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RESEARCH ARTICLE

Long-term effects of temperature and nutrient concentrations on the phytoplankton biomass in three lakes with differing trophic statuses on the Yungui Plateau, China

Jing Dong[1,2,a], Qichao Zhou[3,4,a], Yunni Gao[2], Qianhong Gu[2], Genbao Li[1,*] and Lirong Song[1]

[1] State Key Laboratory of Freshwater Ecology and Biotechnology, Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan 430072, PR China
[2] College of Fisheries, Henan Normal University, Xinxiang 453007, PR China
[3] Yunnan Key Laboratory of Pollution Process and Management of Plateau Lake-Watershed, Yunnan Institute of Environmental Science (Kunming China International Research Center for Plateau Lake), Kunming 650034, PR China
[4] Taihu Laboratory for Lake Ecosystem Research, State Key Laboratory of Lake Science and Environment, Nanjing Institute of Geography and Limnology, Chinese Academy of Sciences, Nanjing 210008, PR China

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Abstract – Long-term annual (1990–2010) monitoring data were analyzed to test the responses of phytoplankton biomass in three lakes in the Yungui Plateau, China, to increasing temperature and increasing nutrient concentrations. The three studied lakes (Lake Fuxian, Lake Erhai and Lake Dianchi) all exhibited significant increases in algal biomass from 1990 to 2010, with increases of 0.111 μg/L, 0.662 μg/L and 3.07 μg/L per year, respectively. The study also indicated that the relative influences of warming and nutrient concentrations on chlorophyll a concentration varied among the lakes and was dependent on trophic level and phytoplankton composition. In Lake Fuxian, the increase in algal biomass was correlated with the rapid growth of *Mougeotia* spp., and the total phosphorous concentration was the key factor driving this increase in algal biomass. In Lake Erhai, the dominant species shifted from *Dolichospermum* spp. to *Microcystis* spp. Additionally, the increase in algal biomass in Lake Erhai (involving mainly an increase in *Microcystis* spp.) was significantly associated with an increase in total nitrogen (TN) concentration. In Lake Dianchi, warming and increases in TN concentration were the strongest predictors of biomass change.

Keywords: Phytoplankton ecology / warming / eutrophication / algal biomass increase

1 Introduction

In recent decades (especially since the 1990s), numerous lakes worldwide have shifted from an aquatic vegetation-dominated clear state to a phytoplankton-dominated turbid state. Water transparency has greatly reduced during this process, and the landscape and drinking water values of affected lakes have sharply decreased. Although many studies have been conducted on this topic, the primary factors that promote phytoplankton development remain debated and require further elucidation (Elliott *et al.*, 2006; Wagner and Adrian, 2009; Jeppesen *et al.*, 2010; Elliott, 2012; Zhang *et al.*, 2012; Rigosi *et al.*, 2014). Nevertheless, it is commonly assumed that eutrophication and climate change associated with anthropogenic activities are major threats to lake ecosystems and are the main factors driving phytoplankton development (*e.g.*, cyanobacterial blooms).

Previous studies have revealed the interactive effects of increased nutrient concentrations and warming in promoting the frequency and magnitude of cyanobacterial blooms (Jöhnk *et al.*, 2008; Paerl and Huisman, 2009; Liu *et al.*, 2011; Huber *et al.*, 2012; O'Neil *et al.*, 2012; Paerl and Paul, 2012; Gkelis *et al.*, 2014). Additionally, Elliott (2012) reported that climate warming can accelerate the negative effects of eutrophication on aquatic ecosystems, whereas nutrient dilution alleviates the adverse effects of climate warming on lake systems. However, the factor that exerts the predominant effects on phytoplankton abundance and biomass in lake systems remains unclear. In an open-air microcosm study (at the University of Liverpool Botanic Gardens at Ness on the Wirral Peninsula, UK), Moss *et al.* (2003) found that eutrophication was a major factor that influenced algal abundance and that the effects of climate warming on phytoplankton in shallow lakes were negligible. In Lake Müggel, cyanobacteria were found to not directly benefit

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*Corresponding author: `ligb@ihb.ac.cn`
[a] Co-first authors.

Table 1. Characteristics of Lake Fuxian (Gao *et al.*, 2013), Lake Erhai (Li *et al.*, 2015) and Lake Dianchi (Zhou *et al.*, 2016).

	Lake Fuxian	Lake Erhai	Lake Dianchi (Waihai)
Latitude	24°21′28″–24°38′N	25°36′–25°58′N	24°30′–25°02′N
Longitude	102°49′12″–102°57′26″E	100°05′–100°17′E	102°36′–102°47′E
Nutrition status	Oligotrophic	Mesotrophic	Eutrophic
Surface area (km^2)	212	252.91	298.2
Maximal depth (m)	157.3	21.5	11.2
Mean depth (m)	87	10.8	4.4

from warming; rather, nutrient reductions caused a bloom decline (Köhler *et al.*, 2005; Wagner and Adrian, 2009). Additionally, Anneville *et al.* (2005) analyzed monitoring data from European plateau lakes from 1974 to 2000 and showed that the phosphorous level was the key determinant of algal composition. Additionally, Brookes and Carey (2011) suggested that controlling nutrients is extremely important for increasing the resilience of aquatic ecosystems to cyanobacterial blooms. In a study of 143 lakes ranging from subarctic Europe to southern South America, Kosten *et al.* (2012) showed that the percentage of the total phytoplankton biovolume attributable to cyanobacteria increased steeply with temperature. Furthermore, Paerl and Huisman (2008) and Posch *et al.* (2012) indicated that warming played a more important role than nutrient level increases in promoting cyanobacterial blooms.

The influences of eutrophication, climate change or other main and interactive effects on algal growth are complex, debated and difficult to predict (Brookes and Carey, 2011). In many recent studies, lake type, lake nutrient level and species composition have been used to predict the responses of phytoplankton to changes in nutrients and climate. Previous studies have indicated that temperature is a key factor in determining cyanobacterial abundance in stratified bodies of water (Becker *et al.*, 2010; Taranu *et al.*, 2012), whereas nutrient levels, such as the total phosphorous (TP) concentration, are important determinants of the cyanobacterial biomass of mixed bodies of water (Wagner and Adrian, 2009; Taranu *et al.*, 2012). According to the 31-year monitoring data set from Lake Geneva presented by Tadonléké (2010), phytoplankton exhibited positive responses to warming when the TP concentration in the lake water exceeded 0.022 mg/L (eutrophic conditions), whereas negative responses were observed at low TP concentrations (nutrient-poor conditions). Furthermore, some studies have suggested that the sensitivity of cyanobacterial abundance to temperature and nutrients depends on the species composition (Rigosi *et al.*, 2014; Deng *et al.*, 2016). Taxa such as *Dolichospermum* spp. are more sensitive to nutrients, whereas *Microcystis* is more sensitive to temperature.

Lake Fuxian, Lake Erhai and Lake Dianchi, which are located on the Yungui Plateau, China, are the main local water resources, providing potable water for Yuxi City, Dali City and Kunming City, respectively. Currently, the three lakes are undergoing different increases in nutrition concentrations and rapid algal growth. Although nutrient enrichment has been commonly identified as a key predictor of phytoplankton development and dominance in freshwater, warming also plays a role (Zhou *et al.*, 2015). The driving force of phytoplankton biomass change has not yet been studied in these three lakes. Quantifying and analyzing the variability in lake responses to environmental changes will provide crucial information for lake assessments, which are important for lake management and protection. In the present study, the following are investigated: (1) temporal changes in the environmental variables and algal biomass of the three lakes, each having a different trophic status; (2) the key environmental factors correlated with phytoplankton biomass in each lake; and (3) the role of phytoplankton composition in the responses of each lake to environmental variables. Here, the functional group concept is applied, as this method can precisely predict species occurrence and reflect habitat characteristics (Reynolds *et al.*, 2002; Padisák *et al.*, 2009).

2 Methods

2.1 Descriptions of the three lakes

Lake Fuxian (area 21 km^2, maximum depth 157.3 m, mean depth 87 m) (Tab. 1) is the second-deepest lake in central Yunnan Province, China. The lake is in a subtropical zone with a monsoon climate and an annual precipitation of approximately 800–1100 mm (Gao *et al.*, 2013). Currently, the lake is oligotrophic.

Lake Erhai (area 252.91 km^2, maximum depth 21.5 m, mean depth 10.8 m) (Tab. 1) is the second largest freshwater lake in Yunnan Province, China. This lake, characterized by a plateau mountain and monsoon climate, is a vital potable water source for Dali city. With the rapid development of industry and agriculture in the region, the lake has been subjected to serious pollution since the 1980s. The lake is now mesotrophic.

Lake Dianchi, located in southwestern China and characterized by a subtropical plateau mountain monsoon climate, is the largest freshwater lake in Yunnan Province. Lake Dianchi covers 309 km^2 and is partitioned into two sections: Caohai Lake (area 10.8 km^2) in the north and Waihai Lake (298.2 km^2) in the south (Zhou *et al.*, 2016). The present study focuses on Waihai, a typical eutrophic lake in China that has experienced cyanobacterial blooms since the 1990s (Sheng *et al.*, 2012; Li *et al.*, 2014).

All three lakes studied here have different nutrient levels and are located on the Yungui Plateau, China. The locations of the three lakes are shown in Figure 1.

2.2 Data collection

Water quality data, including algae biomass (characterized by chlorophyll a concentration (Chl. *a*)), water transparency (SD), total nitrogen (TN) and TP concentrations, for Fuxian Lake from 1990 to 2010 were originally obtained from the

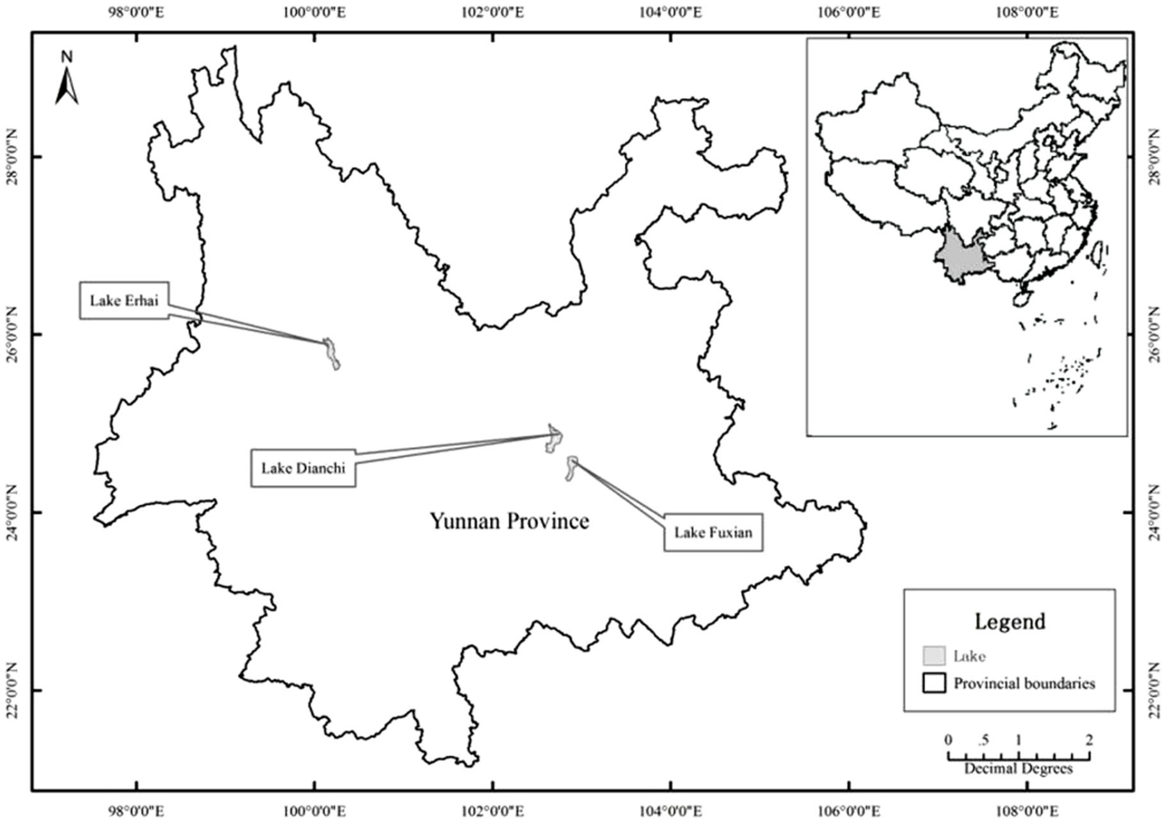

Fig. 1. The locations of Lakes Fuxian, Erhai and Dianchi in Yunnan Province, China.

Yuxi Institute of Environmental Science and Yuxi Environmental Monitoring Center (Gao *et al.*, 2013). The water quality data for Erhai Lake (1990–2010) were obtained from the Erhai Authority (Fu *et al.*, 2013), and the data for Dianchi Lake (1990–2007) were collected from the Kunming Environmental Monitoring Center (Yu *et al.*, 2013; Ouyang *et al.*, 2015; Zhou *et al.*, 2016). The air temperature data (AT) for areas surrounding Lake Fuxian, Lake Erhai and Lake Dianchi were obtained from the meteorological information center of each local city (Dong *et al.*, 2008, 2012; Gu, 2008; Huang *et al.*, 2010). Between 2008 and 2010, the environmental variable data and phytoplankton data from Lake Dianchi were obtained by the present authors, with sampling performed according to Dong *et al.* (2015). In each year, water was sampled each month to determine the algal biomass and the levels of environmental variables. A Secchi disk was used to evaluate the SD of each water body. The TN, TP and Chl. *a* concentrations were measured according to the Protocols for Standard Observation and Measurement in Aquatic Ecosystems of the Chinese Ecosystem Research Network (CERN) (Huang et al., 2000; Cai 2007). All the annual data were calculated based on 12-month (24 sampling sites) averages. The dominant phytoplankton compositions in the three lakes were obtained from our previous study (Dong *et al.*, 2014).

2.3 Statistical analysis

Data exploration was performed before data analysis. Time series analyses of Chl. *a*, TP, TN, SD and AT were conducted to identify long-term trends related to AT and water quality data, and temporal autocorrelation was assessed for all the variables using an autocorrelation function. Then, Spearman correlation analyses were conducted to identify the correlations between all potential pairs of variables (standardized values) in each lake. Finally, stepwise regression of Ln(Chl. a+1) on Ln(AT+1), Ln (SD+1), Ln(TN+1) and Ln(TP+1) was performed for each lake to determine the main explanatory variables; the significant variables in the model were selected based on *t*-tests. Additionally, the standardized beta coefficient was used to estimate the relative contribution of each environmental factor to the phytoplankton biomass. The analyses were performed with IBM SPSS Statistics (version 22.0).

3 Results

3.1 Long-term trends in environmental variables in Lakes Fuxian, Erhai and Dianchi

The variations in mean AT were more pronounced in Lake Erhai and Lake Dianchi than those in Lake Fuxian (Fig. 2). The surrounding ATs of Lake Erhai (slope = 0.075, $p < 0.01$, Tab. 2) and Dianchi (slope = 0.071, $p < 0.01$, Tab. 2) increased significantly from 1990 to 2010. However, no significant increase in temperature near Lake Fuxian was detected ($p > 0.05$) over the studied time period.

Significant TN increases of 0.017 mg/L and 0.434 mg/L per year were observed from 1990 to 2010 in Lakes Erhai and Dianchi, respectively (Tab. 2). In contrast, no significant

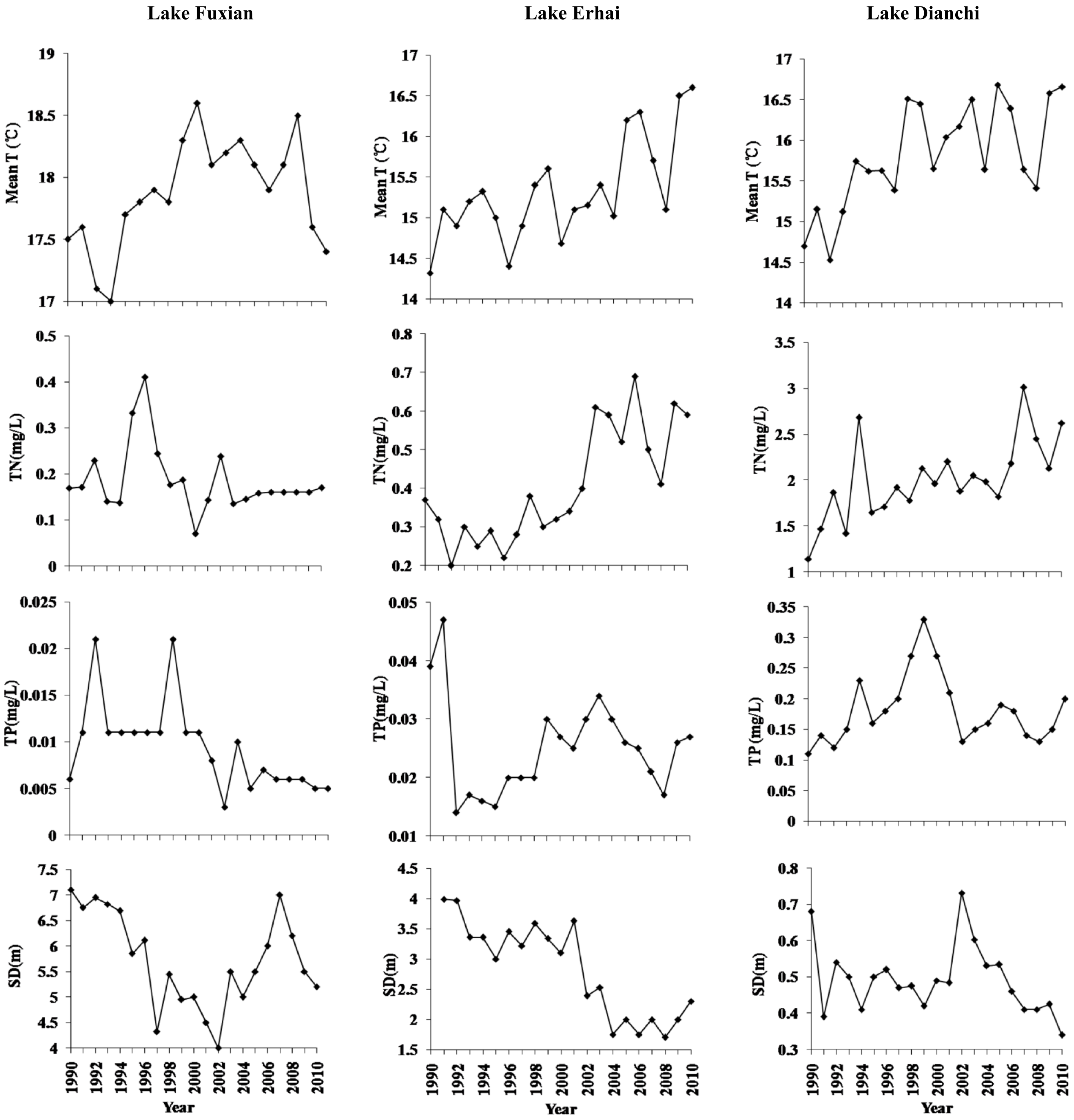

Fig. 2. Trends in environmental variables in Lakes Fuxian, Erhai and Dianchi from 1991 to 2010 (AT, annual mean air temperature; SD, annual mean water transparency; TN, annual mean total nitrogen; TP, annual mean total phosphorus).

change in TN concentration was detected for Lake Fuxian over the time period under study. However, from 1990 to 1996, an obvious increase in TN concentration in Lake Fuxian was detected, with a peak in 1996 (0.41 mg/L) (Fig. 2).

An obvious decrease in TP concentration in Lake Fuxian was observed. The TP concentration decreased by 0.0004 mg/L between 1990 and 2010 (Tab. 2). No significant change in TP concentration from 1990 to 2010 was observed for Lakes Erhai and Dianchi; however, a significant increase was observed in Lake Erhai from 1992 to 2003 (0.0017 mg/L per year, $p < 0.01$). Thereafter, an obvious decrease of 0.0012 mg/L per year ($p < 0.01$) occurred in the lake. The TP concentration of Lake Dianchi exhibited trends similar to those of Lake Erhai, including a significant increase of 0.021 mg/L per year from 1991 to 1999 and a decrease of 0.01 mg/L per year from 1999 to 2010 ($p < 0.01$) (Fig. 2).

There were no significant changes in SD for Lake Fuxian and Lake Dianchi from 1990 to 2010. In contrast, the SD of

Table 2. Linear regressions between each variable over the study period.

Lake	Variable	Slope	p	N	Year range
Fuxian	Chl. a^*	0.111	<0.01	20*	1990–2010
	AT*	–	>0.05	20*	1990–2010
	SD*	–	>0.05	20*	1990–2010
	TN*	–	>0.05	20*	1990–2010
	TP	−0.0004	<0.01	21	1990–2010
Erhai	Chl. a*	0.662	<0.05	20*	1990–2010
	AT*	0.075	<0.01	20*	1990–2010
	SD	−0.115	<0.01	20	1991–2010
	TN*	0.017	<0.01	20*	1990–2010
	TP*	–	>0.05	20*	1990–2010
Dianchi	Chl. a*	3.07	<0.05	20*	1991–2010
	AT	0.071	<0.01	21	1990–2010
	SD	–	>0.05	21	1990–2010
	TN	0.434	<0.01	21	1990–2010
	TP*	–	>0.05	20*	1990–2010

Chl. *a*, annual mean chlorophyll *a* concentration; AT, annual mean air temperature; SD, annual mean water transparency; TN, annual mean total nitrogen; and TP, annual mean total phosphorus. "*" indicates that there was an temporal autocorrelation in the ordinary regression, as demonstrated using modified linear models by autoregression (AR-1).

Lake Erhai markedly decreased (0.115 m per year, $p < 0.01$) from 1991 to 2010 (Tab. 2). In Lake Fuxian, SD decreased by 0.27 m over this period, although it increased by 0.15 m per year after 2002. The SD of Lake Dianchi exhibited a significant decrease from 2002 to 2010 (0.041 m per year, $p < 0.01$) (Fig. 2).

3.2 Long-term trends in the phytoplankton biomass (Chl. *a*) levels in Lakes Fuxian, Erhai and Dianchi

Significant increases in Chl. *a* concentration were observed for Lake Fuxian (slope = 0.111, $p < 0.01$, Tab. 2), Lake Erhai (slope = 0.662, $p < 0.05$, Tab. 2) and Lake Dianchi (slope = 3.07, $p < 0.05$, Tab. 2) over the time period under study. The between-year variation in Chl. *a* was most pronounced in Lake Dianchi (Tab. 2; Fig. 3).

3.3 Variations in Chl. *a* and its driving factors in Lakes Fuxian, Erhai and Dianchi

The relationships between pairs of variables, as determined from Spearman correlation analysis, are shown in Table 3. Chl. *a* content was significantly correlated with TP concentration in Lake Fuxian; AT and TN concentration (particularly the latter) in Lake Erhai; and TP, AT and TN concentration (particularly AT and TN) in Lake Dianchi. Based on the stepwise regression of Ln(Chl. a+1) against Ln(AT+1), Ln(SD+1), Ln(TN+1) and Ln(TP+1) for Lake Fuxian, TP was the main contributing factor to phytoplankton biomass ($p < 0.05$). This relationship is described by the model as shown in Table 4. The significant driving factors affecting Chl. *a* in Lake Erhai were TN concentration ($p < 0.05$) and SD ($p < 0.05$). For Lake Dianchi, AT ($p < 0.01$) and TN concentrations ($p < 0.05$) were the significant driving factors (Tab. 4; Fig. 4).

3.4 Phytoplankton variation in the three lakes from 1990 to 2010

According to our previous study (Dong *et al.*, 2014), the dominant species in Lake Fuxian are *Mougeotia* spp. (phytoplankton group T). Moreover, the dominant species in Lake Erhai shifted from *Cyclotella* sp. (C), *Aphanizomenon flos-aquae* (H1), and *Anabaena sporoides* (H1) to *Microcystis flos-aquae* (M). In Lake Dianchi, the dominant species shifted from green algae *Pediastrum* sp. (J) and *Scenedesmus* sp. (J) to *Microcystis flos-aquae* (M).

4 Discussion

In Lakes Erhai and Dianchi, the nutrient levels varied significantly over the period under study. The TN concentrations in Lake Erhai and Lake Dianchi increased over the study period. However, we did not detect significant changes in TP concentration in Lake Erhai or Lake Dianchi from 1990 to 2010. Previous studies have shown that nutrient increases drive increases in algal biomass (Moss *et al.*, 2003; Köhler *et al.*, 2005; Wagner and Adrian, 2009). Accordingly, such increases considerably influenced algal biomass in these two lakes. To determine the role of warming, we focused on the ATs of these two lakes. We found that Lake Erhai and Lake Dianchi experienced climate warming, with temperature increases of 0.075 °C and 0.071 °C per year, respectively, from 1990 to 2010. This finding is in accordance with the findings of Coumou *et al.* (2013) and Deng *et al.* (2016), who reported that the mean AT of Lake Taihu increased by 0.065 °C per year from 1992 to 2013. In our study, the Spearman correlation analysis indicated that the increases in algal biomass in the two lakes were significantly correlated with both temperature and TN concentration. This result is in agreement with the results of Mooij *et al.* (2005) and Elliott (2012), who suggested that climate warming and eutrophication play vital roles in phytoplankton structuring and are important indicators of phytoplankton dynamics. However, it remains unclear which factor is more important and the best predictor of algal biomass. In the present study, the stepwise regression analyses indicated that algal biomass was associated with TN concentration in Lake Erhai and with AT and TN concentration in Lake Dianchi. This difference might be related to differences in species composition between the two lakes. Different species react differently to climate change and eutrophication, and their tolerance to key environmental factors differs (Adrian *et al.*, 2006; Feuchtmayr *et al.*, 2012; Walters *et al.*, 2013; Rigosi *et al.*, 2014).

In Lake Erhai, the dominant cyanobacterial species changed significantly over the study period of 1990–2010. A cyanobacterial bloom first occurred in 1996, and *Dolichospermum* sp. was predominant from 1996 to 2006. Our previous studies (details in Dong *et al.*, 2014) indicated that the dominance of *Microcystis* has become increasingly pronounced in recent years, and the overwhelmingly dominant

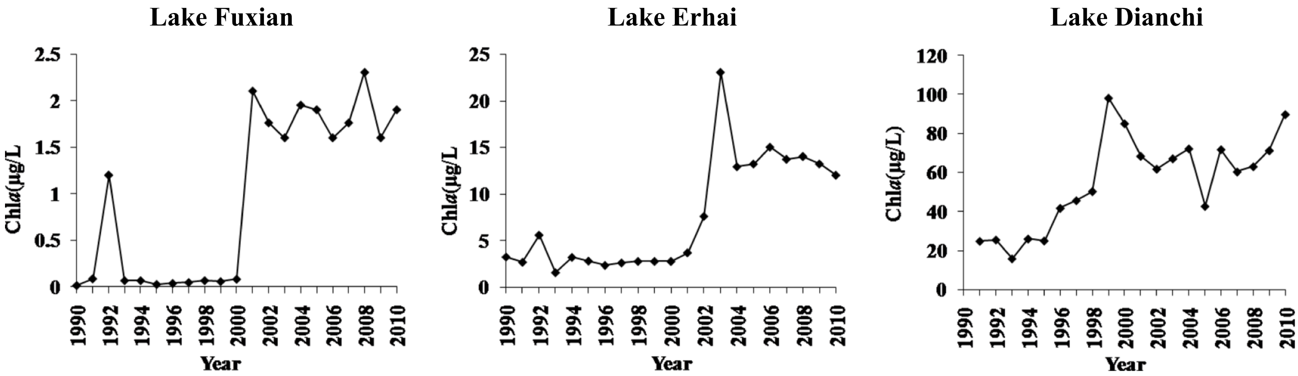

Fig. 3. Trends in the annual mean chlorophyll *a* (Chl. *a*) concentrations in Lakes Fuxian, Erhai and Dianchi from 1991 to 2010.

Table 3. Spearman correlations between the standardized variables of the three lakes.

Lake	Variables	*Z*-score (Chl. *a*)	*Z*-score (AT)	*Z*-score (SD)	*Z*-score (TN)	*Z*-score (TP)
Fuxian	*Z*-score (Chl. *a*)	1	0.092	−0.224	−0.415	-0.607^{**}
	Z-score (AT)	–	1	-0.665^{**}	−0.018	−0.062
	Z-score (SD)	–	–	1	−0.063	0.176
	Z-score (TN)	–	–	–	1	0.183
	Z-score (TP)	–	–	–	–	1
Erhai	*Z*-score (Chl. *a*)	1	0.500^{*}	-0.739^{**}	0.783^{**}	0.172
	Z-score (AT)	–	1	−0.418	0.647^{**}	0.116
	Z-score (SD)	–	–	1	-0.729^{**}	−0.183
	Z-score (TN)	–	–	–	1	0.485^{*}
	Z-score (TP)	–	–	–	–	1
Dianchi	*Z*-score (Chl. *a*)	1	0.637^{**}	−0.263	0.666^{**}	0.450^{*}
	Z-score (AT)	–	1	−0.150	0.439^{*}	0.521^{*}
	Z-score (SD)	–	–	1	-0.556^{**}	−0.319
	Z-score (TN)	–	–	–	1	0.263
	Z-score (TP)	–	–	–	–	1

Z-score, standardized values. Chl. *a*, annual mean chlorophyll *a* concentration; AT, annual mean air temperature; SD, annual mean water transparency; TN, annual mean total nitrogen; and TP, annual mean total phosphorus.

* Significance at $p < 0.05$.

** Significance at $p < 0.01$.

Table 4. Stepwise regression between Ln(Chl. *a*+1) and Ln(AT+1), Ln(SD+1), Ln(TN+1) and Ln(TP+1).

Lake	Stepwise model	Standardized beta	R^2	*P*	VIF
Fuxian	$\mathrm{Ln(Chl.}\ a+1) = 1.066^{**} - 54.118\ \mathrm{Ln(TP+1)}^{*}$	Ln(TP+1), −0.504	0.254	<0.05	1
Erhai	$\mathrm{Ln(Chl.}\ a+1) = 2.768^{*} + 3.326\ \mathrm{Ln(TN+1)}^{*} - 1.468\ \mathrm{Ln(SD+1)}^{*}$	Ln(TN+1), 0.493; Ln(SD+1), −0.437	0.790	<0.00001	3.090
Dianchi	$\mathrm{Ln(Chl.}\ a+1) = -17.481^{*} + 7.051\ \mathrm{Ln(AT+1)}^{**} + 1.35\ \mathrm{Ln(TN+1)}^{*}$	Ln(AT+1), 0.524; Ln(TN+1), 0.372	0.577	<0.001	1.217

Chl. *a*, annual mean chlorophyll *a* concentration; AT, annual mean air temperature; SD, annual mean water transparency; TN, annual mean total nitrogen; and TP, annual mean total phosphorus.

* Significance at $p < 0.05$.

** Significance at $p < 0.01$.

species changed from *Dolichospermum* sp. to *Microcystis* sp. in Lake Erhai in 2010 (Wen and Ma, 2011). *Microcystis* sp. significantly contributed to the recent algal biomass in Lake Erhai. *Dolichospermum* sp. belong to functional group H1 (Reynolds *et al.*, 2002; Padisák *et al.*, 2009), which is particularly tolerant to low nitrogen and carbon conditions. This tolerance occurs because some H1 species possess nitrogen-fixation mechanisms, which favor them under

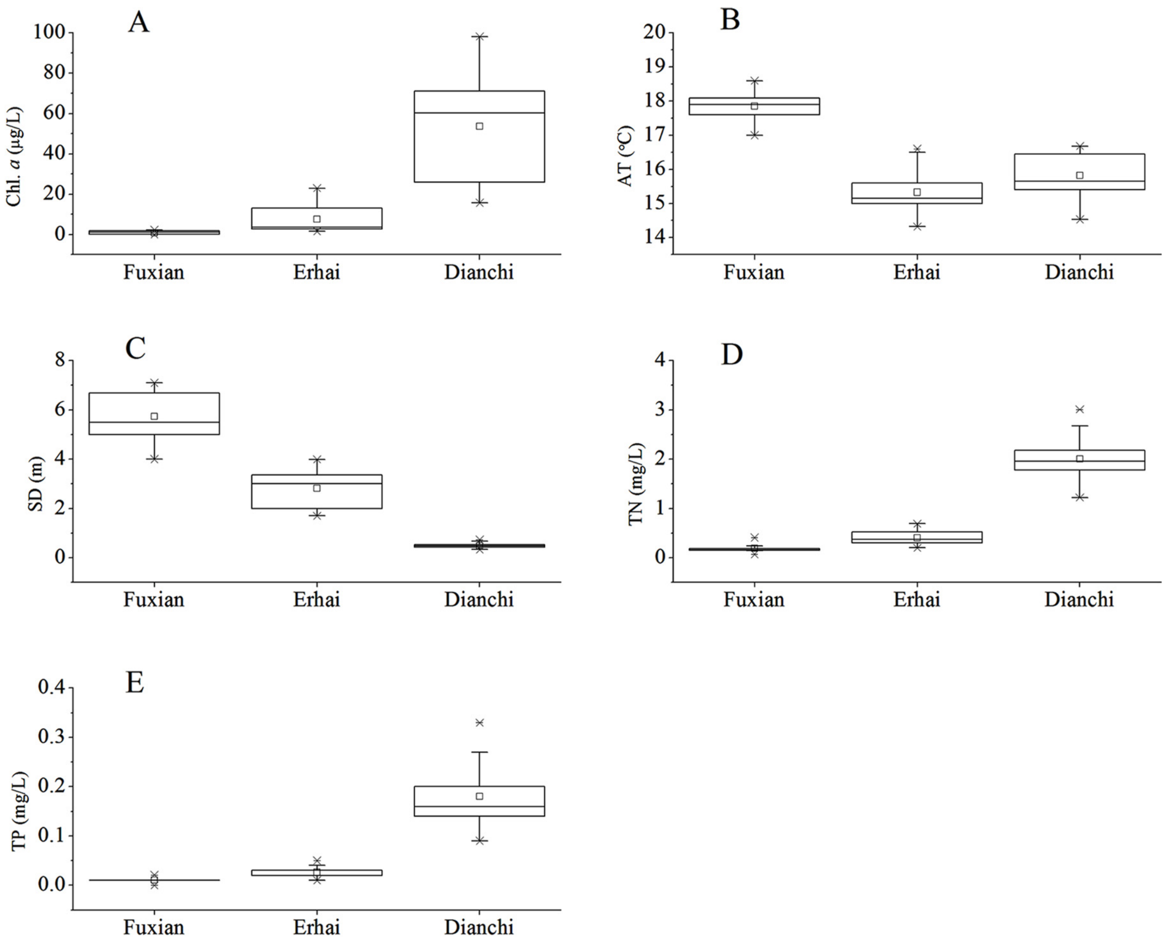

Fig. 4. ;Box chart of annual mean chlorophyll *a* (Chl. *a*), air temperature (AT), water transparency (SD), total nitrogen (TN) and total phosphorus (TP) in the three lakes.

ambient low-nitrogen conditions. In the present study, the TN concentration in Lake Erhai increased by 0.017 mg/L per year from 1990 to 2010 and might have played a role in disrupting the dominance of *Dolichospermum* sp. This hypothesis is concordant with our results, which suggested that the increase in the algal biomass of Lake Erhai during the study period was positively correlated with TN concentration. From 1990 to 2010, the algal biomass of Lake Erhai was significantly negatively correlated with SD. This result is expected because *Microcystis* sp. is believed to be a resilient, shade-tolerant species. A similar result was reported by Kumagai (2000), who suggested that an increase in algal biomass associated with nutrient loading increased light attenuation in Lake Constance, thereby reducing water transparency. In addition, Rinke *et al.* (2010) demonstrated that this effect could promote thermal stratification, in turn creating a more stable environment for cyanobacterial growth. Although *Microcystis* sp. does not perform well in low light environments, it competes advantageously with other primary producers for light by vertically migrating to the surface (Rinke *et al.*, 2010).

Lake Dianchi is hypereutrophic, and it currently exhibits year-round cyanobacterial blooms dominated by *Microcystis* sp. During the study period of 1990–2010, the dominant algae species in Lake Dianchi shifted from functional group J (consisting of *Scenedesmus* sp., *Pediastrum* sp. and *Coelastrum* sp.) to assemblage M (consisting of *Microcystis* sp.) (details in Dong *et al.*, 2014). Findlay *et al.* (2001) and Elliott *et al.* (2005) suggested that climate warming can modify existing phytoplankton communities and reported that warming is a predictor of algal biomass in this shallow lake, as high temperatures are more favorable to cyanobacteria than to green algae. During the study period, the increase in algal biomass of Lake Dianchi was significant and highly correlated with TN concentration and AT. This result agrees with those of Paerl and Paul (2012), who found that *Microcystis* sp. prefer high temperatures. Positive synergistic effects of warming and nutrition increases on *Microcystis* sp. biomass have also been observed in Lake Taihu (Deng *et al.*, 2016) and Lake Pamvotis (Gkelis *et al.*, 2014). Additionally, based on global-scale field data, Kosten *et al.* (2012) suggested that warming and increasing nutrient concentrations can increase cyanobacterial dominance in shallow lakes from subarctic Europe to southern South America.

Lake Fuxian was influenced by the AT increase during the 1960s (Dong *et al.*, 2014). However, in the present study, unlike Lake Erhai and Lake Dianchi, Lake Fuxian exhibited no significant increase in AT or TN concentration from 1990 to 2010. However, significant increases in algal biomass were detected in Lake Fuxian. Based on an analysis of changes in phytoplankton composition, the filamentous green algae

Mougeotia sp. is currently the most predominant species in Lake Fuxian (details in Dong *et al.*, 2014). Additionally, the increase in the algal biomass of Lake Fuxian since the 1990s has been primarily associated with a sharp increase in the density of these green algae (Pan *et al.*, 2009). In the present study, the increase in algal biomass in Lake Fuxian was negatively correlated with TP concentration. This result is consistent with that of Tapolczai *et al.* (2015), who indicated that meso-oligotrophic conditions (TP < 20 μg/L) were favorable for *Mougeotia* sp. Additionally, Padisák *et al.* (2010) suggested that *Mougeotia* sp. is a permanent element of the phytoplankton flora in deep lakes, and its success is partially due to its ability to compete for phosphorus under low ambient concentrations (Reynolds, 2006).

The different responses of the three studied lakes to environmental conditions were very similar to those reported by Rigosi *et al.* (2014), who suggested that the effects of climate warming and eutrophication on cyanobacterial biomass were dependent on lake trophic state and taxon composition.

5 Conclusion

Lakes Fuxian, Erhai and Dianchi all exhibited increases in algal biomass over the studied time period of 1990–2010. Analyzing the effects of warming and nutrient levels on phytoplankton biomass in the three studied lakes revealed that the best predictor of algal increase varied among the lakes. The present findings demonstrated that nutrient levels had stronger effects than temperature in the oligotrophic lake (Lake Fuxian), whereas both nutrient levels and temperature affected algal biomass in the eutrophic and hypereutrophic lakes. This result supports the hypothesis that effects of climate warming and eutrophication on phytoplankton biomass are dependent on taxon composition of the lake.

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