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Effect of flow velocity on phytoplankton biomass and composition in a freshwater lake

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HIGHLIGHTS

- Chl-a concentration and flow velocity are negatively correlated in a lake.
- Flow turbulence significantly inhibits phytoplankton growth.
- Flow turbulence influences phytoplankton species composition.
- A universal critical velocity for algae inhibition probably does not exist.

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ABSTRACT

Water flow has been widely accepted as a target to suppress algae blooms. However, the effectiveness of the flow regulation is unclear due to lack of hard evidences to illuminate the direct cause–effect relationship between hydrodynamic forces and algae growth. In this study, a field observation at a freshwater lake was conducted weekly or biweekly from July 2007 to December 2009. Phytoplankton biomass and composition were investigated at flow velocities of 0.03 m/s, 0.06 m/s, 0.10 m/s, 0.15 m/s and 0.30 m/s in field enclosure experiments. The results from the field observation indicated that phytoplankton biomass and spatial distribution largely depend on the flow condition. A strong negative correlation ($R^2 = -0.618$, $n = 222$, $P < 0.001$) was found between Chl-a concentration and flow velocity. The results of enclosure experiments showed that turbulent flow has the inhibition effect on phytoplankton biomass, but less impact on composition. The average Chl-a concentrations in the flowing enclosures were 20.3%–37.5% lower than that in their corresponding still water enclosures during the entire experiment period. Shear stress within pumps might have caused up to 10% of cell damage. The present study highlights that a universal critical velocity for suppressing algae growth probably does not exist in freshwater bodies, for each has its unique physical, chemical and ecological characteristics. It is therefore suggested that sufficient experiments should be conducted for each water body before a critical flow condition is applied to reduce the algae bloom occurrence.

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1. Introduction

In aquatic ecosystems, the continual water flow provides a unique character that affects the phytoplankton growth. Decrease of discharge and flow velocity, for example, is known to lead freshwater bodies to eutrophication (Sabater et al., 2008). In China, algae bloom has occurred frequently in many tributaries of the Three Gorge Reservoir since its operation. The main reason is that this reservoir has caused tributaries more stagnant (Yang et al., 2010; Wang et al., 2011). Some studies on large rivers have provided

the direct evidences that the river hydrodynamics plays an important role in determining the extent and timing of phytoplankton populations (Marker and Collett, 1997; Salmaso and Braioni, 2008). Chlorophyll-a (Chl-a) concentration was significantly decreased during flow and flood pulses in comparison to isolation conditions in river-floodplain ecosystems (Palijan, 2012). Moreover, some key regulators of phytoplankton community can be identified like discharge (Salmaso and Braioni, 2008), flow velocity, inflow (Vidal et al., 2012) and turbulence (Petersen et al., 1998; Leland et al., 2001; Mitrovic et al., 2003; Guven and Howard, 2006). Four events of algae bloom occurred in the middle and lower reaches of Hanjiang River in China were observed with strong correlation with low flow velocities (Xie et al., 2004). The use of water flows to suppress cyanobacterial blooms was practiced in Australia (Maier et al., 2004; Mitrovic et al., 2006; Mitrovic et al., 2011). It appears that

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altering the hydrology to enhance vertical mixing and/or flushing may be the more promising way to counter formation of surface blooms of buoyant cyanobacteria (Paerl et al., 2011). On the other hand, although water flows have been provided to the Murray–Darling River systems in Australia, it is still not sufficient to prevent blooms (Mitrovic et al., 2008). Although the effectiveness of suppression of phytoplankton blooms remains unclear, there has been an ongoing interest in the possible role of turbulence flow as a factor of inhibiting the phytoplankton growth (Reynolds et al., 1983; Hondzo and Lyn, 1999; Istvanovics et al., 2010; Tolotti et al., 2010). Recently in China, many researchers have started to study the effect of flow velocity on algae blooms (Ding et al., 2007; Huang et al., 2008; Wang et al., 2010; Long et al., 2011). It is suggested that a critical discharge or flow condition exists, which can serve as a flow target for suppressing harmful algae growth.

The hydrodynamic force can influence algae growth in various ways, which can be classified in two groups (Verhagen, 1980). One is that advection and diffusion processes may disturb the effect of vertical migration of the phytoplankton or alter the level of algae biomass temporarily through flushing. The other is that the hydrodynamic force imposes significant effects on the suspension of sediments, contributing to algae growth through nutrient release, light attenuation and grazer changes. Intensified water turbulence may also lead to species replacements from buoyant cyanobacteria to green algae and diatoms in freshwater ecosystems (Reynolds et al., 1983; Harris and Baxter, 1996; Visser et al., 1996; Sherman et al., 1998). This species interaction is not only due to algae traits related to resource use, but also due to the different capability of movement of these organisms (Arin et al., 2002; Huisman et al., 2004). Understanding of the interplay between the different characteristics of phytoplankton species and the physical environmental is a key requirement in developing our insight into the structure and variability of plankton ecosystems (Ross and Sharples, 2008).

The inhibitory effect of turbulence flow on physiological characteristics of phytoplankton in laboratory has been reported by many researchers (Odum, 1956; Koch, 1993; Thomas et al., 1995; Hondzo and Lyn, 1999). Over the last 25 years, interest has also been widened to take into account direct effects of water motion, mainly small-scale turbulence, on physiological process of individual phytoplankton (Peters and Marrase, 2000). Many researchers have proposed that the water flow experienced by an algae organism can have a large effect on its metabolic process, such as photosynthesis, changes of pigmentation and cell division (Koch, 1993; Thomas et al., 1995). The increase in the nutrient flux into the cells due to small-scale turbulence was found to be size dependent (Karp-Boss et al., 1996; Peters et al., 2006). Hondzo and Lyn (1999), in their laboratory experiments, revealed the formation of aggregates of dead and living cells of *Scenedesmus quadricauda* in a turbulence flow and argued that high shear flow rates caused cell destruction, and therefore inhibited algae growth. Most of these researches focus on laboratory studies using stirred beakers or shake flasks with algae sensitive to fluid flow (Ruiz et al., 2004; Hondzo and Warnars, 2008). Few experimental studies have dealt with the effect of fluid motion on natural phytoplankton communities confined in enclosures.

Hard evidence of direct cause–effect relationships between flow rate and algae growth is not easy to find (Peters and Marrase, 2000; Zhu et al., 2010). While how we extrapolate laboratory experiment results investigating potential responses of phytoplankton in a turbulent flow to the corresponding field conditions is a challenging research question (Hondzo and Warnars, 2008). In this study, a 2.5-year-long field observation of algae growth and various physical environmental factors in a small freshwater lake was conducted and enclosure experiments of algae growth under different circulating flow velocities were carried out. The data from the study were analyzed in order to illustrate the effect of water flow on the phytoplankton growth and community composition in freshwater bodies.

2. Materials and methods

2.1. Observation site

Zhongxin Lake (31.72° N, 121.51° E) is a freshwater lake located on Chongming Island, the third largest island of China, with a total surface area of 10 ha and average water depth of 1.3 m, as shown in Fig. 1. Isolated from other water bodies, the Lake is served as a landscape scenery and is replenished by pumping from surrounding rivers, if necessary. There are no anthropogenic pollution sources or natural rainfall-runoff discharged into the Lake. Five locally connected watercourses form the whole water area and two earth dams (A and B in Fig. 1) separate between some of them. Intensive observation was conducted on the east watercourse (E), south watercourse (S), west watercourse (W), north watercourse (N) and middle watercourse (M) from late July 2007 to December 2009, as shown in Fig. 1. Sampling was performed biweekly from late autumn to spring and gradually shifted to weekly interval in summer and early autumn, when algae had higher metabolic rates. The average flow velocity of these watercourses was determined by measuring velocity at 60% of the water depth.

2.2. Enclosure experiment

The field enclosure experiments were conducted in the west watercourse and consisted of three sets. An enclosure flume with still water condition was performed as a control treatment for all the three sets of experiment. As shown in Fig. 1, the enclosure flume is 1.5 m long, 0.4 m wide and 1.5 m high (net size), with the bottom inserted into the lake bed. Therefore water in the flumes was isolated from the surrounding lake water. The flow was generated by different types of submersible pumps. There was partition in each flowing flume to remain a circulating flow. Flow velocities of 0.03, 0.06, 0.10, 0.15 and 0.30 m/s were chosen because generally they can reflect the flow conditions in Zhongxin Lake where significant spatial variation of phytoplankton biomass was observed.

The first set of enclosure experiment performed from August 29 to November 18, 2007, had a circulating flow velocity of 0.15 m/s. The second set of the experiment beginning on March 24, 2008 was controlled with a higher flow velocity of 0.30 m/s and ran continuously for nearly three months. The water flow in both of the two enclosure flumes was controlled by two RS-12000 regulable submersible pumps (Risheng Electrical Products Co., LTD., China) with maximum discharge of 12 m³/h, as shown in Fig. 1. Samples for phytoplankton and nutrient concentration were taken two or three times a week. The third set with three different flow velocities (0.03, 0.06 and 0.10 m/s, respectively) was conducted simultaneously from April 27 to May 20, 2010, controlled by JVP submersible pumps (Yinsen Electrical Products Co., LTD., China) with the discharge ranging from 1.2 to 4.0 m³/h. The flow velocity was measured at the depth of 10 cm from the water surface in six points in the enclosure flume. Water samples were collected and analyzed on a daily basis. Concentrations of nutrients (TN and TP) were kept about 2.10 mg/L and 0.22 mg/L respectively in all enclosures by constantly adding nutrients during the experiment if necessary.

2.3. Sample analysis methods

Water temperature, pH, conductivity and dissolved oxygen (DO) were measured with multi-parameter analyzing instrument for water quality (HQ40d, HACH). DO levels on the surface and at the bottom were measured by an electrode placed at the depth of 0.1 m and 1.0 m, respectively. Flow velocity was measured with intelligent velocity instrument LGY II provided by Nanjing Hydraulic Research Institute. Water samples (0.5 m in depth) were collected from each site using organic glass hydrophore and stored in 1-L plastic

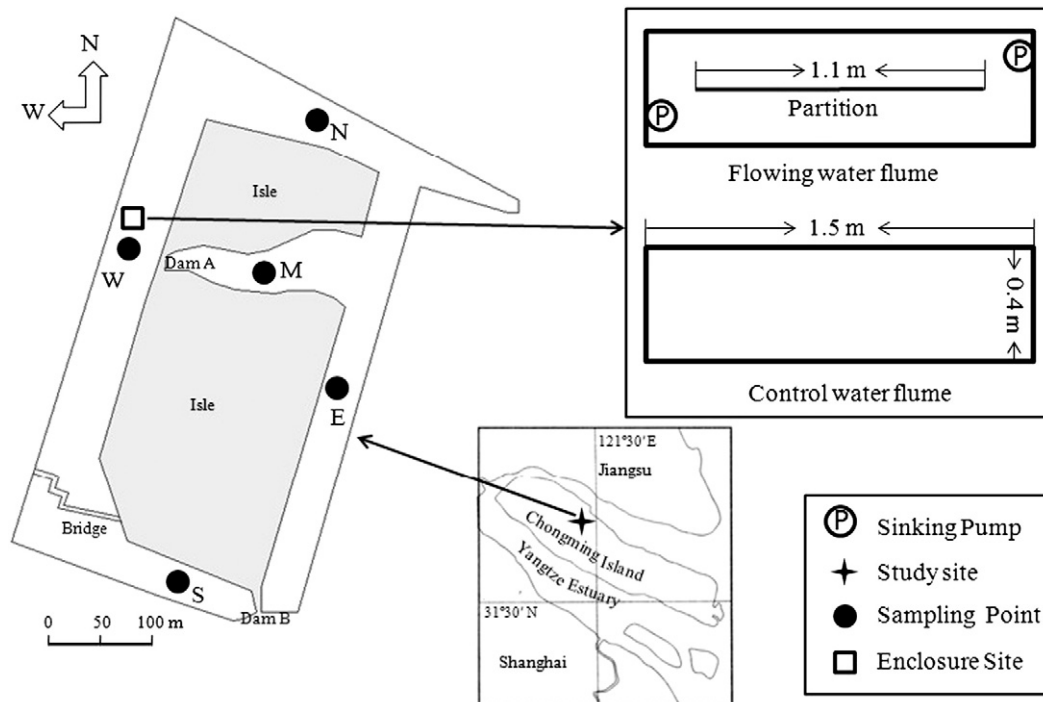


Fig. 1. Map of Zhongxin Lake and locations of sampling points and enclosure experiments.

bottles. Chl-a concentration which represents phytoplankton biomass was measured by hot-ethanol extraction and spectrofluorometric method (Chen et al., 2006). Abundance of phytoplankton groups in the Lake and in the enclosures was calculated using the Olympus CX21 System Microscope and taxa were classified according to “Fresh-water Microorganisms Atlas” edited by Zhou and Chen (2005). 5 L of water sample was filtered in situ through phytoplankton net (64 μm) during the observation in Zhongxin Lake. The samples were fixed and concentrated by sedimentation for assistance in taxonomic identification. Phyto-PAM phytoplankton analyzer (Walz, Germany) was also occasionally used to measure phytoplankton biomass and identify algae groups. Turbidity was measured with a turbid meter. Nutrients including ammonia (NH_4^+-N), total nitrogen (TN) and total phosphorus (TP) were analyzed with spectrofluorometric methods (Huang, 1999). SPSS 13.0 was applied for the paired-sample *T* test and Pearson correlation analysis.

3. Results

3.1. Physical and chemical variables of Zhongxin Lake

The main water source of the Lake is atmospheric rainfall and wind is the only force for water movement. On Chongming Island, the prevailing wind direction is north and northeast in winter and southeast and south in summer. With the north and south wind, wind-driven flow is formed in west watercourse and east watercourse. Shallow circulation flow often occurs in north watercourse affected by southeast and northeast wind. Spatial and seasonal changes of flow velocity were shown in Fig. 2 during the observation period from July 2007 to July 2008. Higher flow velocities were often recorded in the north watercourse with the average flow velocity of 0.13 m/s, significantly different from all other watercourses ($P < 0.001$). The flow velocity in the south watercourse (average flow velocity was 0.07 m/s), was

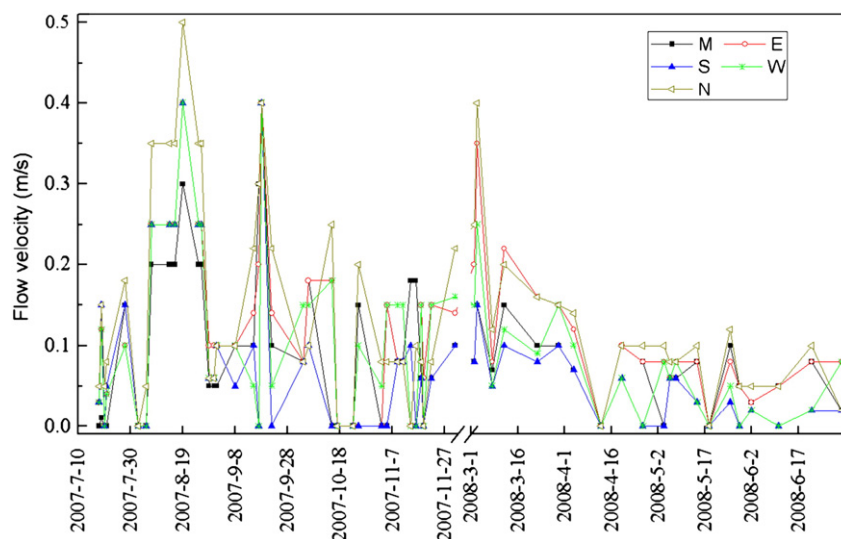


Fig. 2. Flow velocities on each water course from July 2007 to July 2008.

significantly different from that in the west and east watercourses, with average values of 0.09 m/s and 0.08 m/s, respectively (both $P < 0.001$). The south and middle watercourses, both of which are separated from other water courses in one end by dams, showed insignificant difference ($P = 0.169$). The flow velocities in the east and west watercourses were insignificantly different from each other ($P = 0.057$).

Water temperature in Zhongxin Lake during the observation period ranged from 7.2 °C in the winter of 2009 to 35.2 °C in the summer of 2008. The lake has a weak alkaline environment, with pH ranging from 7.92 to 8.85, which is favorable for phytoplankton growth. The turbidity varied within the range of 20.3 to 110 Nephelometric Turbidity Unit (NTU), which is of positive correlation with wind velocity ($R^2 = 0.740$, $n = 193$, $P < 0.001$). Average DO concentration ranged from 3.43 mg/L in the AM 7:00 to 8.41 mg/L in the PM16:00 and DO at the bottom (about 1.0 m from the surface) was in general 30% lower than that on the surface. Seasonal changes of TN and TP were closely related to Chl-a concentration ($R^2 = 0.662$, $n = 174$, $P < 0.001$ and $R^2 = 0.845$, $n = 174$, $P < 0.001$, respectively). The average TN and TP concentrations were 2.13 mg/L (0.53 mg/L to 3.41 mg/L) and 0.21 mg/L (0.06 mg/L to 0.30 mg/L), respectively. TP had significant positive correlation with turbidity ($R^2 = 0.756$, $n = 174$, $P < 0.001$). Wind-induced sediment resuspension might be the primary reason that caused high rate of phosphorus release from the sediment in shallow water bodies (Schindler, 2006; Li et al., 2010).

3.2. Spatial and temporal dynamics of phytoplankton

The spatial distribution of phytoplankton biomass (Chl-a) during the entire observation period of July 2007 to December 2009 is shown in Fig. 3. Phytoplankton bloom occurred from June to late November and the Chl-a concentration peaked above 100 $\mu\text{g/L}$ from late August and early September. Phytoplankton recovery started from March and had a continuous increasing from late April to May. Different watercourses showed different Chl-a concentrations at the same period of time. The north watercourse with the highest flow velocity had the lowest average Chl-a concentration (35.24 $\mu\text{g/L}$) in all watercourses. While the south watercourse with the lowest flow velocity had the highest average Chl-a concentration, 9.1%–31.7% higher than other water courses. Correlation analysis showed negative correlation ($R^2 = -0.618$, $n =$

222, $P < 0.001$) between Chl-a concentration and flow velocity. There was no significant difference on nutrient concentrations among all the watercourses (NH_4^+-N : $P = 0.879$; TN: $P = 0.317$; TP: $P = 0.376$). Fig. 4 shows the distribution of Chl-a concentrations with different flow velocities over July 2007 to July 2008. During the period of phytoplankton bloom (from June to November), the higher Chl-a concentrations ($> 100 \mu\text{g/L}$) were often recorded in the condition with lower flow velocities ($< 0.15 \text{ m/s}$). The velocity of over 0.30 m/s would remarkably inhibit the yield of phytoplankton biomass. In the phytoplankton recovery season (from March to May), flow conditions with flow velocities ranged from 0 to 0.10 m/s are most favorable for rapid proliferation of phytoplankton.

Seasonal phytoplankton succession in the Lake was observed. Green algae (*Volvox*, *Ankistrodesmus* and *Ulothrix*) and diatoms (*Melosiraceae*) dominated in spring and autumn, cyanobacteria (*Microcystis*) in summer and diatoms in winter. However the phytoplankton composition showed less site-specific in the Lake. Some exceptions was recorded in the north watercourse that the cyanobacteria were often replaced by green algae as the dominated groups in summer, probably associated with strongly windy weather.

3.3. Phytoplankton abundance and composition in enclosure experiments

Under flow conditions of 0.15 m/s and 0.30 m/s, the Chl-a average concentrations were 37.5% and 26.1% lower than that in the still water control during the experiment period. It was found that the turbidity in the turbulent enclosures (around 82.3 NTU) was nearly 1.8 times higher than that in the still enclosures. Dominant phytoplankton groups in the enclosure experiment with flow velocity of 0.15 m/s is shown in Table 1, which indicates that changes in the turbulent environment were accompanied by the shift of dominance from cyanobacteria at still water to green algae after one week operation. In October and December, both enclosures were dominated by green algae, probably owing to the temperature change (Li et al., 2009). Under the condition of flow velocity of 0.30 m/s, the dominant phytoplankton group was remarkably less than these in the still water enclosure. The flowing enclosure was dominated by the green algae (*Ankistrodesmus*) and diatoms (*Cyclotella* and *Pleurosigma*), while in the still water enclosure, other genera like *Scenedesmus*, *Schroederia* and *Melosira* were also dominant.

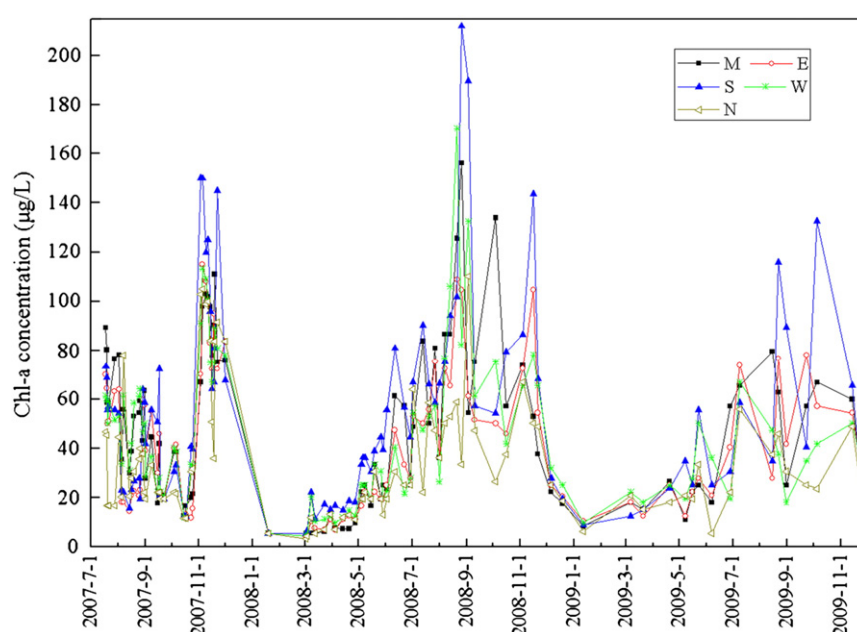


Fig. 3. Seasonal changes of phytoplankton biomass on each watercourse during the observation period.

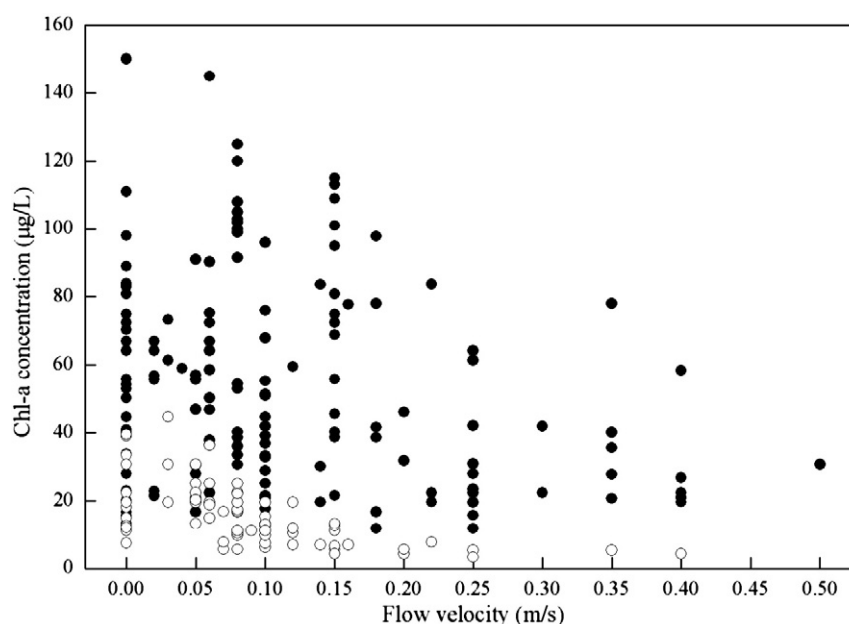


Fig. 4. Distribution of Chl-a concentrations in different ranges of flow velocity over July 2007 to July 2008. (open circles: colder seasons from March to May; solid circles: warmer seasons from June to November).

Daily variations of phytoplankton biomass observed in the four enclosures with the flow velocity of 0 m/s, 0.03 m/s, 0.06 m/s and 0.1 m/s, respectively in the third set of experiment are shown in Fig. 5. The average Chl-a concentrations in the three turbulent enclosures were 20.3%–36.7% lower than that in the still enclosure (35.64 µg/L). From May 10 to May 17, phytoplankton had a favorable growth condition of sunny and calm days with a continuous temperature rise. As a result, Chl-a peaked on May 17 or 18 with 33.89 µg/L, 51.58 µg/L, 45.21 µg/L and 81.33 µg/L under the velocity conditions of 0.10 m/s, 0.06 m/s, 0.03 m/s and 0 m/s, respectively. The result showed a clear inhibition effect of water flow on phytoplankton biomass. The turbidity under turbulent conditions was only 4.5% to 8.9% higher than that under the still water condition. All the four flowing enclosures had almost identical environmental conditions except for the circulating flow velocity.

The variation of phytoplankton composition under different flow velocity conditions was insignificant. In the first days, the cyanobacteria accounted for nearly 60% and the diatoms accounted for above 40% of the total phytoplankton biomass. After six days of pump running, the cyanobacteria disappeared and the green algae dominated under the velocity conditions of 0.06 m/s and 0.10 m/s. In the still water condition, the cyanobacteria survived one day longer than that in the turbulent conditions. In the last 5 days, diatoms were dominant in the still enclosure, while in the velocity conditions of 0.06 m/s and 0.10 m/s, it was the green algae that accounted for nearly 55% of the total phytoplankton biomass.

During the period of the third set of experiment, there were two heavy rainfall events on May 5 and May 18–19 with the rainfall depth of 10.2 mm and 18.6 mm respectively. As shown in Fig. 4, the Chl-a concentrations in all four enclosures were significantly decreased on May 6 and May 19.

4. Discussions

4.1. Shear effect of pump

The flow velocity in the enclosures was generated by submersible pumps, near which turbulence is much higher than the whole enclosure. Moreover, the flow circulating rate in the enclosures reached up to once per every 3 min, or circulation frequency of 0.0056/s, in the experiments. Therefore mechanical damage to algae cells might have occurred within the pumps. Very few studies have directly examined the shear effect which is caused both by high shear stress and pressure in pump. Bronnenmeier and Markl (1982) examined, among other algae, two green algae *Chlamydomonas reinhardtii* and *Chlorella vulgaris* and one cyanobacterium *Anacystis nidulans* which are often observed in freshwater bodies. Using post-shear cell proliferation rate and release of intracellular substances as indicators, the authors found that the critical stress values (below which no essential damage of the microorganism cultures will occur) were 15–20 bar and 2400 rpm (round per minute, corresponding to rotating velocity of pump rotor) for *C. reinhardtii*, and around 100 bar and 3000 rpm for

Table 1
Dominant phytoplankton species in enclosure with flow velocity of 0.15 m/s and in still water enclosure.

| | Before pump running | After pump running | | |
|----------------------------------|---|---|---|--|
| | 2007-09-01 | 2007-09-08 | 2007-10-04 | 2007-11-14 |
| Enclosure with 0.15 m/s velocity | Cyanobacteria (<i>Microcystis</i> , <i>Merismopedia</i>), Green algae (<i>Ankistrodesmus</i> , <i>Scenedesmus</i> , <i>Schroederia</i> , <i>Crucigenia</i>) | Green algae (<i>Ankistrodesmus</i> , <i>Scenedesmus</i> , <i>Schroederia</i>) | Green algae (<i>Ankistrodesmus</i> , <i>Schroederia</i>) | Green algae (<i>Ankistrodesmus</i>), Diatoms (<i>Pleurosigma</i>) |
| Still enclosure | Cyanobacteria (<i>Microcystis</i> , <i>Merismopedia</i>), Green algae (<i>Ankistrodesmus</i> , <i>Scenedesmus</i> , <i>Schroederia</i> , <i>Crucigenia</i>) | Cyanobacteria (<i>Microcystis</i> , <i>Merismopedia</i>), Green algae (<i>Ankistrodesmus</i> , <i>Scenedesmus</i> , <i>Schroederia</i>) | Green algae (<i>Ankistrodesmus</i> , <i>Scenedesmus</i> , <i>Schroederia</i>) | Green algae (<i>Ankistrodesmus</i> , <i>Scenedesmus</i>), Diatoms (<i>Pleurosigma</i>) |

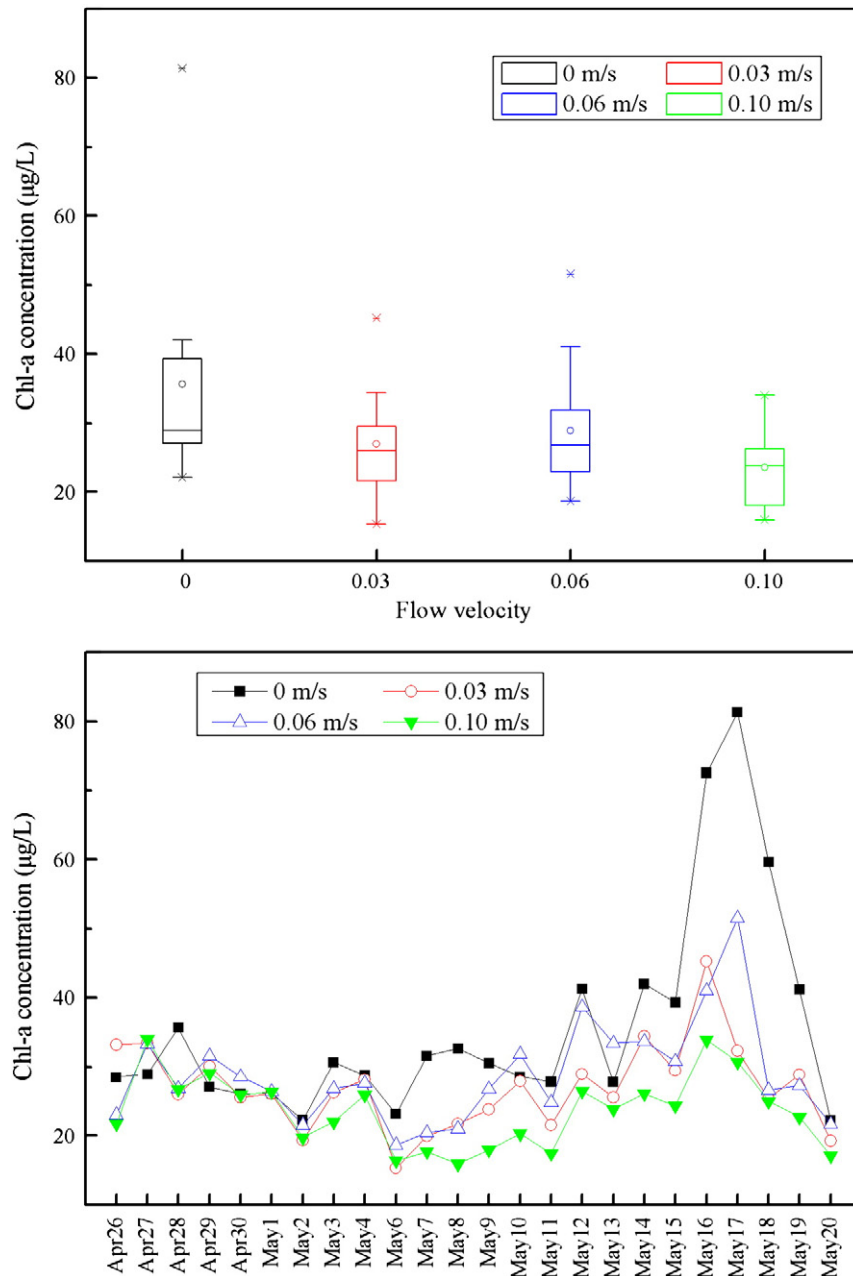


Fig. 5. Daily variation of phytoplankton biomass under different flow conditions in the enclosure experiment.

C. vulgaris. *A. nidulans* was found to have higher stress capacity compared to these 2 green algae. The submersible pumps used in the present study are centrifugal pumps, specifically designed for generation of recirculation flow with very low head. The pressure (<0.1 bar) and rotating velocity (<750 rpm) are much lower compared to the critical stress values observed in the study. Vandanjon et al. (1999) studied the effect of the pump circulation on marine diatom *Haslea ostrearia* (three clones with average modal length of 37.1, 65.5 and 77.8 µm, respectively) and concluded that cell damage increased with the increase of circulation frequency, number of rotation of a cell in pump, rotating velocity of pump rotor and algae size, and was related to the type of pump as well. In an experiment with a centrifugal pump, the results indicated that the cell damage rate eventually kept around 10% when number of rotation of a cell in pump exceeds 1000, with the circulation frequency of 0.033/s and rotating velocity of 1320 rpm. Considering the lower circulation frequency (0.0056/s), lower rotating velocity (<750 rpm) and smaller algae size (3–16 µm) applied in the present

study, the cell damage rate due to the shear effect of pump should be far less than 10%, though the exact value is subject to further investigation.

4.2. Inhibitory effects of turbulence flow on phytoplankton biomass

Significant spatial variation of phytoplankton biomass observed in the Zhongxin Lake could be explained by the variation of flow velocity as the result of coupled effects of wind driven flow and lake morphology. With its unique geographical feature, Zhongxin Lake has different average flow velocities in each watercourse associated with prevailing wind. Higher phytoplankton biomasses were often recorded in the south and middle watercourses where shallow-circulation flow could be hardly maintained. While in the north watercourse, higher flow velocities are the primary reason that caused lower phytoplankton biomasses. Results from the enclosure experiments further revealed the inhibitory effect of circulating flow velocities on phytoplankton biomass. Compared with the three turbulent enclosures, for most of the

experiment period, more phytoplankton was found in the still water enclosure. Different flow velocities had different inhibitory effects. Flow velocity of 0.15 m/s had the highest inhibitory effect rate of 37.5%, while the lower inhibitory effect was found under flow velocities of 0.06 m/s and 0.03 m/s (20.3% and 24.3%, respectively). The inhibitory effect of 0.10 m/s was 33.7%, which showed relatively significant inhibition of phytoplankton biomass. However, as discussed in Section 4.1, it should be noticed that shear stress in the pump might have caused up to 10% of cell damage. In the first two sets of enclosure experiment, much higher turbidity was observed in the flowing enclosures compared to the still water enclosures, implying that sediment resuspension might also be the reason that inhibited the phytoplankton biomass by decrease of underwater light intensity. However, in the third set of enclosure experiment with lower flow velocity and very weak sediment resuspension, the inhibitory effect of turbulence flow on phytoplankton biomass was also evident. This result cannot be explained by the sediment resuspension and indicates that turbulence flow may have a direct disturbance effect inhibiting phytoplankton biomass.

4.3. Critical flow velocity

A common paradigm in aquatic ecology is that there may be a critical flow velocity or mixing hydrodynamic conditions for reducing phytoplankton bloom events (Huisman et al., 1999; Mitrovic et al., 2008). Many researchers have tried to explore the critical flow conditions. Mitrovic et al. (2003) recommended that the critical flow velocity of 0.05 m/s applied in Barwon–Darling River of Australia was sufficient for the suppression of *Anabaena circinalis* and the value might have potential to be applied to other rivers in similar climatic zones. Through the enclosed flume experiments with identical environmental conditions (including nutrients, light etc.), Huang et al. (2008) indicated that flow velocity below 0.4 m/s would not inhibit the algae growth and the occurrence of blooms. In the present study, it was found that average flow velocity of 0.13 m/s in the north watercourse resulted in effective inhibition of phytoplankton biomass. In the enclosure experiments, the circulating flow velocities between 0.03 m/s and 0.30 m/s resulted in the decrease of Chl-a concentrations by 20.3% to 37.5% compared with that in still enclosures. No threshold velocities were observed from the field observations and enclosure experiments. Therefore the present study indicates that a universal critical flow velocity might not exist, because each freshwater water body has its unique physical, chemical and ecological features like water body size, morphology, nature of water flow, sediment condition, nutrient level, water temperature, light intensity and species composition, which may all affect the critical velocity value.

4.4. Effects of flow velocity on phytoplankton composition

Existing theory has predicted that in freshwater bodies, intensified turbulent flow will lead to species replacement from buoyant cyanobacteria toward green algae and diatoms. Changes in turbulent mixing inducing shift competition for light between phytoplankton species was indicated by Huisman et al. (2004). In our study, in the enclosures with high flow velocities (>0.15 m/s), it was found that the phytoplankton group was fewer compared with the still enclosures and transition occurred from dominance by cyanobacteria to dominance by green algae. It might be the intensive water flow that brought the green algae to the light enriching areas and stimulated their growth. However, the variation of species group under the lower velocity conditions (<0.10 m/s) was insignificant.

For natural waters, climate change in the turbulence structure may induce major shifts in the species composition of phytoplankton communities (Huisman et al., 2004; Markensten et al., 2010). In the present study, seasonal change, temperature and probably rainfall as well, might be the dominant factors affecting the change of species composition in these small size enclosures with low flow rates.

5. Conclusions

Through 2.5-year-long intensive field observation in Zhongxin Lake, it has been found that phytoplankton abundance in this system does not depend primarily only on the flow velocity, but also on nutrients, morphology and morphometry of the lake, while differences between watercourses can be explained by water flow. A strong negative correlation ($R^2 = -0.618$, $n = 222$, $P < 0.001$) was found between Chl-a concentration and flow velocity. The hydro-meteorological factors such as water flow, rainfall and temperature change significantly relate to the temporal and spatial dynamics of phytoplankton. Enclosure experiments with five different circulating flow velocities have further shown the inhibition effect of water flow on the phytoplankton biomass and composition. The average Chl-a concentrations in the flowing enclosures were 20.3%–37.5% lower than that in their corresponding still water enclosures during the entire experiment period. Shear stress within pumps might have caused up to 10% of cell damage, while the exact value is subject to further investigation. Flow velocities at 0.15 m/s and 0.30 m/s have significant effect on the variation of dominant phytoplankton species, shifting from cyanobacteria in still water enclosure to green algae and diatoms in turbulent enclosures. The study results highlight that a universal value of critical flow velocity in freshwater bodies probably do not exist due to the difference in many influencing factors such as water body size, morphology, nature of water flow, sediment condition, nutrient level, water temperature, light intensity and species composition. Therefore it is suggested that sufficient experiments should be conducted for each water body before the relationship between phytoplankton growth and water flow velocity is applied to suppress its algae bloom occurrence.

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