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RESEARCH ARTICLE

The relationships of meteorological factors and nutrient levels with phytoplankton biomass in a shallow eutrophic lake dominated by cyanobacteria, Lake Dianchi from 1991 to 2013

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Abstract Long-term interannual (1991–2013) and monthly (1999–2013) data were analyzed to elucidate the effects of meteorological factors and nutrient levels on phytoplankton biomass in the cyanobacteria-dominated Waihai basin of Lake Dianchi. The interannual ln(chl. *a*) exhibited positive correlations with the mean air temperature, mean minimum air temperature, and mean maximum air temperature; in addition, a positive relationship between Δln(chl. *a*) and ΔTP was observed throughout the period. Additionally, ln(chl. *a*) exhibited a positive correlation with the TP concentration, negative correlations with the sunshine hours and wind speed during the dry season, and positive correlations with the TN and TP concentrations during the rainy season. Furthermore, TP was the most influential factor affecting cyanobacterial bloom dynamics throughout the entire period and during the dry season, and TN and TP were the most important factors during the rainy season, as determined by relative importance analysis. The results of this study based on interannual analysis demonstrated that both meteorological factors and nutrient levels have important roles in controlling cyanobacterial bloom dynamics. The relative importance of these factors may change according to precipitation patterns. Thus, climate change regulation and eutrophication management should be considered in strategies for bloom control. Decreasing the TP load should be prioritized throughout the entire period and during the dry season, and decreasing the TN and TP loads should be considered initially during the rainy season. In addition, further studies of more frequent and complete data acquired over a longer period of time should be conducted in the future.

Keywords Cyanobacterial bloom · Climate warming · Sunshine hours · Total nitrogen · Total phosphorus · Dry and rainy seasons

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Introduction

The occurrence and expansion of cyanobacterial blooms in aquatic ecosystems cause serious environmental problems worldwide (Paerl and Otten 2013; Sukenik et al. 2015). The dynamics of cyanobacterial blooms involve the combined effects of physical (e.g., light, temperature, turbulence and mixing, and water residence time), chemical (e.g., nutrients, dissolved carbon, and salinity), and biological (e.g., grazing, microbial interactions, and allelopathy) factors and are also affected by the cyanobacterium itself (Dokulil and Teubner

2000; Heisler et al. 2008; O'Neil et al. 2012; Paerl and Otten 2013). Nutrients (particularly nitrogen and phosphorus) play vital roles in bloom formation (Håkanson et al. 2007; Heisler et al. 2008; Paerl et al. 2014), and meteorological factors, climate change (Hu et al. 2009; Paerl and Huisman 2008; Verspagen et al. 2014; Zhang et al. 2012), and their indirect effects (Callieri et al. 2014; Paerl and Huisman 2009; Posch et al. 2012) have also been identified as contributors to the expansion of cyanobacterial blooms.

The primary factors affecting the development of cyanobacterial blooms remain to be elucidated. Nutrient supply is considered the principal force driving bloom formation or cyanobacterial dominance. Wagner and Adrian (2009) have reported that increased nutrient levels play a more important role in driving cyanobacterial bloom growth than climate warming at total phosphorus thresholds of 70 to 215 μg/L. Another study revealed similar results for Lake Constance (Stich and Brinker 2010). Additionally, nutrient control may be more important than climate change for bloom resilience (Brookes and Carey 2011). However, climate change (e.g., warming) favors cyanobacterial growth either directly or indirectly (Carey et al. 2012; Jöhnk et al. 2008; Paerl and Huisman 2008). Previous studies have indicated that cyanobacterial bloom growth is controlled by physical factors, such as temperature, wind speed, and irradiance, when nutrient levels are sufficient (Qin et al. 2010; Zhang et al. 2012). Furthermore, a combined effect of climate change and nutrient levels on cyanobacterial bloom growth has been demonstrated by Liu et al. (2011) and Gkelis et al. (2014). The interactive effect of eutrophication and climate change on the growth of these blooms, particularly future growth, is complex (O'Neil et al. 2012), and it varies according to the lake classification, such as a dimictic or polymictic basin (Taranu et al. 2012), as well as the lake area (Duan et al. 2015), the trophic status (Rigosi et al. 2014, 2015), and the cyanobacterial taxon (Rigosi et al. 2014) or strain (Davis et al. 2009).

Lake Dianchi is the largest lake on the Yungui Plateau and the sixth largest freshwater lake in China. It is characterized by high solar radiation and low-temperature amplitude, as well as weak development of the lakeshore, which provides various natural resources for the local inhabitants. The lake has suffered from severe eutrophication since the 1980s and has been affected by cyanobacterial blooms since the 1990s (Sheng et al. 2012; Li et al. 2014). Climate warming is also a factor at Lake Dianchi (Zhou et al. 2015a). Although several studies have examined the cyanobacterial blooms occurring in this lake (Liu et al. 2009; Sheng et al. 2012; Shan et al. 2014; Wang et al. 2015), the most influential or primary factor (e.g., meteorological factors or nutrient levels) remains unclear, particularly for interannual analysis based on more than two decades of data. Moreover, this lake is characterized by an obvious division between dry and rainy seasons, and the physical and chemical conditions associated with rainfall patterns may differ between these two seasons, which would affect cyanobacterial dynamics (Paerl and Huisman 2008; Reichwaldt and Ghadouani 2012). Thus, the aim of this study was to analyze the effects of meteorological factors and nutrient levels on the dynamics of cyanobacterial blooms in Lake Dianchi based on interannual data from 1991 to 2013 and monthly data from 1999 to 2013 to identify differences between the dry and rainy seasons. In addition, management suggestions are discussed.

Methods

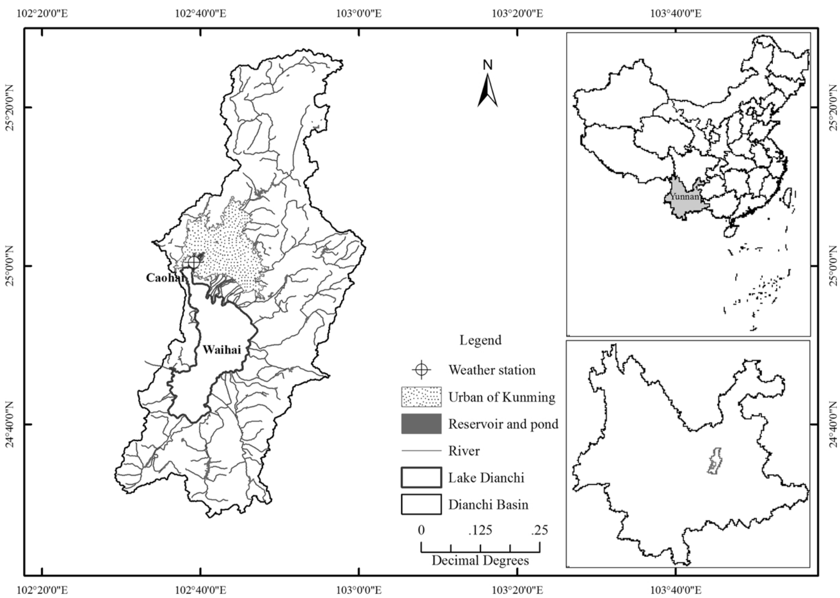
Description of Lake Dianchi

Lake Dianchi (24° 30′ N–25° 02′ N, 102° 36′ E–102° 47′ E, Fig. 1), a warm polymictic and oxic lake (Yuan et al. 1986; Yang et al. 2010), is located in the middle of the Yungui Plateau in southwestern China and is characterized by a northern, low-latitude, subtropical, plateau mountain, monsoon climate. The area of the lake is 309 km^2, and it consists of Caohai, with an area of 10.8 km^2, in the north and Waihai (our study site), with an area of 298.2 km^2, in the south. The mean depth is 4.4 m, and the lakeshore is 163.2 km at a water level of 1887.4 m. More than 20 rivers flow into the lake. Lake Dianchi is located downstream and southwest of Kunming City, and a large amount of pollutants, such as municipal sewage, industrial wastewater, and non-point source nutrients (e.g., nitrogen and phosphorus), are discharged into the lake due to rapid growth resulting from socioeconomic development in the basin. The ecosystem structure and function of the lake are currently simple and vulnerable, e.g., transparency has decreased to 0.6 m, the aquatic macrophyte community covers less than 2.05 % of the lake area, and the phytoplankton and zoobenthos (macroinvertebrate) species richness has significantly decreased (Li et al. 2014; Shan et al. 2014). For additional physicochemical factors in the lake and its basin, such as the nutrients and metal and nonmetal elements, please refer to Liu et al. (2009).

Data acquisition

Meteorological factors, including the sunshine hours (SHs), mean air temperature (ATmean), mean minimum air temperature (ATmin-m), mean maximum air temperature (ATmax-m), precipitation (Pre.), and mean wind speed (WS), were obtained from the National Meteorological Information Center of China. Water quality data, including the chlorophyll *a* (chl. *a*), total nitrogen (TN), and total phosphorus (TP) concentrations, were originally obtained from the Kunming Institute of Environmental Science (1991–1998; cited from Mo et al. 2007) and the Kunming Environmental Monitoring Center (1999–2013), which were part of a single

Fig. 1 Location of Lake Dianchi



institution during the 1990s. The monthly data are presented as the mean value for 8 sampling sites, and the annual data are presented as the mean value for 12 months. Based on the linear relationships between the log(cell chl. *a* concentration) and log(cell volume) of phytoplankton, such as cyanobacteria, chlorophytes, and diatoms (Reynolds 2006), and between the chl. *a* concentration and the MODIS normalized spectral index related to the cyanobacterial bloom area (Shi et al. 2015) and because cyanobacteria have become completely dominant since the 1990s in Lake Dianchi (Li et al. 2014), the chl. *a* concentration was selected to represent the bloom degree (phytoplankton biomass) in the present study.

Statistical analysis

Time series analysis was conducted to identify long-term trends related to meteorology and water quality, and autocorrelation of all variables was detected using an autocorrelation function (acf), which provided estimates of temporal autocorrelation using lagged time series data (Table 1). The *t* test (0.05 significance level) was conducted using Statistical Product and Service Solutions software (SPSS, version 22.0) to assess all variables to detect differences between the dry and rainy seasons. Then, one-dimensional linear regressions were performed with SPSS to determine the direction (positive or negative) of the relationship between ln(chl. *a*) and each independent variable. If autocorrelation was detected, then the linear models were modified based on the residual correlation structure by AR-1 autocorrelation, i.e., order 1 differencing. To quantify the relative contribution of each of the eight explanatory variables to the phytoplankton biomass, generalized linear models (GLMs) between ln(chl. *a*) or ln(Δchl. *a*) and the independent variables were applied using the "glmulti" package of R software (version 3.1.3) (Calcagno and Mazancourt 2010). Model selection was based on the Akaike information criterion (AIC) and Akaike weight (w_i); w_i was also used to define the relative importance of each predictor (Burnham and Anderson 2002).

Results

Long-term trends in meteorological factors

Generally, there were no significant variations ($P > 0.05$) in the annual SHs (Fig. 2a), ATmin-m (Fig. 2c), Pre. (Fig. 2e), or WS (Fig. 2f); however, the annual ATmean (slope = 0.045, $P < 0.05$, Fig. 2b) and ATmax-m (slope = 0.068, $P < 0.01$, Fig. 2d) increased significantly over time. The monthly SHs, ATmean, ATmin-m, ATmax-m, Pre., and WS (mean ± SD) were 221.27 ± 41.22 h, 12.86 ± 3.21 °C, 7.79 ± 2.93 °C, 19.46 ± 3.31 °C, 17.96 ± 19.92 mm, and 2.50 ± 0.83 m/s, respectively, during the dry season and 140.53 ± 42.00 h, 19.36 ± 1.72 °C, 16.07 ± 1.76 °C, 24.25 ± 1.79 °C, 137.27 ± 73.73 mm, and 1.98 ± 0.49 m/s, respectively, during the rainy season (1999–2013). There was an obvious division between the dry (from November to April) and rainy (from May to October) seasons at the study site, and all climatological variables significantly differed between the two seasons (Fig. 3a–f, $P < 0.01$).

Long-term trends in water quality

In general, the TN (slope = 0.034, $P < 0.01$, Fig. 2g) and chl. *a* (slope = 2.43, $P < 0.05$, Fig. 2i) concentrations increased significantly throughout the study period. There was no significant change in the TP concentration ($P > 0.05$, Fig. 2h), but an obvious peak was observed in 1999, followed by a steady

Table 1 Autocorrelation function (acf) for all variables (1991–2013, $N = 23$)

Lag	acf (r)								
	SHs	ATmean	ATmin-m	ATmax-m	Pre.	WS	TN	TP	Chl. *a*
1			0.520			0.860		0.616	0.671
2						0.720			0.525
3						0.588			
4						0.448			
5	−0.351								
6									
7									
8								−0.462	
9									
10						−0.377			
11						−0.426			
12					−0.362	−0.424			
13			−0.364			−0.419			
14						-0.361			

SHs annual sunshine hours, *ATmean* annual mean air temperature, *ATmin-m* annual mean minimum air temperature, *ATmax-m* annual mean maximum air temperature, *Pre.* annual precipitation, *WS* annual mean wind speed, *TN* annual mean total nitrogen, and *TP* annual mean total phosphorus. Lags with autocorrelation coefficients (absolute values) of greater than or equal to $r = 0.35$ are presented

decline from 1999 to 2002. The average TN, TP, and chl. *a* concentration were 2.28 ± 0.59 mg/L, 0.185 ± 0.082 mg/L, and 59.47 ± 30.13 μg/L, respectively, during the dry season and 2.17 ± 0.45 mg/L, 0.177 ± 0.082 mg/L, and 84.56 ± 35.76 μg/L, respectively, during the rainy season. The chl. *a* concentration (Fig. 3i, $P < 0.01$) differed between the dry and rainy seasons, but not TN (Fig. 3g, $P > 0.05$) or TP (Fig. 3h, $P > 0.05$) concentration.

Influences of meteorological factors and nutrient levels on interannual cyanobacterial bloom dynamics

During the entire period from 1991 to 2013, ln(chl. *a*) was highly positively correlated with the ATmean ($R^2 = 0.377$, $P < 0.01$), ATmin-m ($R^2 = 0.426$, $P < 0.01$), and ATmax-m ($R^2 = 0.411$, $P < 0.01$). A positive correlation was also observed between Δln(chl. *a*) and ΔTP ($R^2 = 0.204$, $P < 0.05$), as shown in Table 2. The best model describing ln(Δchl. *a*) contained 1–3 predictor variables (Table 3) that explained 23 to 39 % (R^2) of the variance. ΔTP was the most predictive of ln(Δchl. *a*), as shown in Table 3; with a relative importance of 81 %.

Influences of meteorological factors and nutrient levels on cyanobacterial bloom dynamics during the dry and rainy seasons

During the dry season, ln(chl. *a*) was negatively correlated with the SHs ($R^2 = 0.082$, $P < 0.01$, Fig. 4a) and WS ($R^2 = 0.078$, $P < 0.01$, Fig. 4f) and positively correlated with the TP concentration ($R^2 = 0.099$, $P < 0.01$, Fig. 4h). During the rainy season, ln(chl. *a*) was positively correlated with the TN ($R^2 = 0.134$, $P < 0.001$, Fig. 4g) and TP ($R^2 = 0.157$, $P < 0.01$, Fig. 4h) concentrations. The best model describing ln(chl. *a*) during the dry season contained two to three predictor variables (Table 4) that explained 16–18 % (R^2) of the variance and included TP. The best models describing ln(chl. *a*) during the rainy season contained two to three predictor variables (Table 4) that explained 24–26 % (R^2) of the variance and included TN and TP. In addition, the TP concentration was the best predictor of ln(chl. *a*) during the dry season, and the TN and TP concentrations were the best predictors during the rainy season based on their relative importance (greater than 90 %), and the SHs represented the second most important variable (58 %) during the dry season (Fig. 5).

Discussion

Influences of meteorological factors and nutrient levels on cyanobacterial bloom dynamics

Cyanobacterial growth, dominance, and bloom formation in lakes are the comprehensive result of environmental factors, such as light, temperature, turbulence and mixing, and nutrient levels. Our findings revealed that both meteorological parameters and nutrient levels were important factors affecting interannual cyanobacterial

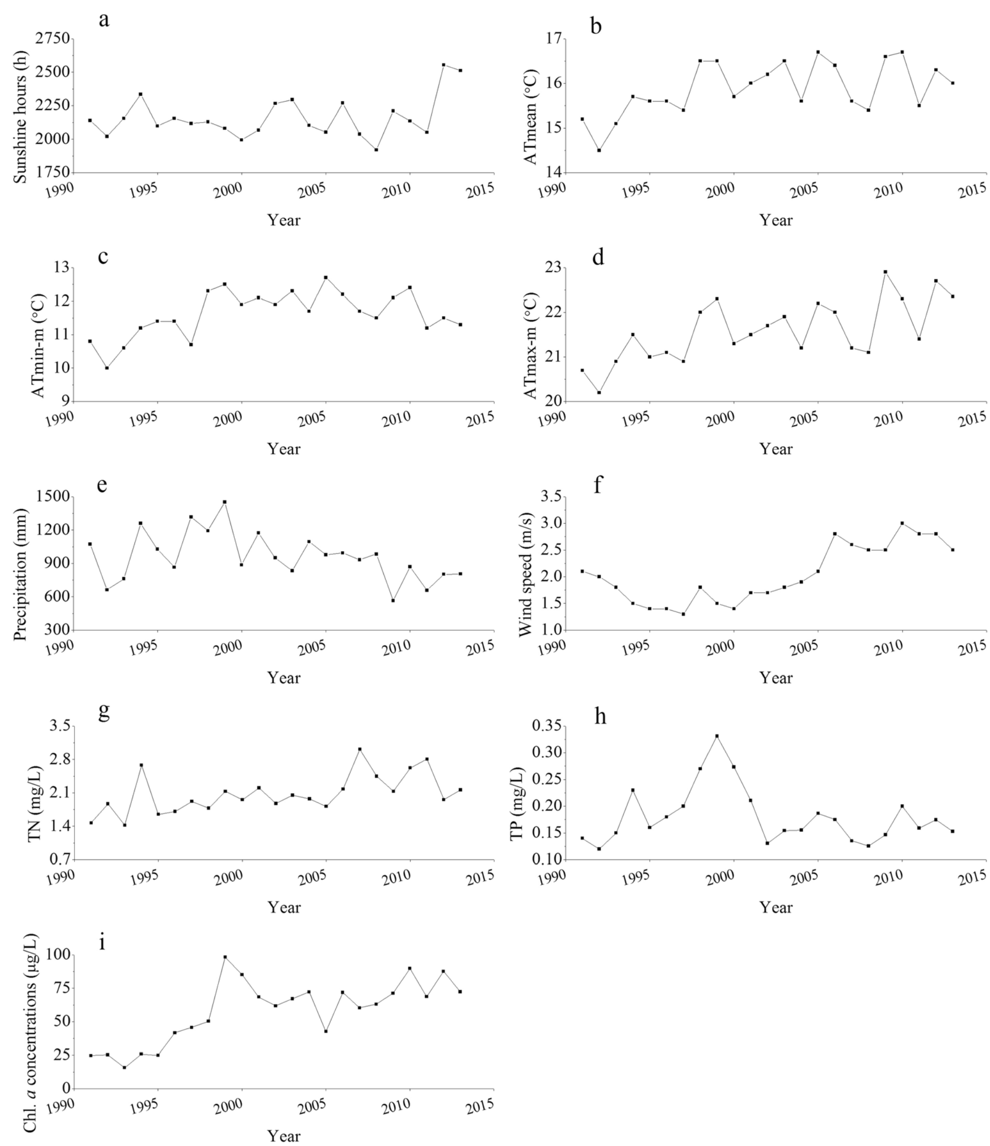


Fig. 2 Annual sunshine hours (**a**), mean air temperature (**b**), mean minimum air temperature (**c**), mean maximum air temperature (**d**), precipitation (**e**), mean wind speed (**f**), mean TN (**g**), mean TP (**h**), and mean chl. *a* concentrations (**i**) from 1991 to 2013

bloom dynamics and that these factors were heterogeneous between the dry and rainy seasons.

Solar radiation is the energy source of aquatic ecosystems and particularly of primary producers (e.g., cyanobacteria) for photosynthesis. Previous studies have indicated that phytoplankton populations increase with increasing incident light intensity (Huisman 1999), which has also been reported in Lake Taihu (Zhou et al. 2014), a lake where the duration of the cyanobacterial bloom was found to increase when the annual SHs exceeded 1650 h (Zhang et al. 2012). Light might be a limiting factor when the euphotic zone (Z_{eu}) is much smaller than the mixing zone (Z_{mix}) (Kalff 2002). However, according to our recent field study and Yuan et al. (1986), the Z_{eu} of the lake was 1.79 ± 0.44 m, and the Z_{mix} was approximately equal to the depth (4.4 m), respectively; in addition, the SHs had no significant effect on phytoplankton biomass in our study. These results indicated that the SHs were sufficient for phytoplankton growth in the low-latitude plateau region of Lake Dianchi, which features a relatively high level of solar radiation and a predominance of cyanobacteria with gas vesicles (Li et al. 2014). An exceedingly high light intensity induces algal photoinhibition, and a low population density does not allow for sufficient self-shading for protection (Gerla et al. 2011). Our previous in situ study conducted from March to April (dry season) revealed the presence of photoinhibition in Lake Dianchi (Zhou et al. 2015b). In the present study, low phytoplankton biomass was detected during the SHs of the dry season (with a relative increase in SHs and a lower bloom biomass compared to the rainy season), which might have resulted from less self-shading and more photoinhibition (Gerla et al. 2011).

Temperature is an important factor affecting phytoplankton growth and cyanobacterial bloom dynamics, with warm weather favoring cyanobacterial bloom formation

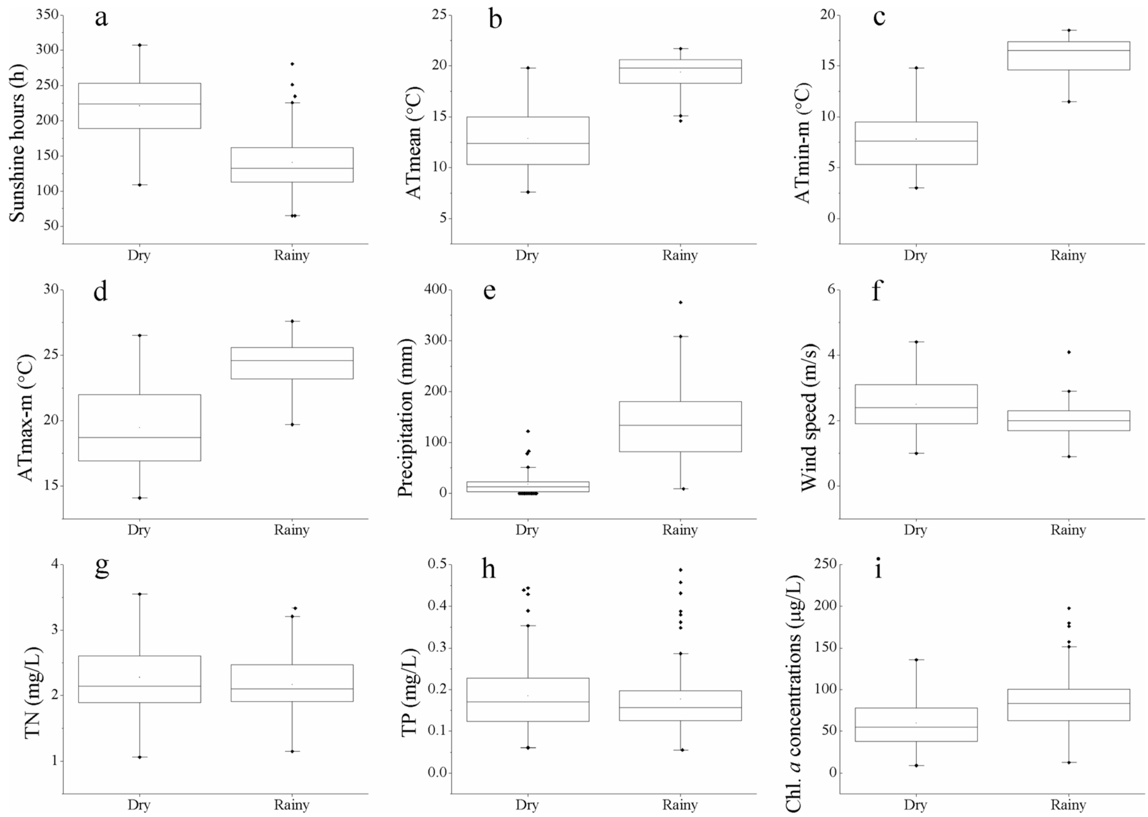


Fig. 3 Box plot of monthly sunshine hours (**a**), mean air temperature (**b**), minimum air temperature (**c**), maximum air temperature (**d**), precipitation (**e**), mean wind speed (**f**), mean TN (**g**), mean TP (**h**), and mean chl. *a* concentrations (**i**) during the dry and rainy seasons from 1999 to 2013

(Kanoshina et al. 2003). Several other studies have also reported that warming temperatures promote cyanobacterial dominance (Kosten et al. 2012) and bloom formation and duration (Jöhnk et al. 2008; Liu et al. 2011; Zhang et al. 2012). However, previous studies have also indicated that temperature is not a predominant controlling factor for cyanobacterial biovolume (Rigosi et al. 2014) or a driver of bloom formation (Wagner and Adrian 2009). For example, the expansion of *Cylindrospermopsis raciborskii* has been partially attributed to increasing temperatures (Sinha et al. 2012); furthermore, oligotrophication has been reported to outweigh the effects of global warming in Lake Constance (Stich and Brinker 2010), and temperature has been demonstrated to be a more important factor in mesotrophic lakes than in oligotrophic and eutrophic lakes (Rigosi et al. 2014). In the present study, the chl. *a* concentration was found to increase with increasing air temperature (ATmean, ATmin-m, and ATmax-m) interannually, but there was no significant correlation between the chl. *a* concentration and air temperature during either the dry or rainy season; this lack of correlation might be attributed to the time scale of the observations.

Table 2 Linear regressions between ln(chl. *a*) and SHs, ATmean, ATmin-m, ATmax-m, Pre., WS, TN, and TP (1991–2013)

Independent variable	Slope	R^2	P	N
SHs	–	0.071	>0.05	22*
ATmean	0.53	0.377	<0.01	23
ATmin-m	0.48	0.426	<0.01	23
ATmax-m	0.47	0.411	<0.01	23
Pre.	–	0.096	>0.05	22*
WS	–	0.019	>0.05	22*
TN	–	0.092	>0.05	22*
TP	3.06	0.203	<0.05	22*

SHs annual sunshine hours, *ATmean* annual mean air temperature, *ATmin-m* annual mean minimum air temperature, *ATmax-m* annual mean maximum air temperature, *Pre.* annual precipitation, *WS* annual mean wind speed, *TN* annual mean total nitrogen, and *TP* annual mean total phosphorus. "*" indicates that there was an autocorrelation in the ordinary regression, as demonstrated using modified linear models based on the residual correlation structure by AR-1 autocorrelation (order 1 differencing)

Precipitation (e.g., rainfall) is thought to influence the dynamics of cyanobacterial blooms under changing climatic conditions (Reichwaldt and Ghadouani 2012). Although different effects of some factors on phytoplankton biomass were observed between the dry and rainy seasons, precipitation did not directly influence bloom dynamics, according to our results. The wind pattern was another important factor. Strong wind is a

Table 3 Best-fit regression models of ln(Δchl. *a*) and meteorological factors and nutrient concentrations (1991–2013)

N	Meteorological factors						Nutrients		R^2_{adj}	*P*	AIC	w_i
	ΔSHs	ΔATmean	ΔATmin-m	ΔATmax-m	ΔPre.	ΔWS	ΔTN	ΔTP				
22								+	0.194	<0.05	−14.734	0.112
			+					+	0.214	<0.05	−13.396	0.057
	+	+						+	0.288	<0.05	−13.349	0.056
	+			+				+	0.272	<0.05	−12.849	0.044
	+							+	0.191	0.052	−12.736	0.041
Relative importance	0.37	0.26	0.24	0.20	0.18	0.17	0.16	0.81	–	–	–	–

Δ the value of "$Year_t$-$Year_{t-1}$", *SHs* annual sunshine hours, *ATmean* annual mean air temperature, *ATmin-m* annual mean minimum air temperature, *ATmax-m* annual mean maximum air temperature, *Pre.* annual precipitation, *WS* annual mean wind speed, *TN* annual mean total nitrogen, *TP* annual mean total phosphorus, *AIC* Akaike information criterion, and w_i Akaike weight. "+" represents the independent variables that were included in a particular model

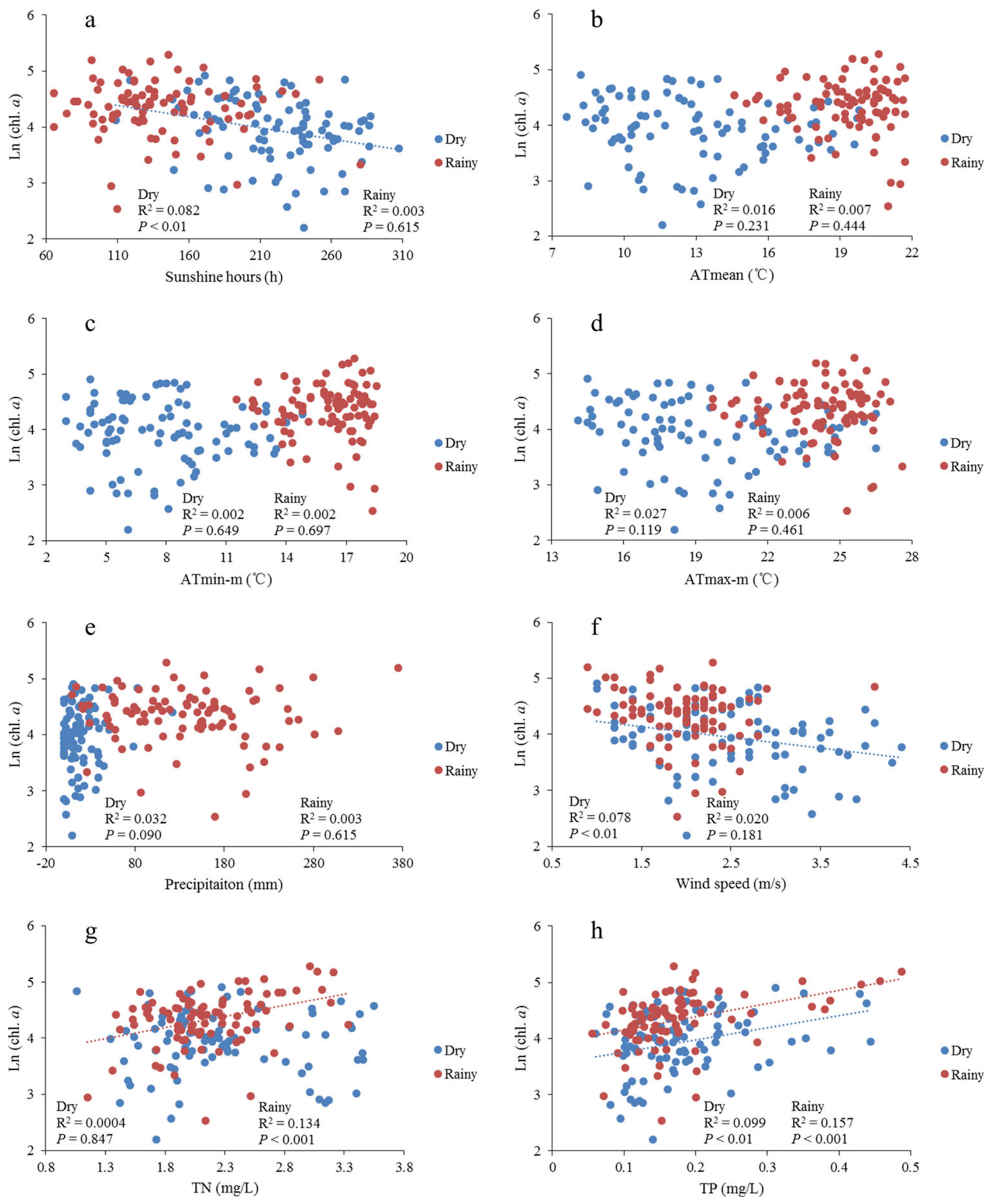


Fig. 4 Correlations between ln(chl. *a*) and monthly sunshine hours (**a**), ATmean (**b**), ATmin-m (**c**), ATmax-m (**d**), precipitation (**e**), mean wind speed (**f**), mean TN (**g**), and mean TP (**h**) concentrations between the dry and rainy seasons from 1999 to 2013 (*N* = 90)

Table 4 Best-fit regression models of ln(chl. *a*) during the dry and rainy seasons from 1999 to 2013 ($N = 90$)

Season	Meteorological factors						Nutrients		R^2_{adj}	*P*	AIC	w_i
	SHs	ATmean	ATmin-m	ATmax-m	Pre.	WS	TN	TP				
Dry	+							+	0.148	<0.001	144.821	0.081
		+	+					+	0.150	<0.001	145.824	0.049
	+					+		+	0.147	<0.001	146.163	0.041
	+		+					+	0.143	<0.001	146.597	0.033
	+				+			+	0.142	<0.01	146.678	0.032
			+	+				+	0.142	<0.01	146.707	0.032
	+	+						+	0.141	<0.01	146.773	0.031
Rainy							+	+	0.232	<0.00001	106.835	0.120
		+					+	+	0.231	<0.0001	108.209	0.061
			+				+	+	0.229	<0.0001	108.419	0.055
					+		+	+	0.229	<0.0001	108.435	0.054
						+	+	+	0.228	<0.0001	108.513	0.052
				+			+	+	0.227	<0.0001	108.657	0.048

SHs monthly sunshine hours, *ATmean* monthly mean air temperature, *ATmin-m* monthly mean minimum air temperature, *ATmax-m* monthly mean maximum air temperature, *Pre.* monthly precipitation, *WS* monthly mean wind speed, *TN* monthly mean total nitrogen, *TP* monthly mean total phosphorus, *AIC* Akaike information criterion, and w_i Akaike weight. "+" represents the independent variables that were included in a particular model

crucial regulator of bloom formation and expansion (Wu et al. 2013; Qin et al. 2015). Bloom area has been shown to be negatively correlated with WS (Wu et al. 2015), and cyanobacterial blooms have been reported to occur earlier and to last longer with an interannual decreasing WS in Lake Taihu (Zhang et al. 2012). In the present study, the WS was negatively correlated with the phytopnankton biomass during the dry season because the cyanobacteria were favored by reduced WS and calm weather (Jöhnk et al. 2008; Kanoshina et al. 2003).

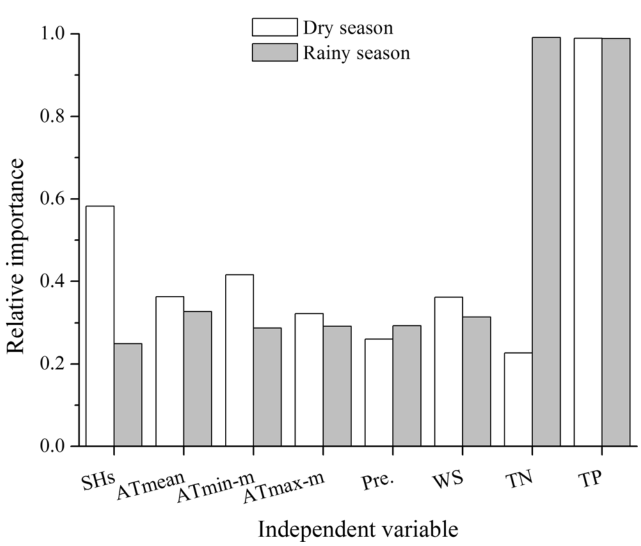


Fig. 5 Relative importance of the independent variables in the models of ln(chl. *a*) during the dry and rainy seasons from 1999 to 2013

Nutrients (nitrogen and phosphorus) are typically considered the principal factors contributing to cyanobacterial bloom formation (Håkanson et al. 2007; Heisler et al. 2008; Paerl et al. 2014). However, cyanobacterial blooms have also been reported to be controlled by physical factors when nutrient levels are sufficient (Qin et al. 2010; Zhang et al. 2012). Although the TN and TP concentrations in the present study were generally higher than the typical classification standards for eutrophication and hypereutrophication (Nürnberg 1996), variation in the TP concentration had significant effects on the phytoplankton biomass both interannually and seasonally. According to the present data, TP was a limiting nutrient controlling bloom dynamics interannually, consistent with the TN:TP ratios recommended by the World Health Organization (WHO), as cited by Salameh and Harahsheh (2011). From 1999 to 2002, the N:P ratios increased and favored non-N_2-fixing cyanobacteria (Posch et al. 2012), and *Microcystis* became a predominant genus (Li et al. 2014). Moreover, a much greater amount of nutrients entered the water body due to rainfall (Reichwaldt and Ghadouani 2012) during the rainy season in combination with appropriate conditions for bloom growth, such as moderate SHs, warm temperature, and low WS. Consequently, phytoplankton biomass was promoted during the rainy season. These results suggest that the relatively high levels of nutrients, particularly TP, remained important for phytoplankton growth; however, they do not indicate that the available forms of N, P, and other nutrients and metal and nonmetal elements had no effects on bloom dynamics in the lake (Liu et al. 2009; Sheng et al. 2012).

Main factors affecting cyanobacterial bloom dynamics and management suggestions

It is difficult to identify the most important factor affecting overall cyanobacterial bloom development due to the differing characteristics of different bloom phases, the individual characteristics of the study site, and the lack of complete information about the aquatic ecosystem. Indeed, long-standing controversy exist with regard to the most important factors affecting cyanobacterial bloom dynamics, as evidenced by the theories of nutrient dominance (Brookes and Carey 2011; Stich and Brinker 2010; Wagner and Adrian 2009), climate or meteorological dominance (Qin et al. 2010; Jöhnk et al. 2008; Zhang et al. 2012), and their combined effects (George et al. 2015; Gkelis et al. 2014; Liu et al. 2011; O'Neil et al. 2012; Paerl and Paul 2012). In the present study, both meteorological factors and nutrient levels had important roles in controlling cyanobacterial bloom dynamics, particularly according to the results of interannual analysis (temperature and TP). Nonetheless, the relative importance of nutrients may change with the precipitation pattern.

Rigosi et al. (2014) have reported that both temperature and nutrient levels are significant drivers controlling the development of cyanobacterial blooms in eutrophic or hypereutrophic lakes; similar findings have been observed in the eutrophic Lake Müggelsee (Wagner and Adrian 2009) and Lake Taihu (Liu et al. 2011) and hypereutrophic Lake Pamvotis (Gkelis et al. 2014). Significant influences of interannual air temperatures and TP were also observed in our study. However, the range of variation in the annual mean temperature has been reported to be suitable for phytoplankton growth in Lake Dianchi (Darley 1982). In other words, the temperature variations observed in this study were not sufficiently extreme to cause limitations. Thus, TP was determined to be a more important factor for phytoplankton growth than the temperature based on analysis of relative importance. Furthermore, the TP concentration significantly decreased from 1999 to 2002 due to the water environment management in the basin (He et al. 2014), whereas the cyanobacterial bloom remained at a high dense, potentially reflecting the combined effects of TN and TP (Paerl et al. 2014). Moreover, TP was the principal factor controlling bloom dynamics during both the dry and rainy seasons. During the dry season, the nutrient input from the watershed was reduced, and the relatively low concentration of TP (compared to that of TN) and high SHs (photoinhibition, as described above) became the major controlling factors. During the rainy season (under appropriate conditions, as described above), the increased nutrient (TN and TP) input promoted phytoplankton growth.

Several challenges, such as climate warming (IPCC 2014), a decline in SHs (Wang et al. 2012), changes in precipitation (Lau et al. 2013), and future eutrophication (Khan and Mohammad 2014), can negatively affect water quality (e.g., cyanobacterial blooms) in lakes. Thus, the development of management strategies for the water environment and lake ecosystems is crucial when facing the effects of climate change combined with those of detrimental human activities. Our interannual results indicated that meteorological factors (temperature) and nutrients (TP) have important roles in controlling cyanobacterial bloom dynamics, which suggests that both climate change regulation (e.g., slowing climate warming) and eutrophication management (e.g., controlling the nutrient load) should be considered in strategies aimed at achieving cyanobacterial bloom control. Moreover, nutrients, particularly TP, were the primary factors affecting cyanobacterial bloom dynamics during the period from 1991 to 2013, as well as during the dry season. During the rainy season, both TN and TP were the main factors affecting cyanobacterial bloom dynamics. These results indicate that strategies aimed at decreasing the TP level should be initially considered during the dry season and that those aimed at decreasing both the TN and TP loads should be considered during the rainy season. Decreasing the TP level (in this study) should also be considered initially, although temperature is also an important factor. Slowing decreases in SHs (e.g., by improving air quality) and WS should also be considered during the dry season in Lake Dianchi.

Additionally, the relatively low R^2_{adj} value obtained in multiple regression analyses suggests that other important factors may affect the phytoplankton biomass or cyanobacterial bloom dynamics in the lake, e.g., the food web structure and trophic interactions (Shan et al. 2014) and other physicochemical environmental factors (Liu et al. 2009; Sheng et al. 2012). Thus, additional similar studies should be conducted with more frequent and complete data acquired over a longer period of time, including water temperatures, the light attenuation coefficient, available forms of N and P, iron (Fe), and the community structure, as well as the environmental factors studied in this paper.

Conclusion

In summary, we analyzed the effects of meteorological factors and nutrient levels on bloom dynamics in Lake Dianchi using the chl. *a* concentration to represent the phytoplankton biomass. The results of our study demonstrated that both meteorological factors and nutrient levels had important roles in controlling cyanobacterial bloom dynamics. Interannual analysis revealed that the phytoplankton biomass increased with increases in air temperature and TP concentration, with TP concentration as the main contributing factor. However, the relative importance of these factors may change according to precipitation patterns. The SHs, WS, and TP concentrations controlled the bloom dynamics during the dry season, among which the TP concentration was the most important factor, whereas the TN and TP concentrations were the primary factors during the rainy season. All of these results suggest that both climate change regulation and eutrophication management should be considered in strategies aimed at controlling cyanobacterial blooms. Decreasing nutrient levels, particularly the TP load, should be initially considered during the entire period and during the dry season, and decreasing both the TN and TP loads should be considered during the rainy season. Further studies should assess the effects of climate change and eutrophication on cyanobacterial bloom dynamics based on data collected over a longer duration and more frequent and complete variables, and appropriate measures should be proposed to control these blooms.

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