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Submerged vegetation removal promotes shift of dominant phytoplankton functional groups in a eutrophic lake

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ABSTRACT

Historical data indicate that the dominance of submerged plants in Dianchi Lake in the 1960s was characterized by low algal density with dominance of non-toxic group J (*Scenedesmus*, *Pediastrum*, etc.). The removal of submerged plants, which began in the 1970s, resulted in the expansion of bloom-forming *Microcystis* (group M). Laboratory experiments suggested that *Microcystis aeruginosa* was inclined to grow and develop at elevated temperatures. The growth of *Scenedesmus obliquus* was slower than that of co-cultivated *M. aeruginosa* in the absence of *Ceratophyllum demersum*, especially at higher temperatures. The existence of submerged plant *C. demersum* could inhibit the growth of the harmful algae *M. aeruginosa* and this inhibitory effect by *C. demersum* was enhanced with an increase in temperature. Instead, with *C. demersum*, the growth of *S. obliquus* was not inhibited, but the co-cultivated *M. aeruginosa* was eliminated in a short time. Combined with the historical data and laboratory experiments, it was indicated that the submerged plants might play important roles in the dominance of the non-toxic group J in the historical succession. Consequently, the introduction of the submerged plant such as *C. demersum* might alter the dominant phytoplankton functional groups from M to J and benefit the restoration of the eutrophic lake.

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Introduction

Eutrophication of shallow lakes is characterized by the disappearance of diverse submerged vegetation and dominance of phytoplankton. Since the 1950s, lakes worldwide changed from clear to turbid because of eutrophication (Blindow, 1992). The coverage of aquatic plants in Dianchi Lake in Yunnan, China, exceeded 90% (Li et al., 1963; Luo et al., 2006), and water transparency was more than 2 m in the 1960s (Yu et al., 2000). From the 1970s to the 1980s, the lake had a low coverage and biodiversity of submerged macrophytes because of the disappearance of numerous species such as the communities of *Ottelia acuminata*, *Chara vulgaris*, and *Ceratophyllum demersum* from the

lake (Dai, 1985; Li, 1985; Dai, 1986; Yu et al., 2000). However, total phytoplankton biomass sharply increased, especially that of *Microcystis*, and water transparency decreased to less than 0.3 m in 2009 (Mo et al., 2007; Zhang, 2007; Wang, 2010; Yu et al., 2010).

Restoration of submerged vegetation in the phytoplankton-dominated lake is crucial in transforming the present state of shallow lakes. Submerged plants and phytoplankton share similar resources essential for growth. Studies indicated that submerged plants could help inhibit the growth of phytoplankton by competing for nutrients or light (Filzgerald, 1969; Boyd, 1971; Phillips et al., 1978; Rørslett et al., 1986; Ozimek et al., 1990; Van Donk et al., 1993; Mjelde and Faafeng, 1997; Lombardo and Cooke, 2003). Submerged plants could also affect phytoplankton biomass

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through allelopathic effects. Release of allelopathically active compounds by submerged macrophytes such as *C. demersum*, *Vallisneria gigantea*, *Najas*, *Chara*, and *Myriophyllum* could significantly inhibit the growth of cyanobacteria, particularly *Microcystis* (Wium-Andersen et al., 1982; Kleiven and Szczepańska, 1988; Saito et al., 1989; Gross et al., 2003; Xian et al., 2006).

Studies on the effects of submerged plants on phytoplankton have thus far focused on algal biomass (Chlorophyll *a* (Chl-*a*)) (Norlin et al., 2005) or selected species (Körner and Nicklisch, 2002). However, aquatic ecosystem restoration entails more than mere reduction in phytoplankton biomass. Changing lake dominance from harmful algae to less harmful algae is also important. Cyanobacterial blooms occur year-round in Dianchi Lake, especially the harmful algae *Microcystis*, producing microcystins and other toxins (Song et al., 1999; Lin et al., 2001). The restoration of this lake involves reduction in both harmful algae and total phytoplankton biomass.

Lu et al. (2012) indicated that restoration of submerged plants in Dianchi Lake could revert the degraded ecosystem into biodiversity levels close to its original state. However, the effect of submerged plants on the composition of dominant phytoplankton during restoration was not investigated. In the present study, we first introduced the phytoplankton functional group theory (Reynolds et al., 2002; Padisák et al., 2009) into the eutrophic lake. We proposed a hypothesis that submerged plants could promote changes in the structure and composition of phytoplankton functional groups in eutrophic lakes.

The present study analyzed the data, collected over 50 years, on submerged plants and phytoplankton functional groups in Dianchi lake (24°40'N–25°02'N and 102°36'E–103°40'E; Yunnan, China). Our analysis focused on the degradation of submerged plants and changes in phytoplankton functional groups. We aimed to identify the relationship between the disappearance of submerged plants and the dominance of phytoplankton functional groups. We'd like to provide some theoretical basis on the roles that submerged plants played in the phytoplankton composition changes and future water restoration.

1. Materials and methods

1.1. Historical data and analysis

Historical data on phytoplankton and submerged vegetation in Dianchi Lake were collected from the literatures. Annual average algal density and biomass in the past 50 years were statistically analyzed; abrupt change points were detected using Change-Point Analyzer 2.3, the Sequential Regime Shift Detection Software version. Annual average coverage and species abundance of aquatic plants were also analyzed.

1.2. Laboratory experiments

1.2.1. Macrophytes and algae culture

Samples of *C. demersum* were collected from Dianchi Lake in Yunan, China. The plants were carefully rinsed with tap water to remove adhering epiphytes and zooplankton (Jasser, 1995; Mulderij et al., 2005; Wu et al., 2007) and then acclimated for three months under laboratory conditions.

Microcystis aeruginosa (a toxic species isolated from Dianchi Lake) and *Scenedesmus obliquus* (also isolated from Dianchi Lake), typical representatives of groups M and J, were provided by the Freshwater Algae Culture Collection of the Institute of Hydrobiology, Chinese Academy of Sciences in Wuhan, China. Prior to the experiments, the algae were batch-cultured in

2000 mL Erlenmeyer flasks with 1600 mL of BG₁₁ medium (Rippka et al., 1979) at room temperature (25°C) under a 12:12 light/dark cycle (25 μmol photons/(sec·m²)).

1.2.2. Experimental design

The highest temperature in Dianchi Lake is about 30°C, occurring in summer. The lowest temperature is about 15°C, occurring in winter. Thus, temperature gradients (15, 20, 25, and 30°C) were set in this laboratory experiment.

M. aeruginosa (initial optical density of 0.06), *S. obliquus* (initial optical density (OD) of 0.06), and a mixture of the two species (OD ratio of 1:1) were cultured, respectively, in the absence or presence of 3 g fresh weight (fw)/L of *C. demersum*. All of the cultures were placed under temperature gradients (15, 20, 25, and 30°C) with a photon supply of about 25 μmol photons/(sec·m²) under a 12:12 light/dark cycle. The cultivation flasks were covered with a parafilm, and each treatment had three replicates. The cultures were shaken manually twice a day to maintain cells in suspension. *C. demersum* exhibited good growth and development during the experimental periods; however, its growth details were not recorded. Regular samplings were conducted every 2 days. The experiments were conducted for 20 days in total.

1.2.3. Measurement of growth

In the absence or presence of *C. demersum*, OD₆₆₅ for single-cultured *M. aeruginosa* and OD₆₈₀ for single-cultured *S. obliquus* (UV/Vis spectrophotometer, TU-1810, Beijing Purkinje General Instrument Co., Ltd., China) were measured every 2 days to monitor their growth.

Chl-*a* was extracted in darkness at 4°C and measured by spectrophotometry, as described by Lichtenthaler and Buschmann (2001). Cells that had been centrifuged (4°C, 12,000 r/min, 10 min) were extracted with 95% ethanol for 24 hr at 4°C in the dark. Then absorbance at 665 (A₆₆₅), 649 nm (A₆₄₉) were measured (UV/Vis spectrophotometer, TU-1810, Beijing Purkinje General Instrument Co., Ltd., China). The Chl-*a* content (C_{Chl-*a*}, mg/L) was calculated by Eq. (1):

$$C_{\text{Chl-}a} = 13.95 \times A_{665} - 6.88 \times A_{649}. \quad (1)$$

When co-cultivating *M. aeruginosa* and *S. obliquus* in the absence or presence of *C. demersum*, cell density of each algae was calculated for measurement of the growth. For each replicate, 2 mL cultures were sampled every 2 days and were fixated with Lugol's fixative. The fixative samples were viewed under an inverted microscope at 400× magnification to count the cell number of each kind of algae.

1.2.4. Measurement of total dissolved phosphorous (TDP)

The concentration of TDP was measured according to Protocols for Standard Observation and Measurement in Aquatic Ecosystems of Chinese Ecosystem Research Network (CERN) (Huang et al., 2000; Cai, 2007).

1.2.5. Data processing

Mean values and standard deviations were calculated from the different replicates (*n* = 3). One-way analysis of variance according to SPSS 18.0 was used to compare differences between treatments, taking *p* < 0.05 as significant.

2. Results

2.1. Changes of dominant phytoplankton composition in Dianchi Lake

This study first examined the historical changes in dominant phytoplankton functional groups of the past 50 years. Group J dominated the lake in the 1960s, and was mainly composed of *Pediastrum simplex*, *Scenedesmus*, and *Coelastrum*. Group M had been rising since the 1980s and replaced assemblage J to become the primary dominant functional group by 2000 (Table 1) (Li et al., 1963; Qian et al., 1985; Zhang et al., 2005; Wu et al., 2010).

2.2. Changes of algal density and biomass (Chl-*a*) in Dianchi Lake

With the shift in the composition of dominant phytoplankton functional groups, algal biomass and abundance quickly increased in the last 50 years (Fig. 1) (Li et al., 1963; Liu, 2001; Mo et al., 2007; Zhang, 2007). As indicated in the survey, two change points have been detected. Algal density shifted from 0.0649×10^7 cells/L in 1957 to 15×10^7 cells/L in 2001, and further to 31×10^7 cells/L in 2011 (Fig. 1a). Biomass shifted from 3.4 $\mu\text{g/L}$ in 1978 to 41.68 $\mu\text{g/L}$ in 1996, and further to 85 $\mu\text{g/L}$ in 2007 (Fig. 1b). The rapid growth and development of both algal density and biomass was found to have started in the late 1990s (Fig. 1).

2.3. Historical changes of aquatic vegetation in Dianchi Lake

The composition and coverage of the aquatic vegetation in Dianchi Lake evidently changed. In the 1960s, Dianchi Lake was clean, characterized by aquatic macrophytes consisting mainly of submerged plants (Fig. 2a and c), which resembled a “flower lake” when plants were in full blossom from spring to autumn (Li et al., 1963; Luo et al., 2006). At that time, the coverage of the submerged vegetation reached 90%, dominated by the species *O. acuminata* (28.1%), *Potamogeton malaianus* (24.1%), *Myriophyllum spicatum* (11.2%), *Potamogeton pectinatus* (9.5%), *Vallisneria spiralis* (5.4%), *Potamogeton maackianus* (4.8%), *Potamogeton crispus* (2.5%), and *C. demersum* (2.5%) (Fig. 2d). However, the submerged plants,

including *O. acuminata*, *C. demersum*, *P. crispus*, *P. maackianus*, *P. malaianus*, and *V. natans*, have gradually disappeared since the 1970s because of eutrophication (Fig. 2d) (Dai, 1985; Li, 1985; Dai, 1986; Yu et al., 2000; Lu et al., 2012). The species biodiversity was reduced from 1.7 in the 1960s to about 0.45 in the 1990s (Fig. 2b). The submerged vegetation was dominated by *P. pectinatus* with 4.4% coverage in the 1990s and 1.8% in 2010 (Fig. 2d) (Yu et al., 2000; Lu et al., 2012).

2.4. Growth of *M. aeruginosa* or *S. obliquus* with or without *C. demersum*

2.4.1. Optical density

In the absence of *C. demersum*, the growth of *M. aeruginosa* was increasing with warming temperature. It was indicated that *M. aeruginosa* grew slowest at 15°C, and fastest at 30°C (Fig. 3a). Statistical analysis indicated that the growth of *M. aeruginosa* was significantly slower at 15°C than that at 20, 25 and 30°C ($p < 0.05$). However, it was demonstrated that *C. demersum* could significantly inhibit the growth of *M. aeruginosa* ($p < 0.05$). Higher temperatures indicated more adverse effects of *C. demersum* on the growth of *M. aeruginosa*. In the presence of *C. demersum*, the decrease of *M. aeruginosa* at 15, 20, 25 and 30°C, occurred at day 12, day 10, day 6 and day 4, respectively (Fig. 3b). Warming temperature could seemingly help eliminate *M. aeruginosa*.

In the present study, *S. obliquus* grew well under all temperatures. There was no significant difference of the growth of *S. obliquus* among temperature gradients ($p > 0.05$). Besides, it seemed that the introduction of *C. demersum* had no inhibitory effects on *S. obliquus* under all temperatures ($p > 0.05$) (Fig. 3c and d).

2.4.2. $C_{\text{Chl-}a}$

Changes of $C_{\text{Chl-}a}$ in *M. aeruginosa* and *S. obliquus* with or without *C. demersum* were similar with OD (Fig. 4). In the absence of *C. demersum*, $C_{\text{Chl-}a}$ in *M. aeruginosa* at 15°C was significantly lower than that at 20, 25 and 30°C ($p < 0.05$) (Fig. 4a). However, the introduction of the submerged plant significantly reduced the $C_{\text{Chl-}a}$ in *M. aeruginosa*, which decreased faster with warmer temperatures. $C_{\text{Chl-}a}$ in *M. aeruginosa* began decreasing at day 4, day 6, and day 12, at 30, 25 and 20°C, respectively (Fig. 4b).

Table 1 – Changes in dominant phytoplankton functional groups from the 1950s (Li et al., 1963; Qian et al., 1985; Wu et al., 2010; Zhang et al., 2005).

Year	Dominant functional groups	Subdominant functional groups	Taxa
1957	J	N P MP Lo	<i>Pediastrum simplex</i> ; <i>Scenedesmus</i> ; <i>Coelastrum</i> <i>Cosmarium</i> <i>Staurodesmus</i> ; <i>Closterium</i> <i>Surirella robusta</i> <i>Ceratium hirundinella</i>
1982–1983	J	P MP M	<i>Pediastrum</i> ; <i>Scenedesmus</i> <i>Melosira granulata</i> <i>Oscillatoria tenuis</i> ; <i>Surirella capronii</i> <i>Microcystis</i> sp.
2001 afterwards	M	J H1	<i>Microcystis aeruginosa</i> ; <i>Microcystis weissenbergii</i> <i>Pediastrum</i> ; <i>Scenedesmus</i> <i>Aphanizomenon flos-aquae</i> ; <i>Anabaenopsis</i>

Fig. 1 – Changes in algal density (a) and biomass (Chl-a) (b) of Dianchi Lake in the past 50 years (Li et al., 1963; Liu, 2001; Mo et al., 2007; Zhang, 2007).

Different from *M. aeruginosa*, there was no significant difference of $C_{\text{Chl-a}}$ in *S. obliquus* under all temperatures ($p > 0.05$) (Fig. 4c). The introduction of *C. demersum* showed no significant inhibitory effects on $C_{\text{Chl-a}}$ in *S. obliquus* under all temperatures ($p > 0.05$) (Fig. 4d), but promoted the accumulation of $C_{\text{Chl-a}}$ in *S. obliquus*.

2.4.3. TDP

The TDP was higher in *C. demersum* treatment than in control at all temperatures in the case of single-cultured *M. aeruginosa*. The TDP of the control at 20, 25 and 30°C was decreasing faster than that under 15°C ($p < 0.05$). There was no significant difference between that at 20, 25, and 30°C ($p > 0.05$). However, in the *C. demersum* treatment, there was no

significant decreasing of TDP at 20, 25 and 30°C cultivation ($p > 0.05$); the TDP was lower at 15°C than at 20, 25 and 30°C ($p < 0.05$) (Fig. 5).

In the case of single *S. obliquus* cultivation, the TDP of all cultures (both control and treatment under all temperatures) were significantly decreased ($p < 0.05$). The TDP in the *C. demersum* treatment cultivation seemed to be higher than that in the control at all temperatures ($p > 0.05$) (Fig. 6).

2.4.4. Growth of co-cultured *M. aeruginosa* and *S. obliquus* with or without *C. demersum*

In the co-cultivation without *C. demersum*, the algae density of *M. aeruginosa* was the lowest at 15°C, whereas the algae density of *S. obliquus* was the highest at this temperature

Fig. 2 – Changes of aquatic plant coverage (a), macrophyte biodiversity (b), submerged plant coverage (c) and submerged plant composition (d) from the 1960s to 2010 in Dianchi Lake.

Data cited from Li et al. (1963), Dai (1985), Li (1985), Yu et al. (2000), Yang et al. (2004), Shen et al. (2010), Ni et al. (2011), and Lu et al. (2012).

Fig. 3 – Optical density (OD) of *M. aeruginosa* (a, b) and *S. obliquus* (c, d) in the absence or presence of *C. demersum* at four temperature gradients.

(Fig. 7a and c). The algae density of *M. aeruginosa* had a faster growth rate with a warmer temperature and the highest algae density of *M. aeruginosa* occurred at 30°C.

The introduction of *C. demersum* significantly inhibited the growth of *M. aeruginosa* ($p < 0.05$). The algae density of *M. aeruginosa* was decreasing faster under 30°C, whereas *S. obliquus* was growing faster at this temperature (Fig. 7b and d).

3. Discussion

Submerged macrophytes in shallow lakes are often associated with high water transparency (Moss et al., 1996). Dianchi Lake was clean before the 1950s, with a high coverage of submerged plants (Li et al., 1963). The present study indicated that the retreat of submerged plants in this lake was followed by rapid algal growth and development (Figs. 1 and 2). The

Fig. 4 – Chl-a content in *M. aeruginosa* (a, b) and *S. obliquus* (c, d) in the absence or presence of *C. demersum* at four temperature gradients.

Fig. 5 – TDP content in *M. aeruginosa* cultivation with or without *C. demersum* at 15°C, 20°C, 25°C and 30°C.

result was consistent with the findings by Phillips et al. (1978) that the rapid algal growth was the effect rather than the cause of the retreat of macrophytes.

The present study indicates that Dianchi Lake was dominated by group J rather than group M in the 1950s in terms of phytoplankton functional groups. At this time, the lake was with high coverage of submerged plants. Later, Most

submerged vegetation species were reduced or disappeared because of eutrophication in the 1970s (Fig. 2). The gradual alteration of dominant phytoplankton functional groups from J to M occurred from the 1980s (Table 1). The rapid increase in algal density and biomass, as well as the, occurred around late 1990s (Fig. 1). The data suggested that the sharp decrease in submerged vegetation seemed to affect the historical

Fig. 6 – TDP content in *S. obliquus* cultivation with or without *C. demersum* at 15°C, 20°C, 25°C and 30°C.

Fig. 7 – Algae density of co-cultivation *M. aeruginosa* (a, b) and *S. obliquus* (c, d) in the absence or presence of *C. demersum* at four temperature gradients.

phytoplankton succession, shifting the dominant group from J to M, then leading the great algae biomass.

Laboratory experiments also seemed to indicate that the presence of submerged plants played important roles in the dominance of group J in Dianchi Lake in the 1960s. The sharp retreat of submerged plants caused the dominance of group M in Dianchi Lake in recent years.

The present laboratory experiments indicated that the growth of *M. aeruginosa* was significantly inhibited in the presence of 3 g/L *C. demersum* ($p < 0.05$; Figs. 3b and 4b). It was suggested that submerged vegetation inhibited algal growth, because the high surface area to volume ratio of these non-root plants make a contribution to the competition for nutrients such as phosphorus (Lombardo and Cooke, 2003). In the present study, in order to exclude the influences of plants competition, the TDP content during the cultural period was also measured. It was indicated that nutrients were not limited factors. The TDP content in the treatment (presence of *C. demersum*) was higher than that in the control (absence of *C. demersum*) (Fig. 5). Besides, the low biomass of *C. demersum* had only a slight effect in shading the light. Thus, the inhibitory effects of *M. aeruginosa* by *C. demersum* might be caused by allelopathy. The result was in agreement with Gross et al. (2003), who also indicated the allelopathic activity of *C. demersum* to *Microcystis*. The experiments also indicated that the effect of *C. demersum* on *M. aeruginosa* is related to cultivation temperature. Metabolic processes have been reported to be profoundly affected by temperature (Rhee and Gotham, 1981; Davidson, 1991). Low temperature can increase the amount of carbohydrates per cell, but decrease the amounts of protein and lipids (Aronson, 1973). In the present study, the inhibitory effect on *M. aeruginosa* by *C. demersum* was increased with warming temperatures (Figs. 3b and 4b).

Different from *M. aeruginosa*, there was no significant inhibitory effect of *C. demersum* on *S. obliquus* at all temperatures (Figs. 3d and 4d). Instead, the introduction of the submerged plant promotes the accumulation of C_{Chl-a} in *S. obliquus*. The growth of *S. obliquus* in the absence or presence of *C. demersum* was accompanied with decreasing TDP (Fig. 6), but the TDP in the *C. demersum* treatment was higher than that of the control without *C. demersum* cultivation.

In the co-cultivation of *M. aeruginosa* and *S. obliquus*, it was indicated that *S. obliquus* was dominant in the presence of *C. demersum*, especially at 30°C (Fig. 7b and d). Without *C. demersum*, *M. aeruginosa* was dominant, which also had the fastest growth at 30°C (Fig. 7a and c).

Therefore, in the 1960s, the coverage of *C. demersum* was about 2.5%. The plants together with other submerged plants might have played important roles in the dominance of functional group J. In the current water restoration, the re-introduction of these submerged plants was necessary (Lu et al., 2012). The present study indicated that it might be of help in changing the dominant phytoplankton from the toxic M to the non-toxic group J. It is better to conduct the re-introduction in summer, when *M. aeruginosa* was of great biomass. *M. aeruginosa* exhibited the tendency to break out at high temperatures in summer and autumn, which was also the appropriate time for *C. demersum* to inhibit the growth of *M. aeruginosa*. The elimination of *M. aeruginosa* by *C. demersum* is higher in summer with high temperature.

4. Conclusions

The historical data on the composition of submerged plants and phytoplankton from the 1950s, combined with the results

of the laboratory experiment, indicated that the disappearance of submerged plants resulted in the dominance of group M in Dianchi Lake. Without submerged plants, *M. aeruginosa* exhibited faster growth than *S. obliquus*, especially at higher temperature. This increase led to an abrupt rise in algal density and biomass in Dianchi Lake, which has been observed in recent decades. Re-introduction of historically dominant species such as *C. demersum* might help for further restoration in Dianchi Lake. It is better to conduct the re-introduction in summer.

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