Journal of Oceanology and Limnology
Vol. 38 No. 1, P. 93-101, 2020
https://doi.org/10.1007/s00343-019-8362-z

Response of benthic algae to environmental conditions in an urban lake recovered from eutrophication, China*

WANG Tao, WANG Qing, XIA Shuang, YAN Chunlan, PEI Guofeng**

Hubei Provincial Key Laboratory for Protection and Application of Special Plant Germplasm in Wuling Area of China, South-Central University for Nationalities, Wuhan 430074, China

Received Dec. 20, 2018; accepted in principle Feb. 13, 2019; accepted for publication Apr. 15, 2019

Abstract Benthic algae communities dominate the primary production in littoral zone of shallow lake. To understand the long-term effect of alteration in the composition of benthic algae community assemblage in such as a lake in China, we analyzed the benthic algae developments and indicators in the Donghu Lake in Wuhan, central China in 2004 and 2014. We compared the benthic algae biomass, compositions, and species richness of aquatic macrophytes and the changes of primary physicochemical parameters. The results show that in the 10-year period, chl *a* and conductivity declined significantly but nutrient level of the whole lake remained largely stable. The benthic algae biomass doubled and the relative proportion of green algae increased, whereas the benthic diatom ratio decreased. The benthic diatom assemblages and taxa differed in a number of ways, showing more epiphytic diatom species, and the relative abundance and species richness changed markedly. The number of aquatic macrophyte species increased from 3 in 2004 to 15 in 2014, presenting a remarkable recovery from previous eutrophication conditions. The changes of water level, chl *a*, and conductivity played a crucial role in governing aquatic macrophytes re-colonization in the littoral zones in the period. The ecological characteristics of littoral benthic diatoms reflect habitat coupling as indicated by redundancy analysis. Therefore, the close link between benthic algae and macrophyte recovery demonstrates that the benthic algae metrics are much more useful than nutrient levels to quantify the process of restoration in the lake.

Keyword: benthic algae; benthic diatom; lake restoration; aquatic macrophyte; water level

1 INTRODUCTION

Algae have been used as bio-indicators to evaluate the environment for almost 100 years (Stevenson, 2014). Bio-indicators cannot necessarily replace physicochemical ones, but are complement to physicochemical factors. Algae biomass, species composition, and diversity tend to reflect the ecological status of a water body more accurately than physicochemical factors (Liu and Shen, 2008). Because benthic algal communities respond quickly to environmental changes, their use as indicators is promoted to provide information on the degradation or restoration of aquatic ecosystems (Gaiser et al., 2011). Benthic algae can attach to a variety of natural substrates, including stones, submerged macrophytes, and soft sediments, as well as artificial substrates. Benthic algae are considered suitable indicators to the trophic status of water bodies, and their assemblages are significantly related to environmental conditions (Poulíčková et al., 2004; Simkhada et al., 2006). Although the routine monitoring of benthic diatoms is less frequently used in lakes than in rivers or streams, several indicators have been developed based on littoral benthic diatoms (Stenger-Kovács et al., 2007; Triest et al., 2012), several studies have suggested that littoral benthic diatoms can respond along environmental gradients, particularly nutrient gradients (Gottschalk and Kahlert, 2012; Bennion et al., 2014).

---

* Supported by the National Natural Science Foundation of China (No. 30970550), the Fundamental Research Funds for the Central Universities, South-Central University for Nationalities (No. CZW18019), and the Major Technological Innovation of Hubei Province of China (No. 2018ABA093)

** Corresponding author: peigf@mail.scuec.edu.cn

Studies on benthic diatoms in freshwater lakes have generally focused on the quantitative and qualitative differences of diatom communities between seasons and/or sites (Lim et al., 2007; Logan and Taffs, 2013). To date, most efforts are directed at investigating sedimentary diatom assemblages to record environmental changes in freshwater lakes, as well as quantifying changes in diatom species composition due to human activities (Smol and Stoermer, 2010; Hadley et al., 2013). However, few studies (Bennion et al., 2015) have examined spatial and temporal variation in diatom compositions during the process of lake restoration.

Donghu Lake is a typical shallow freshwater lake in Wuhan, a mega city in the central China. The lake experienced a period of heavy eutrophication due to the input of domestic and industrial sewage and agricultural runoff in the 1980s and 1990s (Liu et al., 2014). In response to the observed damage to the water quality and loss in the biodiversity, great efforts to improve water quality have been made in recent decades such as overall reduction of external pollution sources, partial dredging of sediment, and sewage interception. In addition, the Donghu Lake is connected with the sand lake and the water level is slightly reduced. These have led to a gradual improvement of environmental conditions in the 2000s, and aquatic macrophytes have recently well recovered in Donghu Lake (Pei et al., 2007).

Littoral zones are areas of high productivity and biodiversity, submerged substrates support abundant quantities of benthic algae (Pei et al., 2015), However, as no detailed full-coverage benthic algae community survey has been conducted before 2004, this study aimed to evaluate temporal changes in benthic algae compositions and abundance in relation to the shifting environmental conditions. Specifically, we explored differences in benthic algae assemblages between any two years from 2004 to 2014, the main reason for the recovery of aquatic macrophytes and how these early improvements developed over the period, and the restoration potential by the present examination of more recent submerged macrophyte community development in the Donghu Lake.

2 MATERIAL AND METHOD

2.1 Study area and sampling sites

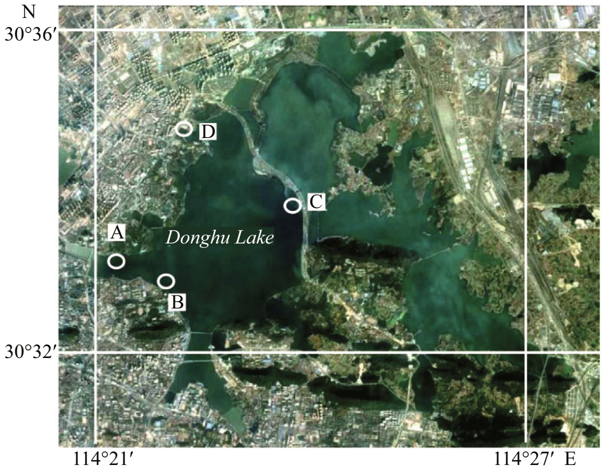

Fig.1 Map of Donghu Lake (picture from Google Earth), notes the sampling sites (A, B, C, and D)

Donghu Lake (33°33′N, 114°23′E) is a shallow urban lake of 32 km^2 in area, and 2.16 m in average depth and 4.66 m in maximum depth. It is located in the northeastern part of Wuhan City, the capital of Hubei Province, China. Donghu Lake is used for a variety of human activities, including water supply, sightseeing, aquatic sports, and commercial fishing. In previous decades, the water level of the lake had been approximately 20 m above sea level, and displayed little seasonal variation. This stability was achieved by pumping water into the lake from Changjiang (Yangtze) River 5 km away during the dry seasons, to ensure a continuous water supply. However, the water level dropped in recent years due to the "Six-Lake Connection Project" implement that completed in 2013. This project was designed to connect the lake with other five neighboring lakes with opening channels in order to transfer water between Donghu Lake and Changjiang River to control the water level.

Four sampling sites were selected along the littoral zone of the lake (Fig.1). Site A (33°33′56″N, 114°20′57″E) is heavily polluted by domestic sewage as the population density around site A is high. Site B (33°32′43″N, 114°22′0″E) is located near a university and is affected by human activities. Site C (33°33′43″N, 114°24′14″E) is vast open, and is seldom affected by people. Site D (33°34′58″N, 114°22′44″E) is far from any major roads with one sewage outlet and some bays in this area. The natural substrate of Donghu Lake littoral zone is mainly natural pebbles. Granite stones were used as artificial substrate and were placed at each site two months before sampling. The size of each granite stone is 15 cm×8 cm×1 cm. About 200 pieces of granite stones were placed in about 0.3 m below water surface of the littoral area at each site where full sunlight could be received. Samples were taken monthly from May 2004 to April 2005 for the 2004 dataset and December 2013 to November 2014 for the 2014 dataset. The sampling methods and schedule were the same in 2004 and 2014.

2.2 Sample handling and identification of diatoms, green algae

Diatom samples are treated in acid. Take (1–2)-mL algae liquid sample into 10-mL glass tube, slowly drop the same volume of concentrated sulfuric acid as the sample, and shake well; in the ventilator, slowly drop concentrated nitric acid, 85°C water bath for 8 h until the sample turns white and the liquid becomes colorless and transparent; finally, acid is washed 3 to 5 times with anhydrous ethanol, and the supernatant of centrifugal discarding is volumed with anhydrous ethanol. Permanent labels of diatoms were prepared with Naphrax™ tablet sealer and observed under an optical microscope (Olympus CX21) 100-fold oil microscope. Specimen identification refers to Chinese Freshwater Algae (Hu et al., 1980).

2.3 Water physical and chemical parameters

To track the changes in trophic status at Donghu Lake over the decade, physicochemical parameters (water temperature, pH, conductivity, phytoplankton chl *a*, total nitrogen (TN), total dissolved nitrogen (TDN), total phosphorus (TP), total dissolved phosphorus (TDP), and soluble reactive phosphorus (SRP)) were examined in 2004 and 2014. On sampling days, the water temperature (WT), pH (portable pH meter, PHB-4, China) and electrical conductivity (portable electrical conductivity meter, DDB-303A, China) were measured in situ. Approximately 1 500-mL water sub-samples were taken from each site to analyze TN and TP. Water sub-samples were filtered through a cellulose acetate membrane (pore size of 45 μm) before analyzing TDN, TDP, and SRP.

2.4 Benthic algae, AFDM, and diatoms

At the same time as collecting water samples, 3–5 pieces of granite stones were sampled randomly from each site. Three parallel benthic algae samples, along with the granite stones to which they adhered, were placed in sealed plastic bags on ice. In the laboratory, any invertebrates on the surface of the benthic algae were carefully removed using forceps. Then, benthic algae samples from an area of 120 cm^2 (15 cm×8 cm) were removed from the granite stones with a scalpel. The surfaces of the selected stones were gently washed with a nylon toothbrush and distilled water. The brushed off algae were collected in a beaker and mixed with the scalpel-scraped algae. All of the benthic algae from the selected area were diluted to 50–100 mL with distilled water (Pei et al., 2015).

Each suspension was divided into two parts in laboratory. The first part was processed to measure the ash-free dry mass (AFDM) based on APHA (2012). The second part was saved in 4% formaldehyde to identify diatoms. Diatom species were identify based on Krammer and Lange-Bertalot (1986, 1988, 1991a, b) and Prygiel and Coste (2000). The relative abundance of individual diatom species was calculated by counting the valves of at least 500 diatoms in each sample.

2.5 Determination of chlorophyll

Sub-samples designated for measuring phytoplankton chlorophyll *a* (chl *a*) were also filtered through a cellulose acetate filter (pore size of 45 μm) and were then extracted with 90% acetone. The chlorophyll measurement method of benthic algae is the same as that of phytoplankton. The analysis of nutrient and phytoplankton chl *a* for water samples was finished using standard procedures (APHA, 2012), with a UV-vis spectrophotometer (UV1750, Shimadzu, Japan).

2.6 Data analysis

The differences between physical and chemical parameters at the four sites were compared using one-way ANOVA (Bonferroni test). Data were analyzed using SPSS 21.0 (IBM). The results were considered significant at $P<0.05$. To compare the temporal and spatial variation between the diatom communities in different years and different sites, redundancy analysis (RDA) was performed on eight samples (years 2004 and 2014, sites A, B, C, and D). We selected the species that were "dominant" for analysis when the relative abundance of the diatom taxa exceeds 10% in at least one sample at one site for 12 months. The data on environmental variables and diatom species were averaged to means over one year and were $\log_{10}(x+1)$ transformed (except pH). RDA was performed using Canoco 4.5.

3 RESULT

3.1 Water physical and chemical parameters

Annual averages of all parameters were calculated based upon monthly recordings. The main change in environmental conditions was phosphorus, chl *a* and conductivity. The water temperature did not change markedly over the timeframe of this study. Similarly,

Table 1 Summary of the physicochemical parameters (mean±SD, *n*=12) at four sites in Donghu Lake sampled in 2004 and 2014

Parameter	Sites in 2004				Sites in 2014			
	A	B	C	D	A	B	C	D
pH	8.49±0.45^{a}	8.50±0.37^{a}	8.30±0.42^{a}	8.21±0.45^{a}	8.10±0.55^{a}	8.16±0.47^{a}	8.25±0.52^{a}	8.03±0.45^{a}
Cond (μS/cm)	614±48^{ab}	659±25^{b}	498±27^{a}	542±22^{ab}	368±43^{c}	375±35^{c}	341±33^{c}	375±36^{c}
Chl *a* (μg/L)	46.8±7.6^{a}	29.5±5.4^{b}	20.7±1.2^{bc}	26.2±3.2^{b}	17.9±5.2^{bc}	21.9±4.8^{b}	8.01±1.2^{c}	18.2±5.1^{bc}
TN (μg N/L)	1358±582^{a}	915±62^{a}	711±50^{a}	763±60^{a}	1011±346^{a}	861±170^{a}	901±56^{a}	936±229^{a}
TDN (μg N/L)	746±51^{a}	756±42^{a}	622±64^{a}	510±52^{a}	837±150^{a}	665±165^{a}	776±94^{a}	551±161^{a}
TP (μg P/L)	304±116^{a}	97±18^{b}	60±11^{b}	91±9^{b}	105±27^{b}	78±20^{b}	49±19^{b}	88±12^{b}
TDP (μg P/L)	60±10^{a}	39±11^{a}	37±9^{a}	40±3^{a}	42±2^{a}	33±4^{a}	21±9^{a}	35±3^{a}
SRP (μg P/L)	51±9^{a}	36±6^{a}	27±3^{a}	33±2^{a}	33±4^{a}	28±6^{a}	17±3^{a}	26±3^{a}

For any one parameter, values with different superscripted letters are significantly different ($P<0.05$) from each other (one-way ANOVA, Bonferroni). Chl *a*: phytoplankton chl *a*; Cond: conductivity.

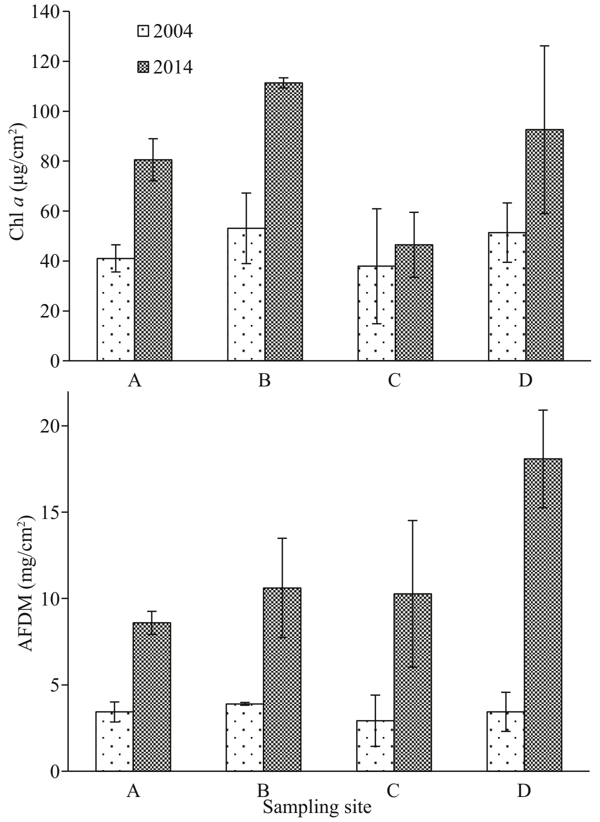

Fig.2 Comparison of the benthic algae chl *a* and AFDM between 2004 and 2014 at each site

pH remained generally stable, and was slightly alkaline (Table 1). The conductivity of Donghu Lake has decreased on average from 578 μS/cm in 2004 to 365 μS/cm in 2014. Phytoplankton chl *a* declined somewhat at all sites, with a significant decrease being detected at sites A and C (A: 46.8→17.9 μg/L; C: 20.7→8.01 μg/L). No significant changes in TN and TDN were observed, though the TN of site A and B slightly decreased (A: 1 358→1 011 μg N/L; B: 915→861 μg N/L) and site C and D slightly increased (C: 711→901 μg N/L; D: 763→936 μg N/L). The most remarkable TP decline was about 70% at site A (304→105 μg P/L). Only weakly changes in the water temperature, pH, TN, TDN, TP, TDP, and SRP were detected at sites B, C, and D between 2004 and 2014.

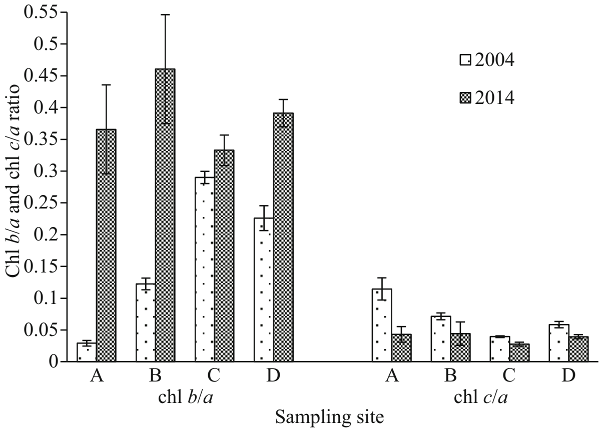

Fig.3 Comparison of the chl *b*/*a* and chl *c*/*a* ratio between 2004 and 2014

3.2 Benthic algae AFDM, chl *a*, chl *b*/*a*, and chl *c*/*a*

Chl *a* and AFDM were used to estimate benthic algae biomass. Benthic algae biomass increased at all sites (Fig.2). Annual mean chl *a* concentration at sites A, B, and D was approximately double that of 2004 in 2014. At all sites, AFDM increased more than 2–3 times and highly significantly ($P<0.001$) from about 3–4 mg/cm^2 in 2004 to 9–18 mg/cm^2 by 2014.

The chl *b*/*a* and chl *c*/*a* ratios were used to assess the relative proportions of green algae and diatoms, respectively. Green algae dominated benthic algae at all sites in 2014 (Fig.3). The relative proportions of green algae increased from 2004 to 2014, whereas the diatom ratio decreased. In 2014, the dominant species of filamentous green algae was *Cladophora glomerata*

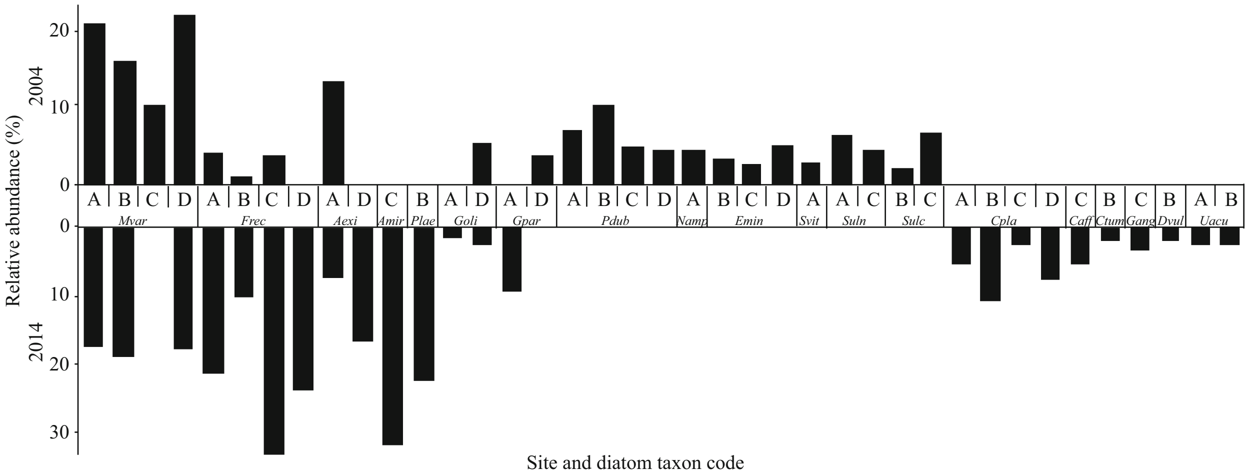

Fig.4 Comparison among the dominant diatoms species of 2004 and 2014

Diatom taxa were accounted for more than 10% in at least one sample at one site for 12 months. Taxon and code: *Melosira varians* (*Mvar*), *Fragilaria recapitellata* (*Frec*), *Achnanthidium exiguum* (*Aexi*), *Achnanthidium minutissimum* (*Amin*), *Pleurosira laevis* (*Plae*), *Gomphonema olivaceum* (*Goli*), *Gomphonema parvulum* (*Gpar*), *Planothidium dubium* (*Pdub*), *Nitzschia amphibia* (*Namp*), *Eolimna minima* (*Emin*), *Sellaphora vitabunda* (*Svit*), *Synedra ulna* (*Suln*), *Synedra ulna var. contracta* (*Sulc*), *Cocconeis placentula* (*Cpla*), *Cymbella affinis* (*Caff*), *Cymbella tumida* (*Ctum*) *Gomphonema angustum* (*Gang*), *Diatoma vulgaris* (*Dvul*), *Ulnaria acus* (*Uacu*).

at all sites. High numbers of *Oedogonium* spp. were observed year-round at site A, and *Spirogyra* spp. was observed at site C in winter and spring. Of note, *Melosira varians* (diatom) contributed most of the benthic algae biomass to site A in 2004, but was essentially replaced by green algae in 2014.

3.3 Benthic diatom

The recorded relative abundance of benthic diatoms and species richness changed markedly during the period of 10 years. Species richness showed a significant increase from 2004 to 2014, 113 diatom species belonging to 18 genera were identified in 2004, while 156 diatom species belonging to 22 genera were identified in 2014. *M. varians* was the dominant contributor to total diatom abundance at all sites in 2004, whereas *Fragilaria recapitellata* was the most abundant species in 2014 (Fig.4). The other dominant species recorded in 2004 were *Planothidium dubium* (each site), *Nitzschia amphibia* (site A), *Eolimna minima* (site B, C, and D), and *Sellaphora vitabunda* (site A). In 2014, *Achnanthidium minutissimum* (site C), *Cocconeis placentula* (site A, B, C, and D), *Cymbella tumida* (site B), *Cymbella affinis* (site C), and *Gomphonema angustum* (site C), *Ulnaria acus* (site A and B) were dominant. Analyses showed that all surveys differed significantly ($P<0.001$) confirming the increase in species richness between 2004 and 2014.

The RDA indicated differences in the composition of diatom assemblages, and well separated the samples obtained in 2004 versus 2014. The eight samples fell into three groups (Fig.5). The first group that were assembled in the third quadrant, included all sites in 2004, with *M. varians*, *P. dubium* and *E. minima* representing the indicator species. The second group included sites A, B, and D from 2014, with *F. recapitellata*, *C. placentula* and *U. acus* representing the indicator species. The third group included just site C from 2014, and was dominated by *A. minutissimum*, *C. affinis*, and *G. angustum*. The four environmental variables explained 32.7% of the

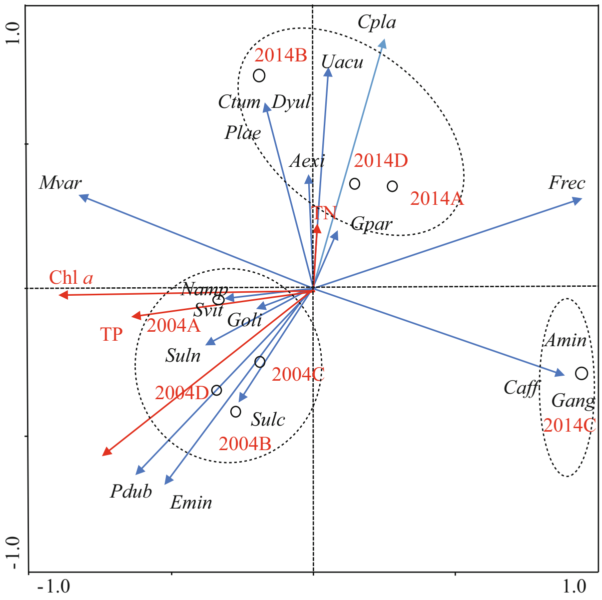

Fig.5 The RDA for benthic diatom communities and environmental factors in 8 samples on 4 locations (A, B, C, D) during 2 years (2004, 2014)

The codes of the diatoms and their corresponding full names are given in Fig.4.

Table 2 Macrophyte species richness and water level in Donghu Lake

Year of sampling	No. of observed species	No. of estimated species (±CI)	Secchi depth (m)	Water level (m)
2004	3	3.2±1.5	0.45 (0.35–0.61)	19.96 (19.8–20.7)
2014	15	15.6±2.1	0.78 (0.58–0.97)	19.50 (19.3–19.8)

CI: confidence interval.

diatom taxa variation. The most important variables, contributing significantly to the RDA axes were the conductivity, concentration of chl *a* and TP.

3.4 Species richness of aquatic macrophytes, transparency, and water level of lake

Species richness of aquatic macrophytes showed a significant increase from just three species in 2004 to fifteen species by 2014. We estimated sample coverage along with species richness at a common base sample for two surveyed years, the richness estimates were very close to the observed values and showed a significant increase from 2004 to 2014 (Table 2). Aquatic macrophytes included emergent macrophytes, Floating-leaved macrophytes, submersed macrophytes, and aquatic mosses in the littoral zone area at all sites in 2014, but only a few submerged macrophyte at sites C in 2004.

Secchi depth readings show a significant increase in water clarity ($P>0.05$) from 0.23–0.36 m. The values fluctuated from 19.8 to 20.7 m in 2004 and 19.3 to 19.8 m in 2014, and a declined greatly water level of Donghu Lake was observed over the 10-year period. The water level dropped by 0.46 m on average between 2004 and 2014 (from 19.96 to 19.50 m).

4 DISCUSSION

Among all environmental variables, many factors might govern the composition and structure of the benthic algae assemblage. Benthic algal biomass tends to be positively correlated with nutrients (Gaiser, 2009), but not always (Chick et al., 2008; Cantonati and Lowe, 2014). Several studies emphasized that the relationship between benthic algae biomass and nutrient concentration is weak, with the addition of nutrient only stimulating algal growth when light intensity increases (Hill and Knight, 1988). In our study, the benthic algae increased markedly from 2004 to 2014, and whilst there was no dramatic change in TP levels between the two years, TP concentrations did experience a decrease (Fig.2 and Table 1). The lack of improved nutrient levels can be partially explained when accounting for some major flood events in summer. Frequent flooding can have sizable effects on lake water quality. Phytoplankton productivity increased along the phosphorus gradient, the total chlorophyll content of phytoplankton is closely related to the phosphorus concentration in water column (Vadeboncoeur et al., 2003). Levels of phytoplankton chl *a* have decreased in conjunction with declining TP levels, suggesting that other factors may have outweighed nutrient effects on benthic algae biomass. Water level and the chl *a* reduction enhanced the underwater light conditions, allowing the expansion of benthic algae. Light is a key factor influencing the competitive interactions between benthic algae and phytoplankton (De Oliveria et al., 2010; DeNicola and Kelly., 2014). In addition to the increase of benthic algae biomass in 2014, the proportion of green algae and diatoms also changed. For benthic algae communities, the eutrophication process decreases the proportion of green algae, which leads to a significant increase in the biomass of diatoms (Ledger and Hildrew, 1998; Roberts et al., 2003). In 2014, the increase in the proportion of green algae, reducing the proportion of diatoms, indicated the restoration and better trophic status of Donghu Lake.

Kelly et al. (2008) supported the use of diatom as a proxy for phytobenthos in ecological status assessments. The change of benthic diatom composition provided more information about the restoration in Donghu Lake. Several diatom species associated with higher-nutrient water columns (Stenger-Kovács et al., 2007), that were dominant in 2004 (specifically *P. dubium*, *N. amphibia*, *E. minima*, and *S. vitabunda*) were rarely observed in 2014. The dominant species present in 2014 could be used to indicating the water quality, such as *A. minutissimum* and *U. acus* are generally found in less polluted waters (Marker and Collett, 1997). In addition, more epiphytic diatom species were found at all sites in 2014 than the dominant species from 2004. Some epiphytic diatoms which are often frequent in waters with relatively good ecological status such as *C. placentula*, *C. tumida*, *C. affinis*, and *G. angustum* (Tornés et al., 2007; Triest et al., 2012), were detected in 2014. *C. placentula* thrives in warm, shallow, and alkaline freshwater environments, enriched with macrophytes (Tunca et al., 2014). Furthermore, taxa from the genus *Cocconeis* tend to be abundant on the macroalgal mats of Cladophora (Reavie and Smol, 1997). Thus, the presence of these species indicated the recovery of submerged plants (He et al., 2016). *C. placentula* was generally observed at all sites throughout 2014, but was completely absent in 2004. The presence of more epiphytic diatoms in 2014, especially *C. placentula* indicated the restoration of Donghu Lake. These changes suggested that the ecological characteristics of littoral benthic diatoms reflect habitat coupling, understanding their changes is critical to determine the causes of the alterations.

Many factors might have contributed to the recovery from eutrophic conditions in Donghu Lake, including water transparency (increase), water level, chl *a*, nutrient levels and conductivity decrease. Those conditions may account for the recovery of aquatic macrophytes communities since the eutrophication peak of the 2000s. Among freshwater ecosystems, shallow lakes are extremely sensitive to fluctuations of water level (Paillisson and Marion, 2011; Levi et al., 2016; Beklioğlu et al., 2017). Small changes of the water level also lead to significant shifts in aquatic plant communities (Coops et al., 2003), making the water level fluctuation a key factor limiting the establishment and expansion of littoral vegetation. Water level reduction indirectly affects submerged macrophytes via a suite of variables, including underwater light conditions, the colonizable substrate area and water current velocity (Rodusky, 2010). Many studies have shown Light intensity primarily regulates the colonization of submerged macrophytes in lakes, especially in shallow eutrophic lakes (Albay and Akçaalan, 2008; Gette-Bouvarot et al., 2015). The water level dropped and water clarity increased (chl *a*, nutrient levels decline) from 2004 to 2014 in Donghu Lake. Thus, a major driving factor that submerged macrophytes were able to re-colonize in the littoral zones was probably the water level drop in recent years, and this data on macrophyte recovery serves to reinforce the importance of continuing studies of Donghu Lake.

There is also growing evidence that filamentous green algae represent an alternative stable state in shallow lakes characterized by a relatively high abundance of filamentous green algae and low abundance, or lack of, submerged macrophytes (Irfanullah and Moss, 2005; Poikane et al., 2016). A comparison between submerged macrophyte dominated lakes and lakes with high abundant filamentous green algae shows similarities among them regarding water nutrient concentrations, physical parameters, and species abundance and composition (Irfanullah and Moss, 2005). Thus, it is no doubt that the increase in species richness of aquatic macrophytes in the littoral zone of Donghu Lake represents the improvement in ecological status. Yet, water chemistry showed weakly change between 2004 and 2014 for the whole lake, and the full-time series of water chemistry data from 2004 to 2014 as per Liu et al. (2014) indicates no obvious improvement in water quality at Donghu Lake during the 10 years. Yet the changes in benthic algae biomass, the ratio of green algae, and benthic diatom compositions indicated recovery from eutrophic conditions in Donghu Lake. Supporting previous studies (Stenger-Kovács et al., 2007; DeNicola and Kelly, 2014; Rimet et al., 2015), benthic algae represent a promising indicator for assessing lake ecology. Changes in water level and physical and chemical factors can also affect the recovery process of shallow lakes (Bennion et al., 2010). The close link between benthic algae and macrophyte recovery supported the conclusion that benthic algae might be a much more informative metric for quantifying the process of restoration in Donghu Lake than physicochemical factors. In addition, the changes in water level and physical and chemical factors also promote the process of restoration in Donghu Lake. However, our finding was based on a single lake and just two years of data, ten years apart, and so might not be applicable for other lakes. Thus, more research is required on more lakes to investigate the replicability of our observation. In conclusion, the recovery from eutrophic conditions indicated by benthic algae improved our understanding of the actual status of the shallow water lake, which will contribute towards implementing appropriate lake management to prevent its deterioration.

5 CONCLUSION

Benthic algae biomass increased two times and the relative proportion of green algae increased, whereas the benthic diatom ratio decreased in 2014 years compared with 2004 years. The ecological characteristics of littoral benthic diatoms reflect habitat coupling, more epiphytic diatom species were found in 2014, and the relative abundance and species richness changed markedly. Reducing water level, chl-*a* and conductivity played a crucial role in governing aquatic macrophytes re-colonization in the littoral zones in recent years. Benthic algae were a much more informative metric for quantifying the process of restoration in Donghu Lake than nutrient levels.

6 DATA AVAILABILITY STATEMENT

The datasets analyzed during the current study available from the corresponding author on reasonable request.

References

Albay M, Akçaalan R. 2008. Effects of water quality and hydrologic drivers on periphyton colonization on *Sparganium erectum* in two Turkish lakes with different mixing regimes. *Environ. Monit. Assess.*, **146**(1-3): 171-181.

APHA. 2012. Standard Methods for the Examination of Water and Wastewater. 22nd edn. American Public Health Association, Washington DC.

Beklioğlu M, Bucak T, Coppens J, Bezirci G, Tavşanoğlu Ü N, Çakıroğlu A. İ, Levi E E, Erdoğan Ş, Filiz N, Özkan K, Özen A. 2017. Restoration of eutrophic lakes with fluctuating water levels: a 20-year monitoring study of two inter-connected lakes. *Water*, **9**(2): 127, https://doi.org/10.3390/w9020127.

Bennion H, Kelly M G, Juggins S, Yallop M, Burgess A, Jamieson J, Krokowski J. 2014. Assessment of ecological status in UK lakes using benthic diatoms. *Freshw. Sci.*, **33**(2): 639-654.

Bennion H, Sayer C D, Tibby J, Carrick H J. 2010. Diatoms as indicators of environmental change in shallow lakes. *In*: Smol J P, Stoermer E F eds. The Diatoms: Applications for the Environmental and Earth Sciences. 2nd edn. Cambridge University Press, Cambridge. p.152-173.

Bennion H, Simpson G L, Goldsmith B J. 2015. Assessing degradation and recovery pathways in lakes impacted by eutrophication using the sediment record. *Front. Ecol. Evol.*, **3**: 94.

Cantonati M, Lowe R L. 2014. Lake benthic algae: toward an understanding of their ecology. *Freshw. Sci.*, **33**(2): 475-486.

Chick J H, Geddes P, Trexler J C. 2008. Periphyton mat structure mediates trophic interactions in a subtropical marsh. *Wetlands*, **28**(2): 378-389.

Coops H, Beklioglu M, Crisman T L. 2003. The role of water-level fluctuations in shallow lake ecosystems — workshop conclusions. *Hydrobiologia*, **506-509**(1-3): 23-27.

De Oliveria D E, Ferragut C, De Campos Bicudo D. 2010. Relationships between environmental factors, periphyton biomass and nutrient content in Garças reservoir, a hypereutrophic tropical reservoir in Southeastern Brazil. *Lakes Reserv. Res. Manage.*, **15**(2): 129-137.

DeNicola D M, Kelly M. 2014. Role of periphyton in ecological assessment of lakes. *Freshw. Sci.*, **33**(2): 619-638.

Gaiser E E, McCormick P V, Hagerthey S E, Gottlieb A D. 2011. Landscape patterns of periphyton in the Florida everglades. *Crit. Rev. Environ. Sci. Technol.*, **41**(S1): 92-120.

Gaiser E. 2009. Periphyton as an indicator of restoration in the Florida everglades. *Ecol. Indic.*, **9**(S6): S37-S45.

Gette-Bouvarot M, Mermillod-Blondin F, Lemoine D, Delolme C, Danjean M, Etienne L, Volatier L. 2015. The potential control of benthic biofilm growth by macrophytes — a mesocosm approach. *Ecol. Eng.*, **75**: 178-186.

Gottschalk S, Kahlert M. 2012. Shifts in taxonomical and guild composition of littoral diatom assemblages along environmental gradients. *Hydrobiologia*, **694**(1): 41-56.

Hadley K R, Douglas M S V, Lim D, Smol J P. 2013. Diatom assemblages and limnological variables from 40 lakes and ponds on Bathurst Island and neighboring high arctic islands. *Int. Rev. Hydrobiol*, **98**(1): 44-59.

He Y, Liu G X, Pei G F. 2016. Effect of artificial macrocosms on water characteristics and benthic diatom communities in Donghu Lake, China. *J. Freshw. Ecol.*, **31**(4): 533-542.

Hill W R, Knight A W. 1988. Nutrient and light limitation of algae in two Northern California streams. *J. Phycol.*, **24**(2): 125-132.

Hu H J, Li Y Y, Wei Y X, Zhu H Z, Chen J Y, & Shi Z X. 1980. Freshwater algae of China. Shanghai Scientific & Technical Publishers, Shanghai, China. p.1-525. (in Chinese)

Irfanullah H, Moss B. 2005. A filamentous green algae-dominated temperate shallow lake: variations on the theme of clear-water stable states? *Arch Hydrobiol.*, **163**(1): 25-47.

Kelly M G, King L, Jones R I, Barker P A, Jamieson B J. 2008. Validation of diatoms as proxies for phytobenthos when assessing ecological status in lakes. *Hydrobiologia*, **610**(1): 125-129.

Krammer K, Lange-Bertalot H. 1986. Bacillariophyceae. 1. Teil: naviculaceae. *In*: Ettl H, Gärtner G, Gerloff J, Heynig H, Mollenhauer D eds. Süßwasserflora von Mitteleuropa, Band 2/1. Gustav Fischer Verlag, Stuttgart.

Krammer K, Lange-Bertalot H. 1988. Bacillariophyceae. 2. Teil: bacillariaceae, epithemiaceae, surirellaceae. *In*: Ettl H, Gärtner G, Gerloff J, Heynig H, Mollenhauer D eds. Süßwasserflora von Mitteleuropa, Band 2/2. Gustav Fischer Verlag, Stuttgart.

Krammer K, Lange-Bertalot H. 1991a. Bacillariophyceae. 3. Teil: centrales, fragilariaceae, eunotiaceae. *In*: Ettl H, Gärtner G, Gerloff J, Heynig H, Mollenhauer D eds. Süßwasserflora von Mitteleuropa, Band 2/3. Gustav Fischer Verlag, Stuttgart.

Krammer K, Lange-Bertalot H. 1991b. Bacillariophyceae. 4. Teil: achnanthaceae, achnanthes and gomphonema. *In*: Ettl H, Gärtner G, Gerloff J, Heynig H, Mollenhauer D eds. Süßwasserflora von Mitteleuropa, Band 2/4. Gustav Fischer Verlag, Stuttgart.

Ledger M E, Hildrew A G. 2002. Temporal and spatial variation in the epilithic biofilm of an acid stream. *Freshw. Biol.*, **40**(4): 655-670.

Levi E E, Bezirci G, Çakıroğlu A İ, Turner S, Bennion H, Kernan M, Jeppesen E, Beklioğlu M. 2016. Multi-proxy palaeoecological responses to water-level fluctuations in three shallow Turkish lakes. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, **449**: 553-566.

Lim D S S, Smol J P, Douglas M S V. 2007. Diatom assemblages and their relationships to lakewater nitrogen levels and other limnological variables from 36 lakes and ponds on Banks Island, N.W.T., Canadian Arctic. *Hydrobiologia*, **586**(1): 191-211.

Liu Y, Shen J Z. 2008. Biological evaluation of algae in water quality monitoring applications. *Reserv. Fish.*, **28**(4): 5-7. (in Chinese)

Liu Z W, Wang Y F, Wang Q Y, Zhang H. 2014. Water body nutrients content change trend analysis in Lake Donghu, Wuhan. *Sci. Technol. Innov. Her.*, (31): 115-116. (in Chinese)

Logan B, Taffs K H. 2013. Relationship between diatoms and water quality (TN, TP) in sub-tropical east Australian estuaries. *J. Paleolimnol.*, **50**(1): 123-137.

Marker A F H, Collett G D. 1997. Spatial and temporal characteristics of algae in the River Great Ouse. II. The epiphytic algal flora. *Regul. River.*, **13**(3): 235-244.

Paillisson J M, Marion L. 2011. Water level fluctuations for managing excessive plant biomass in shallow lakes. *Ecol. Eng.*, **37**(2): 241-247.

Pei G F, Liu G X, Hu Z Y. 2007. Spatial and temporal variation of benthic algal communities in the littoral zone of Lake Donghu. *Acta Hydrobiol. Sin.*, **31**(6): 836-842. (in Chinese with English abstract)

Pei G F, Wang Q, Liu G X. 2015. The role of periphyton in phosphorus retention in shallow lakes with different trophic status, China. *Aquat. Bot.*, **125**: 17-22.

Poikane S, Kelly M, Cantonati M. 2016. Benthic algal assessment of ecological status in European lakes and rivers: challenges and opportunities. *Sci. Total Environ.*, **568**: 603-613.

Poulíčková A, Duchoslav M, Dokulil M. 2004. Littoral diatom assemblages as bioindicators of lake trophic status: a case study from perialpine lakes in Austria. *Eur. J. Phycol.*, **39**(2): 143-152.

Prygiel J, Coste M. 2000. Guide Méthodologique Pour la Mise en Oeuvre de l'Indice Biologique Diatomées NF T 90-354. Agence de I'Eau Artois- Picardie-Cemagref, Bordeaux. France. 134p.

Reavie E D, Smol J P. 1997. Diatom-based model to infer past littoral habitat characteristics in the St. Lawrence River. *J. Great Lakes Res.*, **23**(3): 339-348.

Rimet F, Bouchez A, Montuelle B. 2015. Benthic diatoms and phytoplankton to assess nutrients in a large lake: complementarity of their use in Lake Geneva (France-Switzerland). *Ecol. Indic.*, **53**: 231-239.

Roberts E, Kroker J, Körner S, Nicklisch A. 2003. The role of periphyton during the re-colonization of a shallow lake with submerged macrophytes. *Hydrobiologia*, **506-509**(1-3): 525-530.

Rodusky A J. 2010. The influence of large water level fluctuations and hurricanes on periphyton and associated nutrient storage in subtropical Lake Okeechobee, USA. *Aquat. Ecol.*, **44**(4): 797-815.

Simkhada B, Jüttner I, Chimonides P J. 2006. Diatoms in lowland ponds of Koshi Tappu, Eastern Nepal — relationships with chemical and habitat characteristics. *Int. Rev. Hydrobiol.*, **91**(6): 574-593.

Smol J P, Stoermer E F. 2010. The Diatoms: Applications for the Environmental and Earth Sciences. 2nd edn. Cambridge University Press, Cambridge.

Stenger-Kovács C, Buczkó K, Hajnal É, Padisák J. 2007. Epiphytic, littoral diatoms as bioindicators of shallow lake trophic status: Trophic diatom index for lakes (TDIL) developed in Hungary. *Hydrobiologia*, **589**(1): 141-154.

Stevenson J. 2014. Ecological assessments with algae: a review and synthesis. *J. Phycol.*, **50**(3): 437-461.

Tornés E, Cambra J, Gomà J, Leira M, Ortiz R, Sabater S. 2007. Indicator taxa of benthic diatom communities: a case study in Mediterranean streams. *Ann. Limnol. -Int. J. Lim.*, **43**(1): 1-11.

Triest L, Lung'ayia H, Ndiritu G, Beyene A. 2012. Epilithic diatoms as indicators in tropical African rivers (Lake Victoria catchment). *Hydrobiologia*, **695**(1): 343-360.

Tunca H, Sevindik T O, Bal D N, Arabaci S. 2014. Community structure of epiphytic algae on three different macrophytes at Acarlar floodplain forest (Northern Turkey). *Chin. J. Oceanol. Limnol.*, **32**(4): 845-857.

Vadeboncoeur Y, Jeppesen E, Zanden M J V, Schierup H H, Christoffersen K, Lodge D M. 2003. From Greenland to green Lakes: cultural eutrophication and the loss of benthic pathways in lakes. *Limnol. Oceanogr.*, **48**(4): 1 408-1 418.