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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.

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 *Otellia 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 (Chlophyll *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 BG_{11} medium (Rippka et al., 1979) at room temperature (25°C) under a 12:12 light/dark cycle (25 μmol photons/(sec·m^2)).

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·m^2) 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*, OD_{665} for single-cultured *M. aeruginosa* and OD_{680} 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 (A_{665}), 649 nm (A_{649}) were measured (UV/Vis spectrophotometer, TU-1810, Beijing Purkinje General Instrument Co., Ltd., China). The Chl-*a* content ($C_{Chl\text{-}a}$, mg/L) was calculated by Eq. (1):

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

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.