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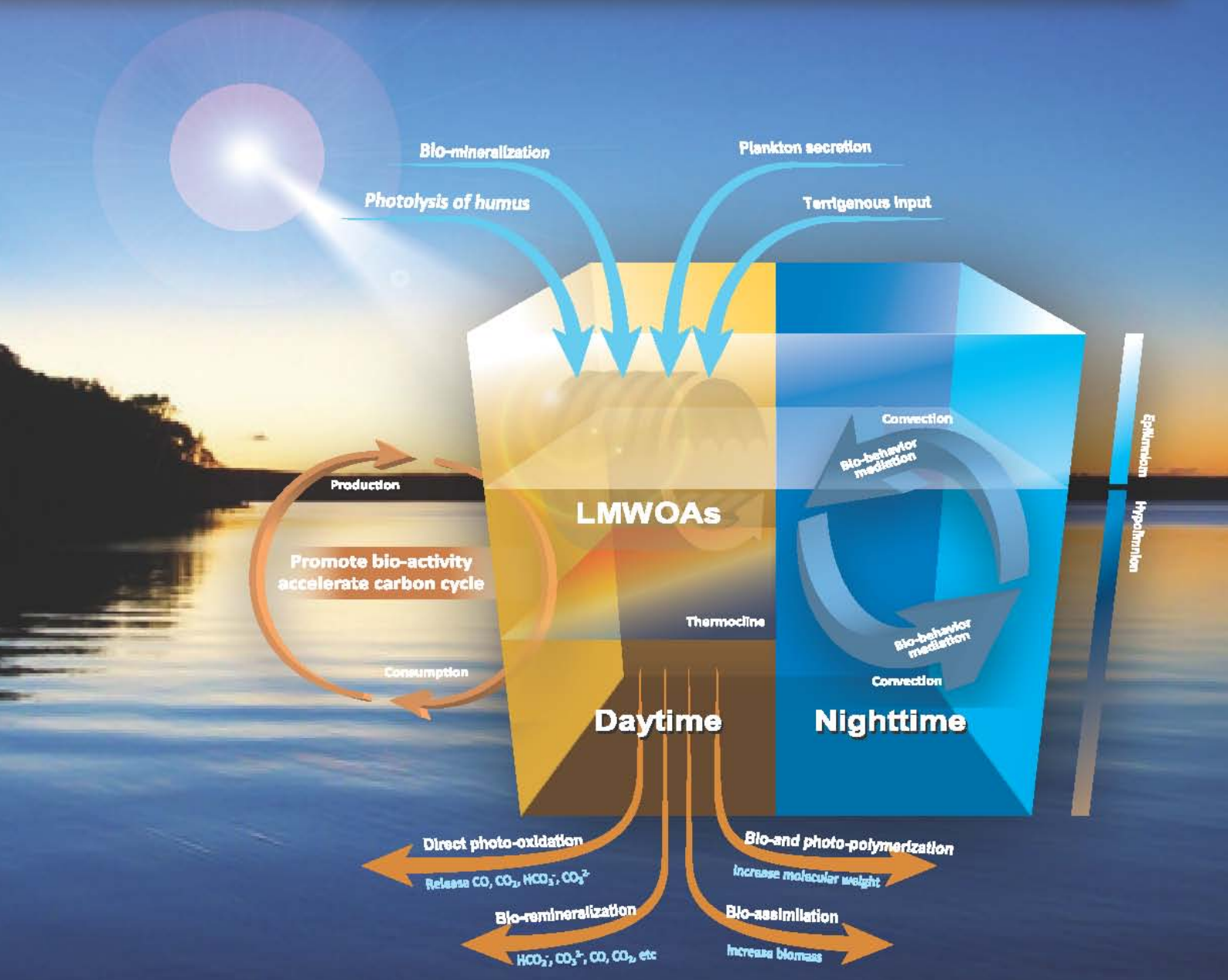

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Growth characteristics of algae during early stages of phytoplankton bloom in Lake Taihu, China

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Abstract

Three treatments, sediment plus lake water (S+W), sterilized sediment plus lake water (SS+W), and sediment plus filtered lake water (S+FW), were recruited to investigate the growth characteristics of algae during pre-bloom and the importance of algal inocula in the water column and sediment. The results showed that in the water column, biomass of all algae increased in all treatments when recruitment was initiated, whereas this tendency differed among treatments with further increment of temperature. The process of algal growth consisted of two stages: Stage I, the onset of recruitment and Stage II, the subsequent growth of algae. Compared with S+W, in Stage I, SS+W significantly increased the biomass of cyanophytes by 178.70%, and decreased the biomass of non-cyanophytes by 43.40%; In Stage II, SS+W notably stimulated the growth of all algae, thus incurring the occurrence of phytoplankton bloom. Further analyses revealed that both metabolic activity and photochemical activity of algae were enhanced in SS+W, which resulted from the releasing of nutrients from sediment. These results suggest that algal growth in Stage II and algal inocula in the water column can be important factors for the formation of phytoplankton bloom. In addition, possible mechanisms promoting algal recruitment and subsequent growth of algae were explored.

Key words: algae; recruitment; phytoplankton bloom; water column; sediment

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Introduction

Phytoplankton bloom has become a common event in many eutrophic lakes worldwide, due to excessive input of nitrogen and phosphorus (Reynolds et al., 1981; Verspagen et al., 2005). In recent years, Lake Taihu (Jiangsu Province, China) has also experienced longer and more severe algal disasters as a result of higher industrial output (Duan et al., 2009). One devastating consequence of phytoplankton bloom was the "2007 water crisis" when the whole city of Wuxi was short of potable water (Guo, 2007). Annual cycling of algae was important in the formation of summer blooms (Aloisie et al., 1998; Schiel, 2006). Therefore, relevant studies are necessary for prevention and control of phytoplankton bloom.

In temperate areas, the growth characteristics of algae vary among seasons. Phytoplankton bloom in summer is preceded by algal recruitment in early spring, and followed by settlement in autumn and overwintering (Kong and Gao, 2005; Reynolds et al., 1981; Takamura et al., 1984). Consequently, the clarification of growth characteristics during recruitment is critical for revealing the profiles of phytoplankton bloom (Kong and Gao, 2005). Most previous studies have estimated the contribution of algal inocula from sediment. These relative values of this source ranged from 0.2%–0.5% (Brunberg and Blomqvist, 2003; Hansson et al., 1994; Reynolds et al., 1981) to 2%–6% (Trimbee and Harris, 1984; Verspagen et al., 2005) due to environmental factors (Schiel and Foster, 2006; Tsujimura et al., 2000; Wichachucherd et al., 2010). Therefore, these contributions were too low to fully explain the origin of massive phytoplankton bloom. On the other hand, simulated experiment addressed the advantages of dominant algal species, cyanophytes over others (Wu et al., 2008). However, in this experiment, the physiological states of algae between in isolated algal strains and in field could be different and the effects of sediment and water column were ignored (Latour and Giraudet, 2004). Subsequently, the relationship between algal recruitment

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and accumulated temperature was identified by Cao et al. (2008), yet in-depth studies on the underlying mechanisms are absent.

Most studies on algal recruitment have concentrated on inocula from sediments (Korpinen and Jormalainen, 2008; Latour et al., 2004; Trimbee and Harris, 1984) due to largest sedimentation in autumn (Brunberg, 1995; Reynolds et al., 1981). However, Verspagen et al. (2005) predicted that the removal of the pelagic population can reduce the magnitude of summer bloom by 64%, although the quantity of the pelagic population is much less than that of the benthic population. In large shallow lakes such as Lake Taihu, the mixing and exchange of algae between the water column and sediment driven by wind (Kong et al., 2009) can reallocate the distribution of algae (Wu et al., 2010). During this process, algae that initially deposited on the sediment surface with photochemical viability in winter, like cyanophytes (Verspagen et al., 2005; Visser et al., 1995), are passively returned to the water column and eventually become holoplanktonic under favorable conditions (Suikkanen et al., 2010). Consequently, in shallow lakes, the potential contribution of inocula in water column for phytoplankton bloom needs to be considered.

In this study, different combinations of sediment and lake water were employed to be recruited with the aim to (1) determine the growth characteristics of algae during the pre-bloom phase; (2) evaluate the importance of algal inocula in the water column and sediment, by experiments with sediment sterilization and the filtration of water column, respectively.

1 Materials and methods

1.1 Sampling site

Lake Taihu (latitude: 30°55′40′′–31°32′58′′N; longitude: 119°52′32′′–120°36′10′′E) is located in the Jiangsu Province of southeastern China and covers an area of 2338 km^2, with an average depth of 2.0 m. Cyanophyte-dominated blooms used to occur in the northern bays due to the calm conditions and high nutrient levels, then spread to other parts of the lake. However, this profile has changed in recent years, and algae initially recruited and returned to the water column in the western and southwestern parts of the lake. Later, algae cells were driven to the northern bay by the monsoon, where they propagated and formed severe blooms (Kong et al., 2009). Consequently, algal inocula in the western and southwestern parts of the lake served a "seed bank" for the blooms and the site "W_2" was selected as sampling site (**Fig. 1**).

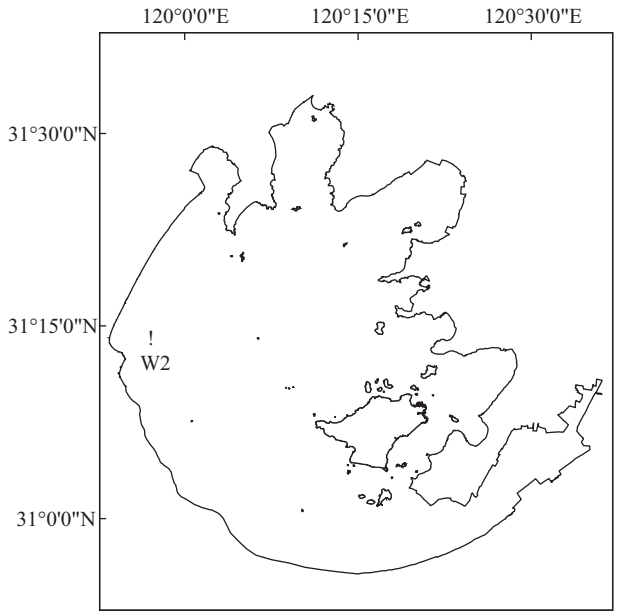

Fig. 1 Sampling site of W_2 in Lake Taihu, China.

1.2 Sample preparation

On March 1, 2010, during the overwintering period (Kong et al., 2009), sediment was collected using a polyethylene corer with a diameter of 10 cm and the upper 0–2 cm of sediment was retained. Meanwhile, a plastic column sampler with a diameter of 10 cm was used to collect integrated water samples with a depth of 0–2 m. All samples were immediately transported to the laboratory.

In the laboratory, 25 ± 0.01 g (fresh weight) homogenized sediment was added to each conical flask, and the total 54 flasks were randomly subdivided into three groups: S+W, sediment + 240 mL lake water, representing algal recruitment in field; SS+W, sterilized sediment (sterilized at 121°C for 20 min) + 240 mL lake water, representing algal recruitment from the water column; and S+FW, sediment + 240 mL filtered lake water (Whatman, GF/C), representing algal recruitment from sediment. Initially, all samples were grown at 6°C (average water temperature in lake) in darkness for 5 day of adaptation. Subsequently, the cultivation lighting conditions consisted of a cold-white fluorescent lamp of 30 μmol photons/(m^2·sec), 12:12 light/dark cycle, and the temperature increased at a rate of 1°C per 5 day, intended to simulate the changes of average water temperature in field (**Fig. 2**). During the entire process, all samples were kept stationary. Small numbers of zooplankton were removed by pipetting when they were observed, in order to avoid potential effects on algal recruitment. On the last day of the series of temperature treatments, 6, 9, 12, 15, 18, and 21°C, nine flasks (three flasks per treatment) were sampled, and the water column and sediment were carefully separated and collected for analysis.

1.3 Pigment measurements

For the determination of phycocyanin, 100 mL of sub-water sample was filtered (Whatman, GF/C). Subsequently, the filter membrane or 2 g (dry weight) freeze-dried sediment was homogenized with 0.05 mol/L Tris-HCl buffer at pH 7.0, and then transferred to centrifuge tubes

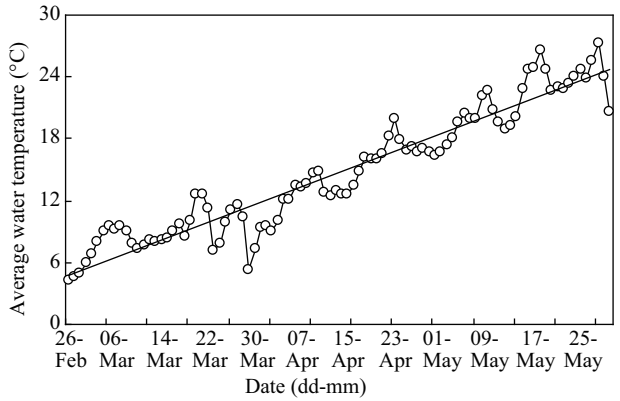

Fig. 2 Changes of average water temperature in field.

and kept in darkness for 8–10 hr at 4°C. The supernatant was collected through centrifugation at 7000 ×*g* for 25 min. The concentration of phycocyanin was measured through colorimetry using a fluorescence spectrophotometer (RF-5301PC, Sahimadzu, Japan). For the determination of chlorophyll *a* (Chl-*a*) and chlorophyll *b* (Chl-*b*), the same procedure was performed except that Tris-HCl buffer was replaced with 90% acetone. Based on the algal species identified in Lake Taihu, the concentrations of Chl-*a*, Chl-*b*, and phycocyanin were indicative of the biomass of total algae, non-cyanophytes and cyanophytes, respectively (Cao et al., 2008).

1.4 Determination of photochemical activity

The method for the determination of photochemical activity was according to Zhang et al. (2008) with minor modifications. Approximately 10 mL of sub-water was kept in darkness for 15 min prior to analysis. Photochemical activity of photosystem II (PSII) was determined using a pulse-amplitude-modulated (PAM) fluorescence monitoring system (Walz, Effeltrich, Germany). Simultaneously, different algal species such as cyanobacteria, chlorophytes, and diatoms/dinoflagellates were distinguished by a specific combination of excitation wavelengths (665, 645, 520, and 470 nm).

The maximum potential quantum yield of PSII (PAM_1) can be expressed as follows:

$$F_v/F_m = (F_m - F_0)/F_m \quad (1)$$

where, F_v represents the difference between F_m and F_0, the maximum and minimum fluorescence values of PSII after darkness adaptation, respectively.

The maximum effective quantum yield of PSII (PAM_{464}) can be expressed as follows:

$$F'_v/F'_m = \left(F'_m - F'_0\right)\Big/F'_m \quad (2)$$

where, F'_v represents the difference between F'_m and F'_0, the maximum and minimum fluorescence values of PSII after activation, respectively.

1.5 Determination of metabolic activity

Metabolic activity was determined according to the method described by Yu et al. (2007). A stock solution (5 mg/mL) of fluorescein diacetate (FDA, Sigma, St. Louis, MO, USA) was prepared and stored at 4°C. The working solution was obtained by 100-fold dilution of the stock solution with distilled water. Up to 25 μL of the working solution was added to 1 mL of the sample filtered through a 50 μm silk. The solutions were homogenized and kept in darkness at room temperature for 8–10 min before measurement. Light at a wavelength of 488 nm was used to excite the fluorescent probes and fluorescent signals were collected from 505–545 nm (Endo et al., 2000) using an Epics Altra flow cytometer (Beckman Coulter, USA).

The results were analyzed using the software WinMDI 2.9. First, algae displayed by side scatter and Chl-*a* fluorescence were classified into different cell aggregations (*i*). The intensity (*I*) and percentage (*P*) of each cell aggregation were obtained from FL_1 histogram (FDA fluorescence). Total metabolic activity was expressed as:

$$\text{Metabolic activity} = \sum_{n=1}^{i} (I_n \times P_n) \quad (3)$$

1.6 Determination of nutrient

The concentrations of total nitrogen (TN) and total phosphorous (TP) were determined using a combined persulfate digestion, as described for soluble reactive phosphorus and nitrate, then detected by spectrophotometric according to the Chinese Standard Methods for Lake Eutrophication Survey (Jin and Tu, 1990).

1.7 Statistical analysis

All data, except for the concentration of nutrients, were collected in triplicates and presented as mean ± standard deviation. The significant changes of algal biomass and physiological parameters with temperature increment across treatments were analyzed using general linear model (univariate GLM; SPSS 13.0) with temperature and treatment being fixed factors. Multiple comparisons between temperatures were conducted via Student-Newman-Keuls test. The difference in treatments at a specific temperature or temperature-span was performed using *T*-tests. Differences were considered significant when $p < 0.05$.

2 Results

2.1 Pigments in sediment

The changes of pigment concentrations in sediment are shown in **Fig. 3**. The statistical analysis showed that the concentrations of Chl-*a* and Chl-*b* across treatments increased significantly at 12°C, while that of phycocyanin increased significantly at 15°C. Therefore, the recruitment

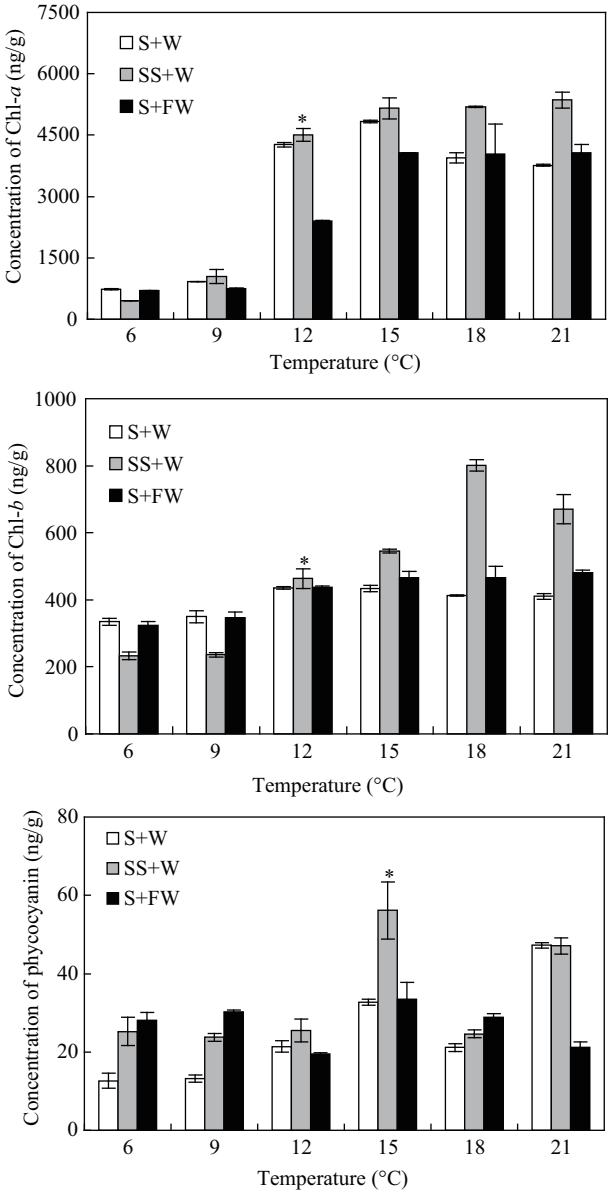

Fig. 3 Concentrations of pigments in sediment of treatments. Data are the averages with SD (bars) of triplicates. * represents the first significant increment; S+W, SS+W and S+FW denotes sediment plus lake water, sterilized sediment plus lake water and sediment plus filtered lake water respectively.

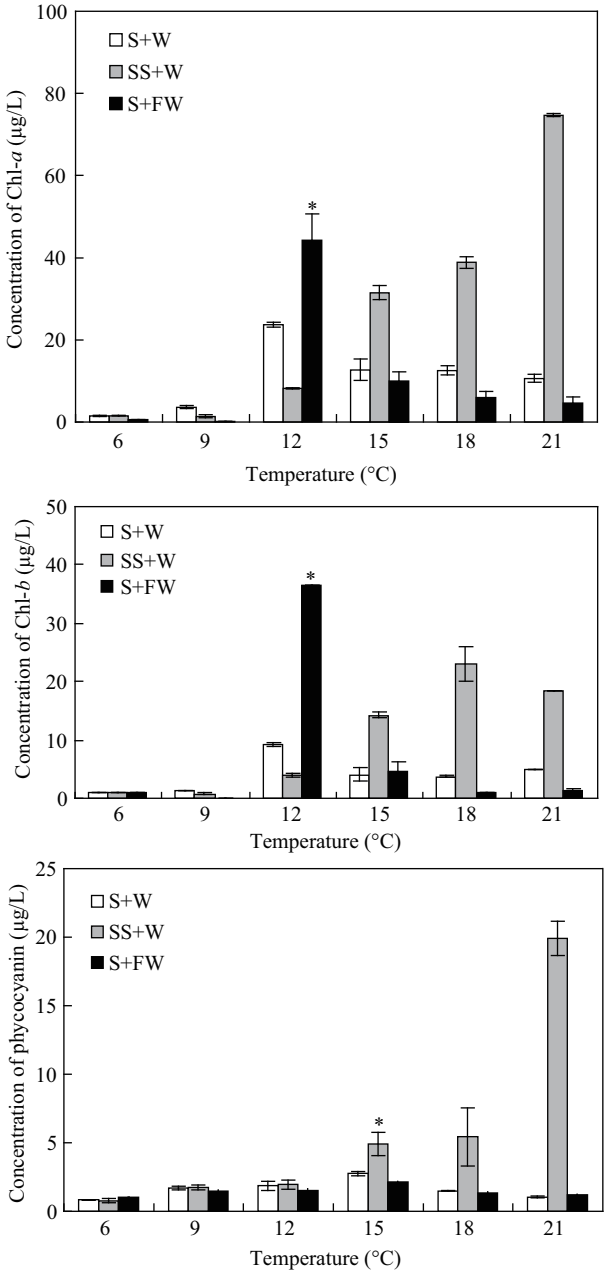

Fig. 4 Concentrations of pigments in water column of treatments. Data are the averages with SD (bars) of triplicates. * represents the first significant increment.

of total algae, non-cyanophytes, and cyanophytes was initiated at 12, 12, and 15°C, respectively.

2.2 Pigments in water column

The changes of pigment concentrations in water column are shown in **Fig. 4**. The concentration of Chl-*a* across treatments increased significantly at 12°C. At 12°C, Chl-*a* concentration in S+W was 23.66 ± 0.60 μg/L, significantly higher than 8.19 ± 0.18 μg/L in SS+W and lower than 44.25 ± 6.44 μg/L in S+FW. Thereafter, the concentration of Chl-*a* in SS+W continued to increase but declined in S+W and S+FW.

The concentration of Chl-*b* across treatments increased significantly at 12°C. At 12°C, the concentration of Chl-*b* in S+W was 9.16 ± 0.28 μg/L, significantly higher than 3.98 ± 0.23 μg/L in SS+W and lower than 36.59 ± 0.02 μg/L in S+FW. Thereafter, the concentration of Chl-*b* continued to increase in SS+W but decreased in S+W and S+FW.

The concentration of phycocyanin across treatments increased significantly at 15°C. At 15°C, the concentration of phycocyanin in S+W was 2.75 ± 0.16 μg/L, lower than 4.92 ± 0.85 μg/L in SS+W and higher than 2.12 ± 0.08 μg/L in S+FW. Thereafter, the concentration of phycocyanin continued to increase in SS+W but decreased

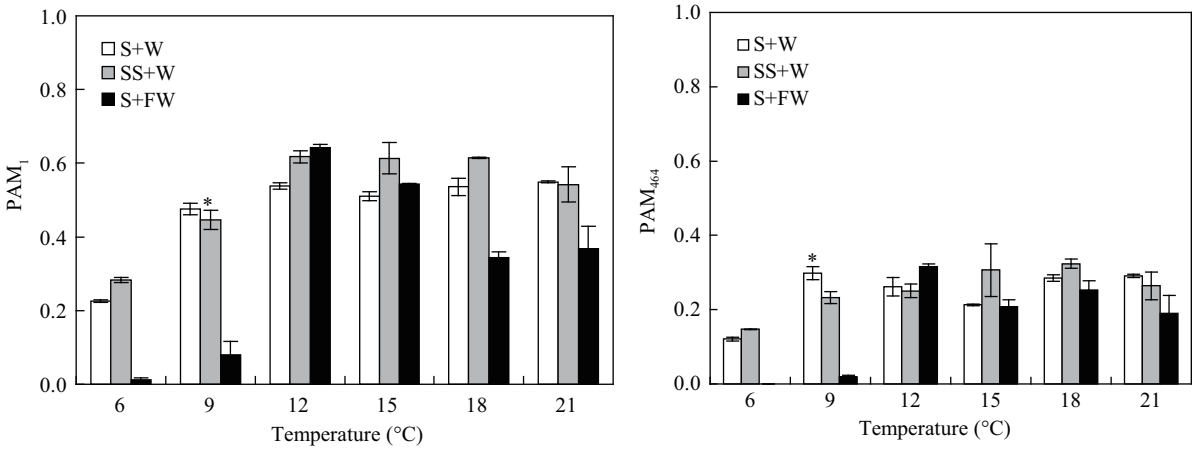

Fig. 5 Photochemical activities of cyanophyte photosystem II (PSII) in treatments. Data are the averages with SD (bars) of triplicates. * represents the first significant increment.

in S+W and S+FW.

2.3 Photochemical activity

The photochemical activities of green algae were not detected during the entire process in all treatments, and those of cyanophytes are shown in **Fig. 5**. The value of both PAM_1 and PAM_{464} across treatments increased significantly at 9°C. From 6 to 21°C, mean PAM_1 in SS+W was 0.539 ± 0.016, significantly higher than 0.477 ± 0.030 in S+W and 0.317 ± 0.008 in S+FW, while mean PAM_{464} in SS+W was 0.258 ± 0.014, higher than 0.247 ± 0.005 in S+W and 0.156 ± 0.005 in S+FW.

2.4 Total metabolic activity

The changes of total metabolic activity are shown in **Fig. 6**. Total metabolic activity across treatments increased significantly at 12°C. From 6 to 21°C, mean total metabolic activity in SS+W was 48.42 ± 1.65, higher than 46.28 ± 2.01 in S+W and 35.84 ± 2.24 in S+FW.

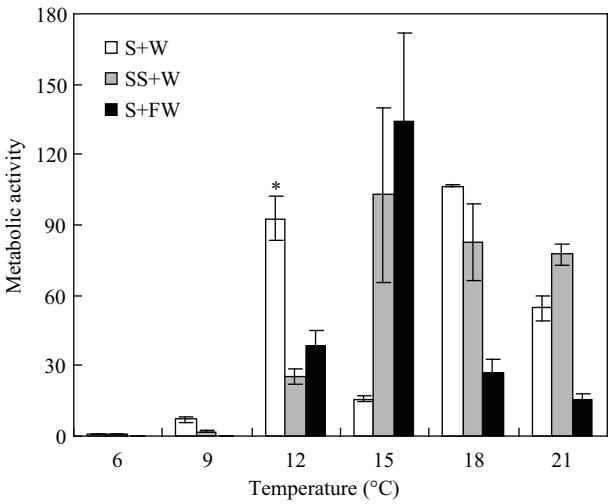

Fig. 6 Changes of the total metabolic activity in treatments. Data are the averages with SD (bars) of triplicates; * represents the first significant increment.

2.5 Concentration of nutrients

The concentrations of TN and TP are shown in **Table 1**. During the entire process, no significant differences of nutrients concentration in sediment across treatments were detected. However, at 6°C, the concentrations of TN and TP in the sediment of SS+W were 72.22% and 82.76% of that in S+W, and at 21°C the concentrations of TN and TP in the water column of SS+W were 246.55% and 250.00% higher than that in S+W.

3 Discussion

At the completion of the experiment, algae had massively propagated and accumulated on the water surface in SS+W even though without the presence of inocula in sediment, whereas this phenomenon was not detected in S+W and S+FW. The changes of pigments showed that algal recruitment did unanimously increase in all treatments, so it can be concluded that algal growth during post-recruitment determines the formation of phytoplankton bloom. The clarification of mechanisms promoting algal recruitment and subsequent growth would undoubtedly offer us insights in understanding the profiles of phytoplankton bloom.

3.1 Growth dynamics

The characteristics of algal growth in early stages are essential for the formation and prevention of phytoplankton bloom. The recruitment of total algae, non-cyanophytes, and cyanophytes were initiated at 12, 12, and 15°C, respectively. Cao et al. (2008) proved that a certain cumulative temperature was needed for the initiation of algal recruitment. As a result, there is difference in accumulative temperatures to initiate algal recruitment among species.

Temperature is important for annual cycling of algae in lakes. In early spring, increasing temperatures activates algal inocula resting on sediment surface and promotes algal migration from sediment to water column (Latour et al.,

Table 1 Concentration of total nitrogen (TN) and total phosphorous (TP) in sediment and water column

Treatment		Sediment (mg/g)						Water column (mg/L)
		6°C	9°C	12°C	15°C	18°C	21°C	21°C
S+W	TN	2.16	1.61	1.58	1.56	1.76	1.56	0.58
	TP	0.29	0.25	0.23	0.21	0.30	0.23	0.04
SS+W	TN	1.56	1.76	1.72	1.57	1.79	1.77	2.01
	TP	0.24	0.30	0.26	0.26	0.30	0.28	0.14
S+FW	TN	1.95	1.72	1.78	1.67	1.78	1.43	0.52
	TP	0.29	0.28	0.28	0.25	0.29	0.22	0.04

2004; Schone et al., 2010). During post-recruitment, the variance of temperature affected the competitiveness and the development of dominance of algae, thus determining the profiles of phytoplankton bloom (Chu et al., 2007). In autumn, decreasing temperature results in algal sedimentation (Visser et al., 1995). Based on these characteristics of algal growth, Kong and Gao (2005) proposed the theory of "four stages" for the formation of phytoplankton bloom, in which overwintering and recruitment are identified as the bottleneck stages of algal growth. Consequently, the identification of the threshold temperatures for algal recruitment offers an opportunity to eliminate the inocula of "problematic algae".

In the water column, the increase of algal biomass at these temperatures and divergent trends above these temperatures implies that the process of algal growth during early stages of phytoplankton bloom can be divided into two stages: Stage I, the onset of recruitment and Stage II, the subsequent growth of algae. In previous studies, although the importance of algal recruitment has been widely acknowledged, the difference of algal recruitment between areas where phytoplankton bloom occurred or not had been paid little attention. The identification of "two stages of algal growth" demonstrated that algal recruitment was independent of the occurrence of phytoplankton bloom and the tendency of algal growth (increasing or decreasing) in Stage II was critical for phytoplankton bloom.

3.2 Effect of sediment sterilization

The sterilization of sediment should have decreased algal biomass because of the absence of inocula in the sediment. In Stage I, the biomass of total algae and non-cyanophytes decreased as expected, but that of cyanophytes increased. In Stage II, the subsequent growth of both cyanophytes and non-cyanophytes was stimulated. Therefore, the effect of sediment sterilization on algal growth is related to algal species and developmental stages.

The presence of sediment can negatively affect algal recruitment by inhibiting photosynthesis (Chapman et al., 2002; Grant, 2000) and physical covering on surviving spores (Eriksson and Johansson, 2003; Schiel and Foster, 2006; Wichachucherd et al., 2010). However, these aspects could be excluded in this study. Therefore, the occurrence of phytoplankton bloom in SS+W ascribed to eutrophication in the water column, as indicated by higher metabolic activity (Brookes et al., 2000). Although the nutrient levels in sediment were not altered significantly, the possible release of nutrients from sediment after sterilization at 6°C could lead to eutrophication in the water column at 21°C (**Table 1**). Consequently, the release of nutrients from the sediment resulted in elevated photochemical ability and metabolic activity, thus stimulating the growth of cyanophytes in Stage I and the subsequent growth of cyanophytes and non-cyanophytes in Stage II.

The enrichment of nutrient is not entirely beneficial for algal growth in early stages, due to the simultaneous increment of predation pressure by herbivores (Hemmi and Jormalainen, 2002; Korpinen and Jormalainen, 2008). However, cyanophytes, unlike non-cyanophytes, can reduce this risk of being consumed through elevated toxin excretions (Yoshida et al., 2007). For this reason, SS+W increased the biomass of cyanophytes, rather than non-cyanophytes in Stage I. Turner (2010) found that once algal recruitment was initiated, the predation pressure would diminish gradually because of the increased algal density. Therefore, decreased predation pressure, together with the stimulation of algal growth under eutrophication (Davis et al., 2009; Moisander et al., 2009) accounted for the rapid increment of biomass of cyanophytes and non-cyanophytes in Stage II.

In addition, it is worth noting that although eutrophication stimulated algal growth, the occurrence of phytoplankton bloom in SS+W confirmed the significance of algal inocula in the water column. This conclusion offers experimental evidence for the prediction that the removal of pelagic populations be useful to suppress or delay the summer bloom (Verspagen et al., 2005). Also, this finding provides clues for policy-makers to adopt more appropriate controlling strategies against phytoplankton bloom.

3.3 Effect of filtration of water column

Filtration of the water column increased the biomass of non-cyanophytes in Stage I. In the experiments, few cladocera and copepods appeared in the treatments except S+FW before algal recruitment, which indicated that not only algal inocula but zooplankton in the water column were eliminated in S+FW. Grazing by zooplankton has been shown to be important in controlling algal quantity (Kampe et al., 2007; Korpinen and Jormalainen, 2008; Turner, 2010). Turner (2010) confirmed that the algal biomass lost by predation would exceed that of algal

growth when algal density was low. Meanwhile, algae during recruitment are vulnerable to predation for their proper size, fine material and concentration (Turner, 2010; Van Alstyne et al., 1999). Therefore, the stimulation on non-cyanophytes in Stage I was associated with decreasing abundance of zooplankton. However, the expected increment of cyanophytes was not detected, which could result from the low quantity and inferior condition of cyanophytes inocula in sediment in terms of the lowest photochemical activity (**Fig. 5**).

The subsequent growth of both non-cyanophytes and cyanophytes were inhibited in Stage II as well as in S+W group. The data of nutrient levels in Lake Taihu showed that the concentration of TN and TP in S+FW (**Table 1**) were equivalent to that in the lake center where phytoplankton bloom usually did not occur (Chen et al., 2003). Therefore, the inhibition of algal growth in Stage II ascribes to the insufficiency of nutrients.

3.4 Growth strategy

Algae have evolved different strategies to cope with stress during long-term adaptation. Two kinds of strategies exist in both marine and freshwater phytoplankton (Jochem, 1999; Zhang et al., 2007). Type I adapts to stress by reducing metabolism, whereas Type II by maintaining metabolic activity, thus incurring greater mortality. Latour et al. (2004) and Wu et al. (2008) confirmed cyanophytes and non-cyanophytes to be Types I and II, respectively. Therefore, it could be deduced that higher metabolic activity existed in non-cyanophytes than in cyanophytes upon recruitment.

As a result, the recruitment and growth of non-cyanophytes in Stage I can be initiated immediately under favorable conditions even without the presence of photochemical activity. Therefore, both the increment of metabolic activity and the recruitment of non-cyanophytes occurred at 12°C. In Stage II, the diverse tendencies among treatments illustrated the subsequent growth was dependent on the external supply of energy. Thus algal growth in Stage II was only stimulated in SS+W due to more nutrient supply.

For cyanophytes, the presence of lower metabolic activity means that the accumulation of energy should proceed ahead of recruitment to provide enough energy. As a result, the significant increment of photochemical ability (at 9°C) was followed by the recruitment of cyanophytes (at 15°C). Tsujimura et al. (2000) and Visser et al. (1995) found that the sedimentation of cyanophytes resulted from the increment of carbonate ballast and collapsing of gas vesicles. Therefore part of this accumulated energy was used to reduce carbohydrate ballast and re-form gas vesicles for migration from sediment to water column. SS+W promoted the growth of cyanophytes in Stage I and Stage II for the enhanced photochemical activity.

4 Conclusions

Algal growth during early stages of phytoplankton bloom consisted of two stages: Stage I, the onset of recruitment, and Stage II, the subsequent growth of algae. The tendency of algal growth in Stage II (increasing or decreasing) was crucial for the formation of phytoplankton bloom. The increment of nutrients enhanced the biomass of cyanophytes in Stage I and stimulated the subsequent growth of all algae in Stage II. Algal inocula in the water column was important for phytoplankton bloom.

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