobacteria was established in the later stages of the experiment. Therefore, the weakening of light intensity is beneficial to the early establishment of the dominance of cyanobacteria in the phytoplankton community structure, accelerating the succession process of phytoplankton community. These findings contribute to the exploration of the effects of reduced light intensity on the establishment of cyanobacterial dominance in spring, providing valuable insights for the management of lake ecosystems.

Keywords Phytoplankton · Cyanobacteria · Reduced underwater light · Turnover

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Introduction

Climate change and human activities have resulted in two-thirds of the globally recorded long-term species exhibiting earlier spring phenology. This has caused alterations in the distribution range, seasonal

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dynamics, and composition of species in freshwater ecosystems (IPCC 2022). Phytoplankton is highly sensitive to changes in the environment. While temperature is considered the primary factor driving phytoplankton succession in spring, light plays a more important role in regulating the phytoplankton biomass or spring blooms (Sommer and Lewandowska 2010). Temperature is a well-established factor that influences the growth and distribution of phytoplankton during spring. However, the effects of light and temperature on phytoplankton growth and distribution are often intertwined, making it challenging to separate their respective impacts in field studies. Consequently, the role of light in the succession of spring phytoplankton communities is not yet fully understood.

Light is a crucial factor that directly affects the growth and productivity of phytoplankton by influencing photosynthesis. The efficiency of photosynthesis is largely determined by the intensity of light, which can further affect the biomass and biological activity of phytoplankton (Gao et al. 2019). However, in the last 60 years, there has been a global trend of radiation dimming, which has caused a decline of 4% to 6% in surface total radiation due to air pollution and increased aerosols from human activities (Wild et al. 2009; Yang et al. 2018). Additionally, the increase in phytoplankton biomass resulting from eutrophication, particularly in bacillariophytes or filamentous cyanobacteria during spring, can further reduce water clarity and enhance light attenuation (Zhang et al. 2018). As a result, the availability of underwater light has been greatly reduced in aquatic ecosystems due to the long-term decrease in incident total radiation and water clarity (Zhang et al. 2020).

Light is the primary energy source for the growth of phytoplankton. The intensity and photoperiod of light affect the amounts of photosynthetic products, thereby influencing the growth of phytoplankton (Happer 1992; Anderson et al. 1997). Different algae have different requirements for light, and appropriate light intensity can improve the light use efficiency of phytoplankton and promote their growth (Guo 2010). Differences in light conditions can also lead to vertical migration and changes in community structure (Zeng et al. 2014). When light intensity weakens, the synthesis of chlorophyll and photosynthetic pigments in Chlorophyta and Bacillariophyta is affected, reducing their light use efficiency. This leads to a slowdown in organic synthesis in cells, thereby affecting their growth and reproduction (Huisman et al. 1999). However, most of cyanobacteria can move vertically in the water by adjusting their own buoyancy and choosing a suitable water layer for living (Šesták et al. 2001). In addition, cyanobacteria have a lower chlorophyll content but larger light absorption cross-sectional area, adjustable photosynthetic pigment composition, special chloroplast morphology and arrangement, and the ability to adapt to different light environments. As a result, changes in light intensity may sometimes have less effect on cyanobacteria than other phytoplankton (Brauer et al. 2012; Gaskill et al. 2020). Therefore, reducing the underwater available light may lead to cyanobacteria dominating in eutrophic lakes, resulting in ecological imbalances (Zhang et al. 2022).

Light intensity not only directly affects algal growth but also plays a crucial role in biomass, community diversity, and species succession (Reynolds 2006; Edwards et al. 2013). Manipulating light conditions is a commonly used technique to study the relationship between light and phytoplankton community dynamics. Shading treatment is a popular method in this regard. Kojima et al. developed the "partial shading method" and discovered that when the shading area exceeded 30%, the growth of cyanobacteria was inhibited. Further, when the shading area exceeded 60%, the biomass of phytoplankton decreased significantly (Kojima 2000). Hence, reducing the available light resources can significantly affect the biomass of phytoplankton (Chen et al. 2009). Environmental factors such as light intensity have a crucial role to play in determining the biodiversity of phytoplankton, including the number and abundance of different species, as well as their interactions. Some indoor studies found that the biomass of phytoplankton reached its lowest point, and the community diversity was at its maximum at a specific light intensity (Yan et al. 2018). Phytoplankton community evolved toward algae species that were tolerant to environmental stress along a decreasing light gradient (Gong et al. 2020). Hence, light intensity can directly impact the survival, reproduction, and interaction of species and is an important factor in altering community structure and species composition.

In this study, we put forward the hypothesis that a decrease in underwater light will result in a variation

of phytoplankton composition, leading to a higher dominance of cyanobacteria and a subsequent decline in phytoplankton diversity. This, in turn, will accelerate the succession process of phytoplankton community. To test this hypothesis, we conducted a field mesocosm experiment under different light intensities to explore the impact of reduced underwater light (100%, 85%, and 65% photosynthetically active radiation levels) on the establishment of cyanobacterial dominance and the dynamic changes in the structure of the spring phytoplankton community.

Methods

Mesocosm experiment

The mesocosm experiment with light manipulation was conducted at the Taihu Laboratory for Lake Ecosystem Research (CERN TLLER) and started on April 1, 2013, and ended on May 17, 2013, during recovering and growing period of phytoplankton. In this experiment, 150 L of water samples was taken from Lake Taihu. To remove large zooplankton, the water samples were filtered through a nylon sieve with 64-μm mesh size before the water samples were placed in plastic tanks (70 cm in height and 58 cm in inner diameter). And these tanks were suspended in a concrete pond (7 m long × 6 m wide × 2 m deep) serving as a water bath to reduce daily temperature fluctuation. The treatment groups of three photosynthetically active radiation (PAR) gradients were formed by shielding the tanks with white gauze, establishing 100% PAR (no white gauze shielding), 85% PAR (one layer of white gauze shielding), 65% PAR (two layers of white gauze shielding). Three replicates were established for each treatment group, and the underwater light intensity was measured using a LI-1400 quantum meter at 8:00, 13:00, and 17:00 every day to determine the average light intensity that reached the water surface.

During the treatment, all mesocosms were left open to allow rainwater to enter. As evaporation rates varied between the mesocosms, deionized water was added every 2–3 days to maintain the same water level in all tanks. Nutrient concentrations were monitored in each tank every other day, and the levels of nitrogen and phosphorus were recorded. Prompt adjustments were made to the nutrient levels by adding KH_2PO_4, NH_4Cl, and $NaNO_3$ as necessary, in order to maintain their relative stability and consistency with the initial status and to minimize the interference of external factors on experimental results. To prevent microorganisms from adhering to the inside walls of the tanks, gentle brushing was performed at 6:30 p.m. every day, except for the tank bottoms.

Sample collection and analyses

Water temperature and pH were measured in each tank using a multiparameter water quality analyzer (HORIBA multi-parameter water quality analyzer U-53). One liter of mixing water was collected from each tank for laboratory analyses. The water samples were filtered using a Whatman GF/C glass-fiber filter membrane with an aperture size of 1.2 μm for the dissolved nutrients before these analyses. The concentrations of total nitrogen (TN, unfiltered), dissolved total nitrogen (DTN), total phosphorus (TP, unfiltered), and dissolved total phosphorus (DTP) were determined after thawing with the use of a combined persulfate digestion, followed by the spectrophotometric analysis. The detection limits for phosphorus (TP and DTP) and nitrogen (TN and DTN) are 0.01 mg/L and 0.05 mg/L, respectively. Nitrate (NO^{3-}) and nitrite (NO^{2-}) were measured using a continuous flow analyzer with a detection limit of 0.07 mg/L (Skalar SA 1000, Breda, The Netherlands).

Phytoplankton samples of 500 mL were collected approximately every 6 days and fixed with 5 mL of acid Lugol's solution. Species or genus identification was performed using the most recent literature (Hu and Wei 2006). Counts were conducted in random fields (more than 30 fields) in sedimentation chambers (30 mL) using an inverted microscope according to the criteria established by Utermöhl (1958). Biovolume was calculated using the method developed by Hillebrand et al. (1999), while biomass was estimated based on the algal volume in each sample and converted to fresh weight assuming a specific gravity of 1 g/cm.^{3}

The maximum optical quantum yield (F_v/F_m) reflects the efficiency of excitation and capture in the reaction center of photosystem II (PSII) and is used to evaluate the distribution ratio of energy in the center of optical system responses, as established by Genty et al. (1989) and Falkowski and Kolber (1993). Although it has been shown in

studies that this ratio does not have a completely linear relationship with the capacity for photosynthesis (Andersen et al. 1997), it is still commonly used to characterize the maximum photosynthetic capacity of PSII (Falkowski and Kolber 1995). The effective quantum yield (F_v'/F_m') is the effective photochemical quantum yield of PSII, which reflects the efficiency of primary light energy capture by open PSII reaction centers. The two indices were measured using a Phyto-PAM fluorometer (Walz, Effeltrich, Germany) equipped with a Phyto-ED emitter–detector unit following the protocol described in a previous study (Guan et al. 2020). The measurements were taken in the same environment as the samples grew, after a 15-min dark adaptation. F_0 is the fluorescence yield of all the reaction centers in PSII when they are fully open, and can be immediately measured using weak probe light after a period of dark adaptation. F_m is the maximum fluorescence signal emitted by all the closed reaction centers of PSII in the dark-adapted state. F_m' is the maximum fluorescence yield of PSII in the light-adapted state, when the reaction centers are open and dynamic equilibrium is maintained. The measurements were measured by a 600-ms pulse of saturating irradiance. F_t was the current instantaneous fluorescence signal in the light-adapted steady state. The fluorescence parameters were calculated using the following equations. The blank fluorescence value was obtained by measuring the fluorescence of a 0.22-μm filtered sample.

$$F_v/F_m = \left(F_m - F_0\right)/F_m$$
$$F_v'/F_m' = \left(F_m' - F_t\right)/F_m'$$

In addition, Phyto-PAM fluorometry is capable of distinguishing different pigmented phytoplankton groups, such as cyanobacteria, chlorophytes, and diatoms/dinoflagellates, by utilizing four distinct excitation wavelengths (665, 645, 520, and 470 nm). This approach enables the independent measurement of the fluorescence signals of each phytoplankton group in a mixed sample.

Calculating species diversity

To evaluate different aspects of species diversity, we used species richness and Pielou's evenness index to assess the number of species and the biomass differences among different species. We also used Simpson's index (Simpson 1949) and Shannon–Wiener index (Shannon and Weaver 1949) to assess the diversity and complexity of community species. Additionally, we used the dominance index to evaluate the dominant species of the community, where a species with a relative abundance of $Y \geq 0.02$ is considered dominant (Sun et al. 2006; Xu and Shen 1995).

Species richness:

$$R = \frac{S-1}{\ln N} \tag{1}$$

Pielou's evenness index:

$$J = \frac{H'}{\ln S} \tag{2}$$

Simpson's index:

$$D = 1 - \sum_{i=1}^{S} P_i^2 \tag{3}$$

Shannon–Wiener index:

$$H' = -\sum_{i=1}^{S} P_i \ln P_i \tag{4}$$

Dominance index:

$$Y = \left(\frac{N_i}{N}\right) f_i \tag{5}$$

where S is the total number in the community and N is the sum of the number of individuals of all species in the community, P_i is the proportion of the number of individuals of species i to the total number of individuals in the community, f_i is the percentage of the quadrat number of species i in the total quadrat number.

Calculating community turnover rate

The concept of turnover refers to the idea that when species are in a dynamic equilibrium state, the total number of species will remain relatively stable over time, but the species composition will change (MacArthur and Wilson 1963; Diamond 1969; Collins et al. 2008). We calculated turnover using the turnover function in the Codyn package with R (Hallett et al. 2016), which includes three metrics: total

turnover, appearances, and disappearances. The formula for calculating the total species turnover rate is as follows:

$$\text{Total turnover} = \frac{\text{appearances} + \text{disappearances}}{\text{Total species observed in both timepoints}} \quad (6)$$

"appearances" refer to the number of new or immigrated species in an ecosystem during a certain time period. "disappearances" refer to the number of species that disappeared or emigrated from the ecosystem during the same time period. "Total species observed in both timepoints" is the total number of species present in the ecosystem at two time points.

Mean rank shifts (MRS) represent the relative change in species rank abundance and indicate the change in relative abundance over time (Collins et al. 2008). We calculated MRS using the *rank_shift* function as:

$$\text{MRS} = \sum_{i=1}^{N} \frac{|R_{i,t+1} - R_{i,t}|}{N} \quad (7)$$

where N is the number of species in common in both time points, t is the time point, and $R_{i,t}$ is the relative rank of species i at time t. The analyses were performed in the R environment (version 4.2.1, R Core Team, 2020).

Data analysis

The mean values and ranges of environmental parameters and nutrients in the collected water samples were calculated and are presented in Table 1. Differences in these variables among groups were compared using Tukey's HSD post hoc test, with statistical significance considered at $p < 0.05$. Prior to analysis, the data were $\log_{10}x$ or $\log_{10}(x+1)$ (if a value of zero occurred) transformed to meet assumptions of normality or homogeneity of variance. No significant differences were found in the environmental parameters and nutrient concentrations among the three experimental groups ($n = 12$, $p > 0.05$). The statistical analysis was performed using SPSS 26.0 (SPSS, Chicago, Illinois, USA) for Windows. The time changes in the metrics indicating biomass, photochemical efficiency, diversity, and changes in community were also tested with Tukey's HSD post hoc test by comparing the significance of adjacent data. We employed a generalized linear mixed model (GLMM) to account for the respective and combined effects of light treatment and time on total and taxonomic group biomass, diversity indices, and community turnover rate. The sampling time was considered as the repeated-measures variable in the models. The fixed effects in our analysis were the light treatments (100%, 85%, and 65% PAR levels), while the group numbers of these treatments were entered as random variables. We conducted this analysis using the Statsmodels package in Python 3.9.

Results

Responses of phytoplankton biomass to declining PAR

The biomass of phytoplankton in the three groups gradually increased over time with an average biomass of 74.62 mg/L and was significantly affected by the declining underwater light ($p < 0.001$, Table 2). The phytoplankton biomass in the 65% PAR group

Table 1 Environmental parameters summarized as the mean values (minimum–maximum value) in the mesocosms from April 2013 to May 2013

	100% PAR	85% PAR	65% PAR
PAR (μmol m^{-2} s^{-1})	629.9 (62.0–1066.0)	535.4 (52.7–906.1)	409.4 (40.3–692.9)
Temperature (°C)	19.0 (12.3–26.0)	19.0 (12.3–26.0)	19.0 (12.3–26.0)
pH	8.70 (8.16–9.52)	8.61 (8.06–9.39)	8.70 (8.16–9.55)
TN (mg/l)	4.56 (3.09–7.22)	4.52 (3.02–7.20)	4.51 (3.02–7.14)
DTN (mg/l)	3.51 (2.74–5.17)	3.47 (2.59–5.16)	3.45 (2.53–5.18)
NO_3^- (mg/l)	1.23 (0.74–1.70)	1.23 (0.77–1.70)	1.21 (0.74–1.70)
NO_2^- (mg/l)	0.10 (0.03–0.24)	0.10 (0.03–0.26)	0.10 (0.03–0.25)
DTP (mg/l)	0.03 (0.01–0.07)	0.03 (0.01–0.07)	0.03 (0.01–0.07)
TP (mg/l)	0.11 (0.03–0.28)	0.11 (0.03–0.25)	0.11 (0.03–0.25)

TN total nitrogen, NO_3^- nitrate nitrogen, NO_2^- nitrite nitrogen, *TP* total phosphorus, *DTP* dissolved total phosphorus

reached an earlier and higher peak compared to the other groups. Specifically, the maximum biomass of phytoplankton in the 65% PAR group occurred on the 35th day, reaching 278 mg/L. On the other hand, in the 85% and 100% PAR groups, the maximum biomass was 165 mg/L and 267 mg/L, respectively, and occurred on the 41st day (Fig. 1).

At the outset of the experiment, the dominant species of phytoplankton were bacillariophytes, dinoflagellates, and some species of Euglena. However, in the middle of the experiment, cyanobacteria showed a recovery in growth and gradually replaced bacillariophytes and other algae to become the dominant species. During the later stage of the experiment, the biomass of Chlorophyta in the 100% PAR group was significantly higher than that in the other two groups ($p < 0.05$). On the other hand, the phytoplankton community in the 65% and 85% PAR groups was dominated by cyanobacteria.

The results showed that there were 21 dominant species totally in the study system, including 7 species of cyanobacteria, 12 species of Chlorophyta, and 2 species of Bacillariophyta. In the 100% PAR group, there were 7 dominant species of cyanobacteria, 12 dominant species of Chlorophyta, and 2 dominant species of Bacillariophyta. *Microcystis* in Cyanophyta has the highest dominance value of 3.206. In the 85% PAR group, there were 5 dominant species of cyanobacteria, 10 dominant species of Chlorophyta, and no dominant species of Bacillariophyta. *Pseudanabaena* in Cyanophyta has the highest dominance value of 2.707. In the 65% PAR group, there were 5 dominant species of cyanobacteria, 4 dominant species of Chlorophyta, and no dominant species of Bacillariophyta. *Pseudanabaena* still has the highest dominance value of 4.615. Furthermore, the types and numbers of dominant species of Chlorophyta and Bacillariophyta were found to decrease with decreasing light intensity (Table 3). The dominant cyanobacteria observed were *Microcystis*, *Pseudanabaena*, *Dolichospermum*, and *Aphanizomenon*, which exhibited higher dominance values. In the 100% PAR group, the biomass of *Microcystis* remained consistently the highest. However, in the 85% and 65% PAR groups, the biomass of *Aphanizomenon* and *Pseudanabaena* was higher than that of *Microcystis*, showing a trend of initially increasing and then decreasing (Fig. 2).

Photosynthetic responses to declining PAR

At the start of the experiment, the F_v/F_m values of cyanobacteria were low in all three groups. However, they increased rapidly from the 29th day in the 65% and 85% PAR groups. In contrast, F_v/F_m values in the 100% PAR group remained low throughout the entire experiment. The F_v/F_m values of Chlorophyta increased earlier than those of cyanobacteria. The F_v/F_m values of Chlorophyta in the 100% PAR group consistently increased and reached a maximum value of 0.56 on the 47th day. In contrast, the F_v/F_m values of Chlorophyta in the 65% and 85% PAR groups decreased since the 29th day. The F_v/F_m values of Bacillariophyta did not differ significantly among the three groups ($p > 0.05$). Moreover, the effective photosynthetic activity of Bacillariophyta was lower than their maximum photosynthetic activity and followed a similar pattern in all three groups (Fig. 3).

Responses of phytoplankton community dynamic to declining PAR

The decreasing light did not have a significant impact on the phytoplankton richness, except during the initial stage of the experiment. However, it did result in a decrease in Pielou's evenness index, Simpson index, and Shannon–Wiener index after the 30th day of the experiment ($p < 0.05$, Fig. 4; Table 2). Moreover, the declining underwater light led to a decrease in the turnover rate of the phytoplankton community, particularly in terms of the total turnover ($p = 0.038$) and disappearance metrics ($p = 0.046$, Fig. 5, Table 2). There was no significant effect observed on the metrics of appearance and MRS ($p > 0.05$).

Discussion

Responses of phytoplankton biomass and photosynthesis to declining PAR

Our findings suggest that the reduction of PAR results in an earlier peak in cyanobacterial biomass during the spring. This is particularly crucial as it can affect the timing and magnitude of the summer cyanobacterial bloom. The timing of the spring cyanobacterial biomass peak is influenced by a multitude of factors,

Table 2 Results of generalized linear mixed model (GLMM) for phytoplankton total and taxonomic group biomass, diversity indices and community turnover rate, using PAR treatment as between-subject factor and day in the experiment (time) as within-subject factor

	Effect	Type III sum of squares	*df*	Mean square	*F*	*P*
Total biomass	Corrected model	430,467.408[a]	26	16,556.439	4.98	< 0.001
	Intercept	386,987.45	1	386,987.45	116.398	< 0.001
	Time	2890.063	2	1445.032	0.414	0.663
	PAR	380,712.024	8	47,589.003	14.313	**< 0.001**
	Time × PAR	47,029.534	16	2939.346	0.884	0.590
Cyano-bacterial biomass	Corrected model	122,875.657[b]	26	4725.987	5.269	< 0.001
	Intercept	59,068.617	1	59,068.617	65.851	< 0.001
	Time	89,821.564	8	11,227.696	12.517	**< 0.001**
	PAR	3254.516	2	1627.258	1.814	0.173
	Time × PAR	29,799.577	16	1862.474	2.076	**0.024**
Richness	Corrected model	1267.354[c]	26	48.744	3.071	< 0.001
	Intercept	31,968.194	1	31,968.194	2013.844	< 0.001
	Time	20.887	2	10.443	0.737	0.483
	PAR	932.122	8	116.515	7.454	**< 0.001**
	Time × PAR	297.308	16	18.582	1.171	0.321
Evenness	Corrected model	3.023[d]	26	0.116	18.187	< 0.001
	Intercept	30.296	1	30.296	4738.64	< 0.001
	Time	0.164	2	0.082	12.744	**< 0.001**
	PAR	2.341	8	0.293	46.298	**< 0.001**
	Time × PAR	0.492	16	0.031	4.812	**< 0.001**
Simpson	Corrected model	2.937[e]	26	0.113	11.033	< 0.001
	Intercept	39.906	1	39.906	3897.593	< 0.001
	Time	1.883	8	0.238	23.24	**< 0.001**
	PAR	0.224	2	0.112	10.959	**< 0.001**
	Time × PAR	0.809	16	0.051	4.939	**< 0.001**
Shannon	Corrected model	25.167[f]	26	0.968	13.261	< 0.001
	Intercept	261.503	1	261.503	3582.528	< 0.001
	Time	1.362	2	0.681	9.34	**< 0.001**
	PAR	18.449	8	2.306	31.759	**< 0.001**
	Time × PAR	5.258	16	0.329	4.502	**< 0.001**
Total turnover	Corrected model	1.265[g]	23	0.055	12.027	< 0.001
	Intercept	20.658	1	20.658	4518.479	< 0.001
	Time	1.148	7	0.164	35.884	**< 0.001**
	PAR	0.032	2	0.016	3.51	**0.038**
	Time × PAR	0.088	14	0.006	1.378	0.202
Mean rank shifts	Corrected model	898.289[h]	23	39.056	2.818	< 0.001
	Intercept	7684.747	1	7684.747	554.553	< 0.001
	Time	735.869	7	105.124	7.586	**< 0.001**
	PAR	6.154	2	3.077	0.222	0.802
	Time × PAR	137.804	14	9.843	0.71	0.753

Significant values of factors ($P < 0.05$) are in bold type

[a] $R^2 = 0.710$ (adjusted $R^2 = 0.567$)

[b] $R^2 = 0.717$ (adjusted $R^2 = 0.581$)

[c] $R^2 = 0.601$ (adjusted $R^2 = 0.405$)

[d] $R^2 = 0.899$ (adjusted $R^2 = 0.850$)

[e] $R^2 = 0.844$ (adjusted $R^2 = 0.768$)

[f] $R^2 = 0.867$ (adjusted $R^2 = 0.801$)

[g] $R^2 = 0.855$ (adjusted $R^2 = 0.784$)

[h] $R^2 = 0.580$ (adjusted $R^2 = 0.374$)

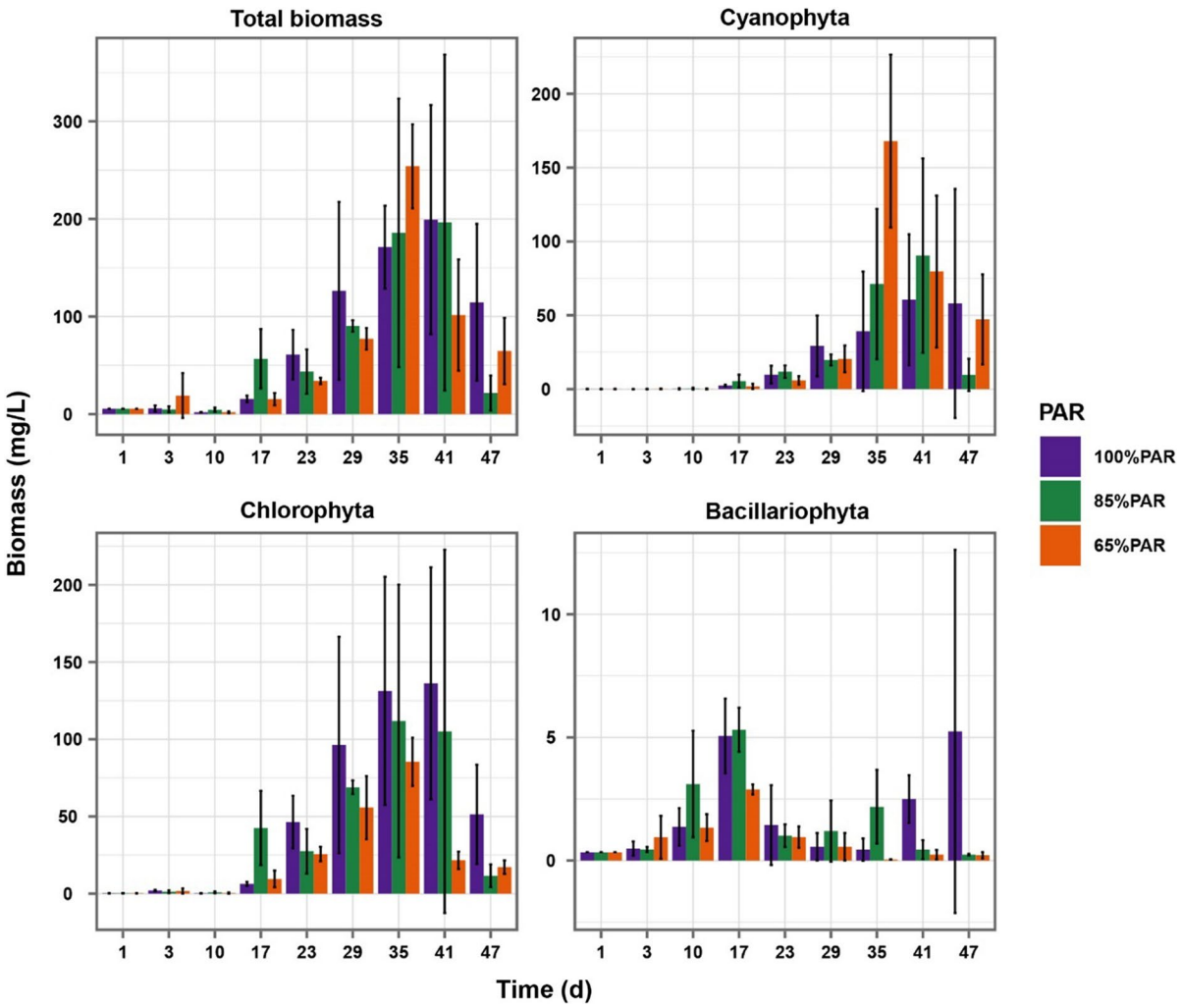

Fig. 1 Under different light conditions (100% PAR group in purple, 85% PAR group in green, 65% PAR group in orange), the variations in total phytoplankton and taxonomic biomass (mean ± sd) along the experiment days

such as water temperature, nutrient availability, and the availability of light (Lewandowska and Sommer 2010; Sommer and Lengfellner 2008; Sommer et al. 2012). Our previous studies have shown that the advancement of the spring timing is influenced not only by relatively high temperatures but also by relatively low light intensity (Zhang et al. 2022). This result is consistent with the findings of previous studies.

Cyanobacteria are known for their adaptability to a wide range of light intensities, including low light conditions (Scheffer et al. 1997; Kong and Gao 2005). To thrive in low light environments, cyanobacteria have evolved diverse mechanisms to optimize their photosynthesis and energy utilization. One mechanism that cyanobacteria use to optimize their photosynthesis and energy use in low light environments is by adjusting their pigmentation in response to changes in light intensity (Zheng et al. 2021). Cyanobacteria have evolved various pigments that can absorb different wavelengths of light, including chlorophyll a, phycocyanin, and phycoerythrin, in order to adapt to changes in light intensity (Cao et al. 2020). When the light intensity is low, cyanobacteria increase the production of pigments such as phycocyanin and phycoerythrin. This allows them to absorb light more efficiently and carry out photosynthesis even under low light conditions (Falkowski and

Table 3 Dominance index values of dominant genus in Cyanophyta, Chlorophyta, and Bacillariophyta under different light conditions

Division	Dominant genus	100%PAR	85%PAR	65%PAR
Cyanophyta	*Microcystis*	3.206	1.370	0.569
	Pseudanabaena	0.271	2.707	4.615
	Dactylococcopsis	0.069	0.075	0.027
	Dolichospermum	0.026	0	0
	Aphanocapsa	0.173	0.125	0.155
	Aphanizomenon	0.133	0.224	0.142
	Merismopedia	0.029	0	0
Chlorophyta	*Scenedesmus*	0.214	0.106	0.021
	Scenedesmus	0.052	0.039	0
	Chlorella	0.700	0.734	0.091
	Chlamydomonas	0.907	0.218	0.046
	Crucigenia	0.085	0.023	0
	Selenastrum	0.055	0.035	0
	Planctonema	0.053	0.066	0
	Dictyosphaerium	0.297	0.096	0.092
	Kirchneriella	0.037	0.023	0
	Oocystis	0.040	0	0
	Actinastrum	0.041	0	0
	Mougeotia	0.029	0.081	0
Bacillariophyta	*Cyclotella*	0.027	0	0
	Synedra	0.039	0	0

A dominance index of ≥ 0.02 indicates a dominant genus, while a dominance index of > 0.1 indicates an absolutely dominant species

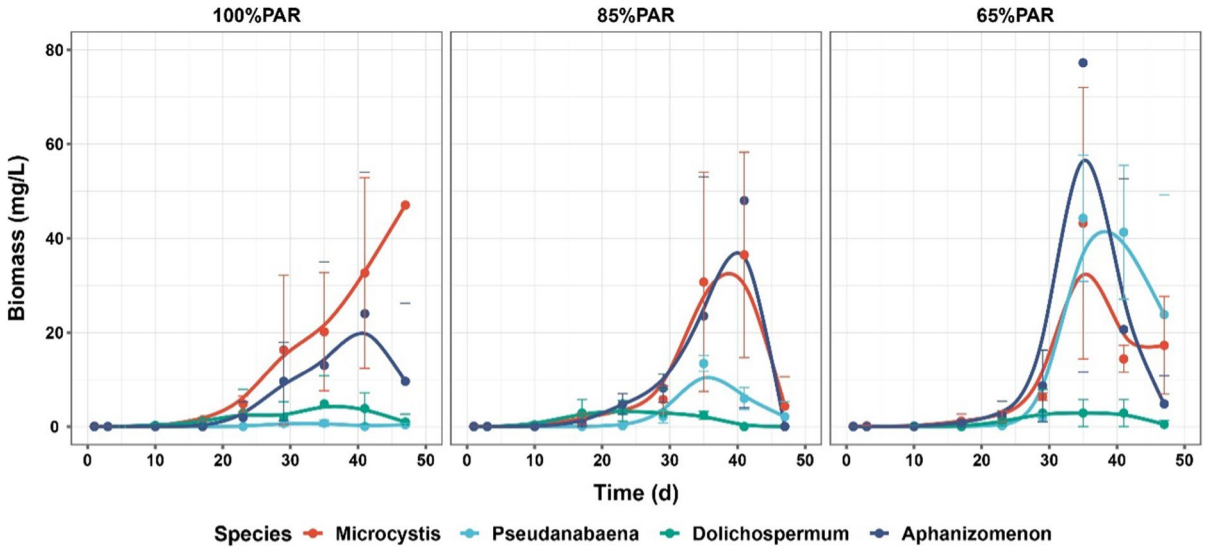

Fig. 2 The variations in the dominant cyanobacterial biomass (*Microcystis*, *Pseudanabaena*, *Dolichospermum*, and *Aphanizomenon*) under different light conditions along the experiment days

Raven 1997). Cyanobacteria also possess the ability to expand their antenna size, enabling them to capture more light energy (Zhang et al. 2012). In addition, cyanobacteria can adjust their cellular metabolism to optimize their energy use and adapt to low light conditions. For example, they can reduce their respiration

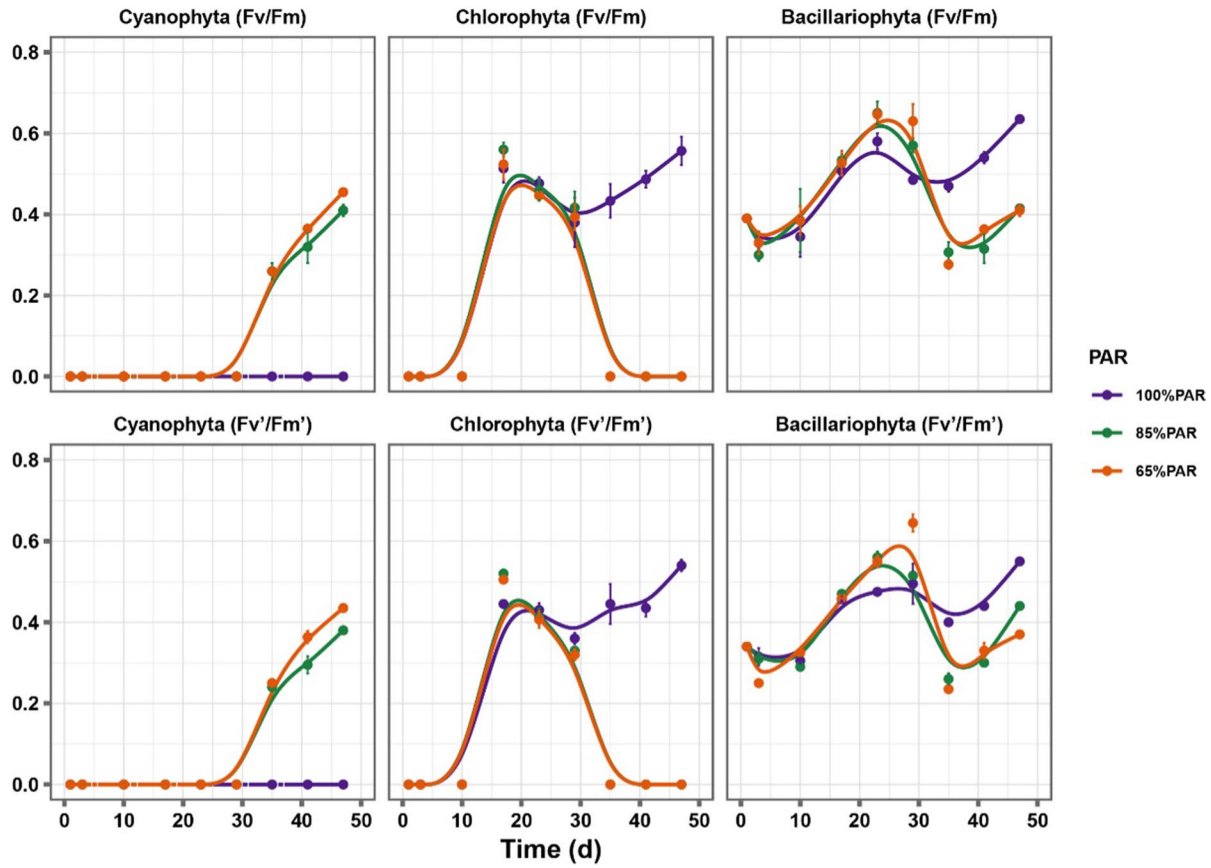

Fig. 3 The variations in the maximum photochemical efficiency (F_v/F_m) and effective photochemical efficiency (F_v'/F_m') of Cyanophyta, Chlorophyta, and Bacillariophyta under different light conditions along the experiment days

rates while increasing their carbon fixation rates, which enables them to maintain a positive energy balance despite the lower light availability (Pierangelini et al. 2015). Our results indicate that reducing PAR enhances the capacity for photosynthesis in cyanobacteria, while decreasing it in Chlorophyta and Bacillariophyta. This suggests that cyanobacteria have a stronger ability to utilize low light and use it to achieve rapid growth, compared to other algae groups. The results indicate that Chlorophyta and Bacillariophyta have a lower capacity for photosynthesis as PAR is reduced, suggesting that they are more sensitive to fluctuations in light intensity. Thus, it is essential to maintain a suitable light intensity to ensure their growth rates remain relatively stable.

Different species of cyanobacteria exhibit varied responses to a decrease in PAR, with some such as *Aphanizomenon* and *Pseudanabaena* exhibiting a stronger capacity to adapt to low light conditions compared to others. Therefore, their biomass is higher in low light conditions, which enables them to outcompete *Microcystis* in terms of biomass production. Meanwhile, *Microcystis* maintained a sustained growth trend in the 100% PAR group and did not reach its peak until the end of the experiment. The growth of *Dolichospermum* did not show a significant response to the reduction of PAR during the experiment. The differences in low light adaptation among different cyanobacteria might be attributed to their varying temperature optima (Edwards et al. 2016). However, the specific mechanisms underlying these differences are still unclear and require further investigation. Furthermore, it is worth noting that in contrast to what is observed in the field, the biomass of total phytoplankton and taxonomic groups did not show a sustained increasing trend in the

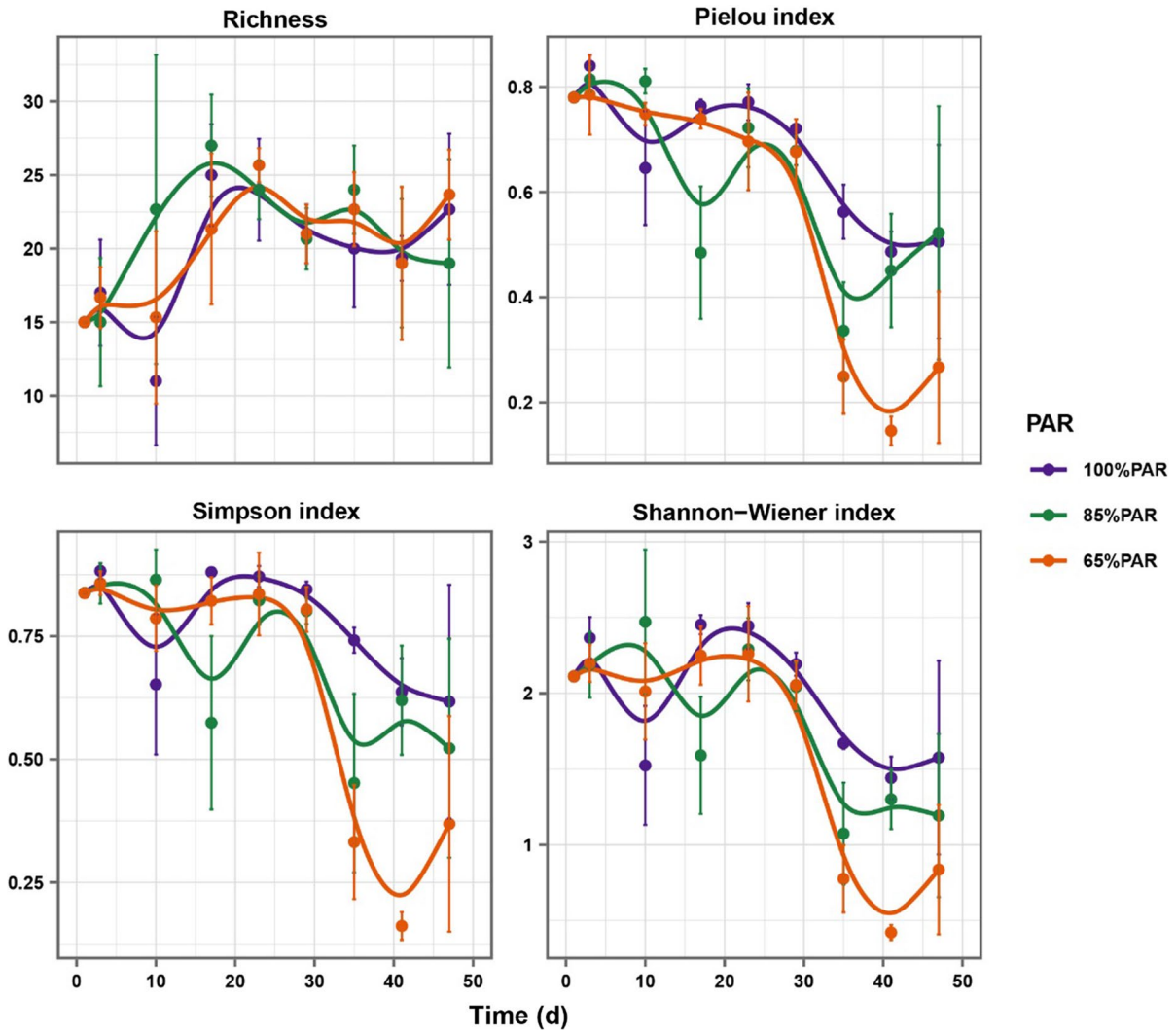

Fig. 4 The variations in the mean values (±sd) of richness, Pielou's evenness, Simpson index, and Shannon–Wiener index at different light conditions along the experiment days

experiment, but rather started to decline toward the end of the study. This could be attributed to the significant increase in biomass during the later stages of the experiment, resulting in high biomass levels in the relatively closed experimental system, and leading to density-dependent effects on the biomass, which ultimately caused a decline in the total phytoplankton and taxonomic groups' biomass.

The photosynthetic efficiency of phytoplankton has been found to decrease significantly with increasing light intensity (Kromkamp et al. 2008; From et al. 2014). In natural phytoplankton samples, F_v/F_m showed light-driven depression when the light intensity exceeded 800 µmol m^{-2} s^{-1} (Vassiliev et al. 1994). Similarly, in a mesocosm experiment with midday light intensity reaching up to 1200 µmol m^{-2} s^{-1}, F_v/F_m also exhibited light-driven depression (Bergmann et al. 2002). In our current study, we observed that the F_v/F_m of cyanobacteria was inhibited when the average PAR was approximately 630 µmol m^{-2} s^{-1}. The difference of key PAR values in different studies might be dependent on the phytoplankton composition. Different species of phytoplankton have varying degrees of adaptation to different levels of light intensity (Falkowski et al. 1993). Some phytoplankton in Bacillariophyta and Chlorophyta are

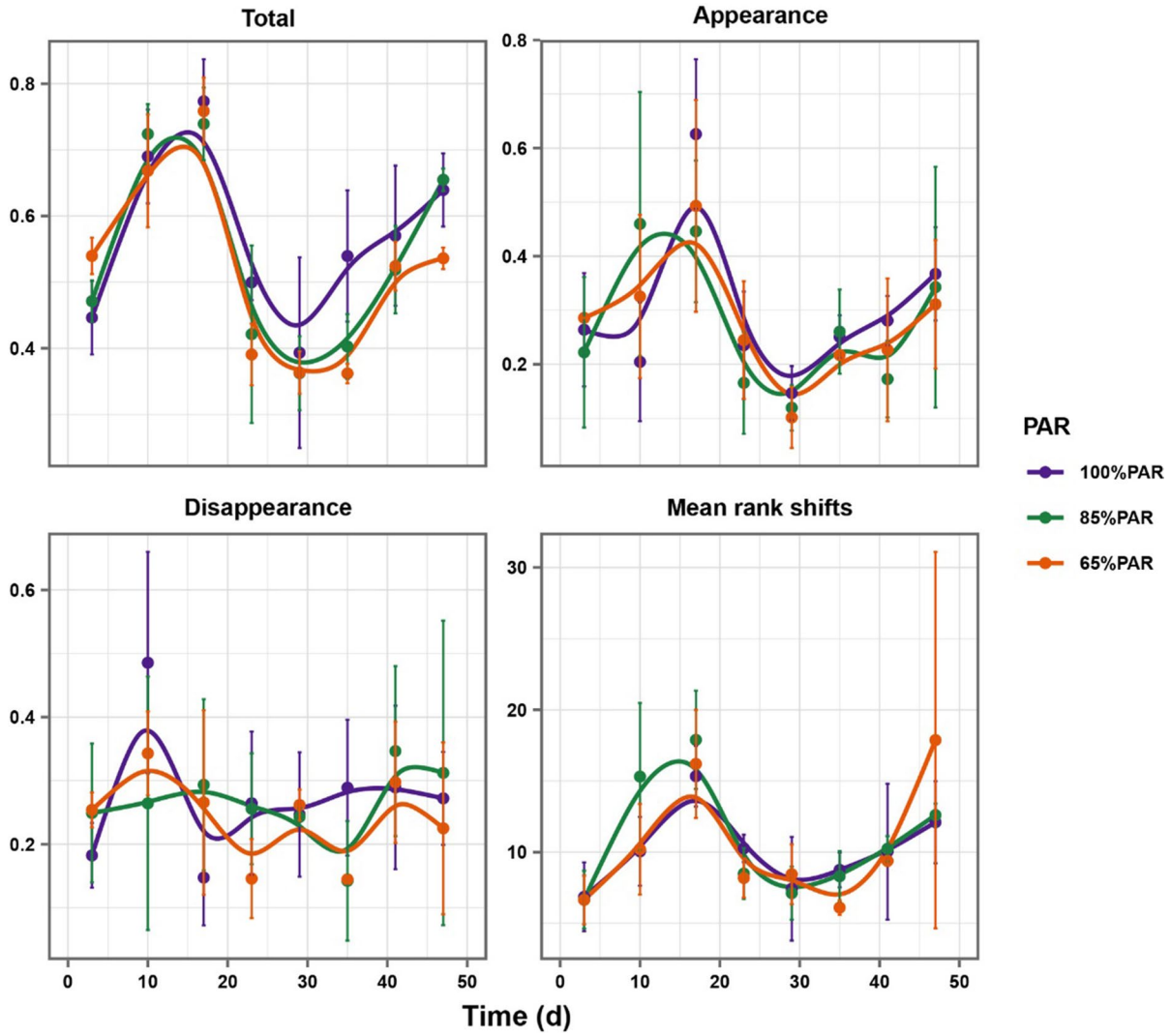

Fig. 5 The variations in the total turnover, the appearance, the disappearance, and the mean rank shifts under different light conditions along the experiment days

adapted to perform photosynthesis under higher light intensity, while others, such as cyanobacteria, have evolved to perform photosynthesis effectively under lower light intensity (Gao et al. 2019). The experimental results confirmed this fact, as the F_v/F_m values of chlorophytes and bacillariophytes in the 100% PAR experimental group showed an increasing trend, whereas the F_v/F_m value of cyanobacteria remained consistently low. In the 85% and 65% PAR experimental groups, the F_v/F_m values of chlorophytes and bacillariophytes decreased and even became zero in the later stages of the experiment, whereas the F_v/F_m value of cyanobacteria continued to increase (Guan et al. 2020). Cyanobacteria are capable of adjusting the composition of their photosynthetic pigments to adapt to different light conditions. In low light conditions, they tend to have relatively high content of carotenoids, which can absorb longer wavelength light in the spectrum and improve photosynthetic efficiency (Li et al. 2020). Therefore, reducing the light intensity can help restore the photosynthetic activity of cyanobacteria and reduce the photosynthetic activity of chlorophytes.

Responses of phytoplankton community dynamics to declining PAR

The impact of light intensity on the richness and diversity of phytoplankton varies depending on the algae species and their ability to adapt to different light conditions. In this study, the impact of light intensity on phytoplankton richness and diversity depended on the species of algae and their adaptability to light. While the richness was less affected by light intensity, the Pielou index, Simpson index, and Shannon–Wiener index showed significant differences with varying light intensities during the experiment, with an overall downward trend. In the experiment, excessive light intensity can lead to the death or inhibition of certain algae species that are unable to adapt to high light conditions in their photosynthetic pathways. This can ultimately result in a decrease in the diversity and richness of the phytoplankton community. It is worth noting that cyanobacteria are capable of thriving in both high and low light environments. Furthermore, there are also mixotrophic phytoplankton species, such as *Cryptomonas* sp. exhibit good adaptability to low light conditions (Dong et al. 2016). Therefore, in high light environment, only algae that have adapted to high light intensity can survive and reproduce in such an environment, leading to a shift in the species composition of the algal community toward relatively low diversity and richness. Similarly, excessively low light intensity may result in a reduced rate of photosynthesis, enabling only those algae that can adapt to low light environments to grow and reproduce. This can ultimately lead to a decrease in the diversity and richness of algal communities (Huisman et al. 1999). Therefore, maintaining an appropriate light intensity is crucial to promote the diversity and richness of algal communities. Excessive or insufficient light conditions can result in a decrease in diversity and richness of algal communities.

The turnover of phytoplankton species in spring is determined by multiple factors (Lu 2017). Initially, the turnover and mean rank shift values were low in all three experimental groups. However, as the water temperature and daylight hours increased in spring, the growth and activity of phytoplankton also increased, thereby promoting the rate of species turnover (Righetti et al. 2019). The different light intensities among the three treatment groups resulted in changes in the relative abundance of the phytoplankton community's species composition, leading to species turnover. Under low light conditions, cyanobacteria exhibit strong competitive abilities, allowing them to occupy the living space and nutrient resources of other phytoplankton, thereby inhibiting the growth and reproduction of other phytoplankton (Ma 2005). During the middle of the experiment, there was an increase in the biomass of cyanobacteria which became dominant, resulting in a decrease in the turnover and mean rank shift values in all three treatment groups. Once the biomass of cyanobacteria reached its maximum level, the turnover and mean rank shift values reached their lowest point. Therefore, the dominant position of cyanobacteria can have a significant impact on phytoplankton species turnover, which may either increase the stability of the community (Xue et al. 2018), or lead to a decrease or disappearance of other phytoplankton, thus altering the ecological structure and function of the water body (Huisman et al. 2018).

Conclusions

In conclusion, our study suggests that reduced light levels promote the growth of cyanobacteria, resulting in an earlier peak in cyanobacterial biomass. Moreover, it also leads to a reduction in species diversity and accelerates the transition from spring to summer in phytoplankton communities. This study provides valuable insights into the responses of spring phytoplankton communities, particularly cyanobacteria, to changes in underwater light conditions. The results can aid in the development of effective lake management strategies and the enhancement of cyanobacterial bloom control, which is of great importance for the maintenance of water quality and the protection of aquatic ecosystems. However, more research is needed to fully comprehend the potential cascading effects on higher trophic levels that may arise from changes in primary producers.

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

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical standard All prevailing local, national and international regulations and conventions, and normal scientific ethical practices have been respected. This study did not include human participants, human data or tissues, neither involving the use of any animals.

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