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Jian Huang

Qiujin Xu

Xixi Wang

Old Dominion University, x4wang@odu.edu

Hao Ji

Edward J. Quigley

See next page for additional authors

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Authors

Jian Huang, Qiujin Xu, Xixi Wang, Hao Ji, Edward J. Quigley, Mohamadali Sharbatmaleki, Simeng Li, Beidou Xi, Biao Sun, and Caole Li



Original Research

Effects of hydrological and climatic variables on cyanobacterial blooms in four large shallow lakes fed by the Yangtze River



Jian Huang^a, Qujin Xu^{b,*}, Xixi Wang^c, Hao Ji^a, Edward J. Quigley^a,
Mohamadali Sharbatmaleki^a, Simeng Li^a, Beidou Xi^c, Biao Sun^d, Caole Li^c

^a California State Polytechnic University Pomona, CA, USA

^b Chinese Research Academy of Environmental Sciences, Beijing, China

^c Old Dominion University, Norfolk, VA, USA

^d Inner Mongolia Agriculture University, Hohhot, China

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ABSTRACT

Shallow lakes, one of the most widespread water bodies in the world, are easily shifted to a new trophic state due to external interferences. Shifting hydrologic conditions and climate change can cause cyanobacterial harmful algal blooms (CyanoHABs) in shallow lakes, which pose serious threats to ecological integrity and human health. This study analyzed the effects of hydrologic and meteorological variables on cyanobacterial blooms in Yangtze-connected lakes (Lake Dongting and Poyang) and isolated lakes (Lake Chao and Tai). The results show that (i) chlorophyll-a (Chl-a) concentration tends to decrease exponentially with increasing relative lake level fluctuations (RLLF) and precipitation, but to increase linearly with increasing wind speed and air temperature; (ii) Chl-a concentrations in lakes were significantly higher when RLLF < 100, precipitation < 2.6 mm, wind speed > 2.6 m s⁻¹, or air temperature > 17.8 °C; (iii) the Chl-a concentration of Yangtze-isolated lakes was more significantly affected by water level amplitude, precipitation, wind speed and air temperature than the Yangtze-connected lakes; (iv) the RLLF and the ratio of wind speed to mean water depth could be innovative coupling factors to examine variation characteristics of Chl-a in shallow lakes with greater correlation than single factors.

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1. Introduction

Globally, the occurrence of CyanoHABs is a serious threat to human health, ecological integrity, ecosystem services, and the sustainability of inland and coastal waters. This is especially true in shallow lakes [1]. Cyanobacteria are photosynthetic prokaryotes, sometimes referred to as blue-green algae, and they generally form large colonies or filaments in lakes. Many species possess the ability to control their buoyancy through intracellular gas vesicles [2]. While this property can lead to unsightly blooms forming near the lake surface, it is the cyanobacteria's ability to produce toxins that

concerns humans the most [3]. There are several types of toxins produced by cyanobacteria including hepatotoxins, neurotoxins and cytotoxins [4]. Hepatotoxins damage the liver, and some types can adversely affect the digestive and respiratory systems. In contrast, neurotoxins directly affect the nervous system. Cytotoxins can cause widespread necrotic injury in mammals and are also genotoxic, causing chromosome loss and DNA strand breakage [5].

In recent decades, studies have been conducted to better understand the mechanisms of algal blooms, specifically in shallow eutrophic lakes. These studies have provided evidence suggesting how human activity [6,7], water-sediment exchange [8,9], and external nutrient load [10,11] affect trophic structure. Ecosystems in shallow lakes, however, are susceptible not only to human activity and pollution but also to climatic conditions and hydrologic characteristics, especially water depth.

There has been growing concern in the field of limnology about how climate change may affect phytoplankton populations, which include cyanobacteria. Cyanobacteria grows faster if

* Corresponding author. Chinese Research Academy of Environmental Sciences, No.8 Dayangfang, Beijing, 100012, China.

E-mail addresses: jianhuang@cpp.edu (J. Huang), jianhuang225@gmail.com, xuqj@craes.org.cn (Q. Xu), x4wang@odu.edu (X. Wang), hji@cpp.edu (H. Ji), equigley@cpp.edu (E.J. Quigley), sharbat@cpp.edu (M. Sharbatmaleki), sli@cpp.edu (S. Li), xibd@craes.org.cn (B. Xi), sunbiao@imau.edu.cn (B. Sun), caole003@sina.com (C. Li).

temperatures are higher than $>25^{\circ}\text{C}$. In the field, high temperatures usually occur in lakes in conjunction with stratification, allowing cyanobacteria with buoyancy-regulating properties to appear in near-surface waters. Regional and global warming trends increase the frequency, magnitude, duration, and distribution of CyanoHABs [1]. Meanwhile, regime shifts, or sudden transitions from one stable state to another alternative state, occur due to the basin morphology and water level fluctuation in shallow lakes [12]. Analyzed how water depth and surface area affected Chl-a concentrations in 90 shallow lakes in China with mean depths less than 2.42 m. They found that Chl-a concentrations in the lakes with surface areas (SA) less than 25 km^2 were significantly higher than those in lakes with SA greater than 25 km^2 . [13]; who analyzed data from 466 lakes in 12 European countries, found that Chl-a concentration increased with higher photon absorption and water alkalinity, but it decreased with greater lake water depth and distance from the coast. In addition, rapidly increasing demand for flood control and secured water availability has stimulated nearly one million dam and sluice constructions globally in the past [14]. The water level control on lakes can cause reduced seasonal water level fluctuations and potential negative effects on ecosystems [15]. Both of these studies concluded that shallow lakes are typically isolated and fragmented in the landscape and are extremely sensitive to hydrologic and climatic variability such as air temperature, water depth, surface area and water level. Shallow lakes are commonly affected by multiple interacting stressors, potentially confounding the analysis of separate individual metrics. Thus, it is difficult to receive the comprehensive, scientific and accurate understanding of the mechanisms of algal blooms in shallow lakes by considering variables individually.

In the middle and lower Yangtze River basins there are 651 lakes with SA greater than 1 km^2 , and 18 of those lakes have SA ranging from 100 to 3841 km^2 [16]. The water depth of the lakes is ranging from 1.31 to 23.5 m. Lake Poyang, Dongting, and Tai are the three largest freshwater lakes in the Yangtze River reaches, and Lake Chao is the fifth largest lake in this region. In the Yangtze River floodplain, hundreds of lakes are considered classified as oxbow or riverine, including Lake Dongting and Lake Poyang. This means that they had, or currently have, hydrologic connections with the Yangtze River or its major tributaries [17]. The frequency and duration of hydrologic connectivity is of great importance to the equilibrium of these lake ecosystems. During the past half-century, the environmental health of lakes in the Yangtze River floodplain has been adversely impacted by stresses resulting from human occupancy and overexploitation of catchment resources [18]. Consequently, most of the lakes in this area (e.g. Lake Chao and Tai) have become reservoir-type and susceptible to algal blooms partially due to undesirable alterations of hydrology, climate and lake shape. The cyanobacteria blooms have been extensively studied in Lake Tai and Chao due to serious eutrophication problems, but comparatively less research has been focused on the large Yangtze-connected lakes such as Lake Dongting and Poyang. Our interest is to better understand the influence of complex and interactive factors related to hydrology and climate on the typical Yangtze-connected and isolated lakes. Albeit such understanding to date is insufficient in existing literature and there is room for improvement.

In order from upstream to downstream, Lake Dongting, Poyang, Chao and Tai are all located in the same drainage river basin along the Yangtze River [19]. There are differences in the hydrological conditions among these lakes, however, because each system is either connected to or isolated from the main course of the Yangtze River [20]. Lake Dongting and Poyang mostly maintain natural connectivity to the Yangtze River, while

Lake Chao and Tai have become mostly reservoir-type lakes controlled by sluice gates. In this study, we examined the interactive effects of hydrological (RLLF and mean water depth) and climatic (wind speed, precipitation, and air temperature) factors on CyanoHABs in lakes connected to the Yangtze River (Lake Dongting and Poyang) and nearby lakes isolated from the Yangtze River (Lake Chao and Tai). For the purposes of this research, the Chl-a concentration was used as a surrogate for the CyanoHABs because of their demonstrated positive correlation [21]. We examined a time series of Chl-a concentrations from 2000 to 2010, along with the corresponding hydrology and climate data. The main objective of this study was therefore to (i) compare and analyze the difference between Yangtze-connected and Yangtze-isolated lakes affected by hydrological and climatic variables; (ii) contrast the impact of single factors (water level, wind speed) with coupling factors (RLLF and wind-speed/water-depth ratio) on Chl-a in the two lake types (isolated and connected); (iii) explain and discuss why air temperature drives cyanobacteria blooms formed and accumulated in specific zones of Yangtze-isolated lakes.

2. Materials and methods

2.1. Study sites

Lake Dongting ($29^{\circ}20'\text{N}$, $112^{\circ}50'\text{E}$), Lake Poyang ($29^{\circ}05'\text{N}$, $116^{\circ}20'\text{E}$), Lake Chao ($31^{\circ}20'$, $117^{\circ}20'\text{E}$), and Lake Tai ($31^{\circ}15'\text{N}$, $120^{\circ}14'\text{E}$) are the four most notable shallow lakes located in the middle to lower reaches of the Yangtze River. The four lakes were selected because they developed in floodplains and their trophic states are limited due to the lake hydrologic climate and geomorphology. For Lake Dongting and Poyang the water levels tend to increase with precipitation, especially for months in which the precipitation exceeds 300 mm; for Lake Chao and Lake Tai, the water levels are independent of precipitation (Fig. 5). This is because the inflow-outflow processes for Lake Dongting and Poyang are not significantly controlled by hydraulic structures such as gates and so experience large inflows and outflows and short retention times. Lake Chao and Tai, however, are heavily regulated by hydraulic structures, with relatively smaller inflows and outflows and longer retention times.

The surface areas of the four lakes are between 769 km^2 and 2933 km^2 with mean water depths between 2.12 m and 6.39 m (Table 1). Mean depth, maximum depth, and water level fluctuation descend in the order of Lake Dongting, Lake Poyang, Lake Chao, and Lake Tai. Additionally, these four lakes were considered shallow lakes in this study because they: 1) have a mean water depth of less than 7 m; and 2) do not have consistent thermal stratification [12]. The inflows and outflows of Lake Dongting and Lake Poyang are larger than those of Lake Chao and Lake Tai, whereas the retention times for Lake Dongting and Lake Poyang are noticeably shorter than those of the other two lakes. As expected, the water quality in Lake Dongting and Poyang is markedly better than that of Lake Chao and Tai, as indicated by the TN, TP, and Chl-a concentrations in the first two lakes being much lower than those in the second pair of lakes (Table 1). Based on Chl-a concentration, Lake Dongting and Lake Poyang can be classified as mesotrophic ($1.7\text{ }\mu\text{g L}^{-1} < \text{Chl-a} < 14.3\text{ }\mu\text{g L}^{-1}$), whereas Lake Chao and Lake Tai can be classified as eutrophic ($\text{Chl-a} \geq 14.3\text{ }\mu\text{g L}^{-1}$) [17].

CyanoHABs are closely related to hydrologic and climatic conditions, especially for shallow lakes. In particular, algal density and nutrient concentration both exhibit visible spatial variations across Lake Chao and Lake Tai. In this study, Lake Chao was subdivided into two zones designated west and east (Fig. 1). The west zone, which experiences severe CyanoHABs, receives direct

Table 1
The morphology, hydrology, meteorology and water quality characteristics of the four study lakes.

Characteristic	Symbol	Lake Dongting	Lake Poyang	Lake Chao	Lake Tai
<i>Morphology</i>					
Surface area (km ²)	SA	2432	2933	769	2425
Mean depth (m)	Z _{mean}	6.39	5.10	2.69	2.12
Maximum depth (m)	Z _{max}	23.50	19.50	3.77	3.30
Volume (10 ⁸ m ³)	V	155.42	83.68	20.70	48.60
<i>Hydrology</i>					
Lake level (m)	LL	26.90	13.60	8.80	3.30
Lake level amplitude (m)	LLA	11.14	9.89	3.09	0.84
Relative lake level fluctuation	RLLF	174	194	115	42
Retention time (d)	t _r	18.20	20.90	210.40	310.50
Inflow (m ³ s ⁻¹)	Q _{in}	9912.48	4613.77	115.77	182.97
Outflow (m ³ s ⁻¹)	Q _{out}	9893.50	4629.60	114.00	181.10
Drainage area (km ²)	DA	257000	162000	13310	36500
<i>Climate</i>					
Air temperature (°C)	T	18.04	20.18	17.34	16.94
Wind speed (m s ⁻¹)	V _w	2.57	2.08	2.27	3.14
Precipitation (mm)	P	313	292	191	94
Sunshine hour (h)	Sun	4.84	5.36	5.28	4.91
<i>Water quality</i>					
Total nitrogen (mg L ⁻¹)	TN	1.33	0.61	2.53	3.57
Total phosphorus (mg L ⁻¹)	TP	0.10	0.15	0.22	0.14
Chlorophyll-a (ug L ⁻¹)	Chl-a	2.01	5.60	19.30	21.00

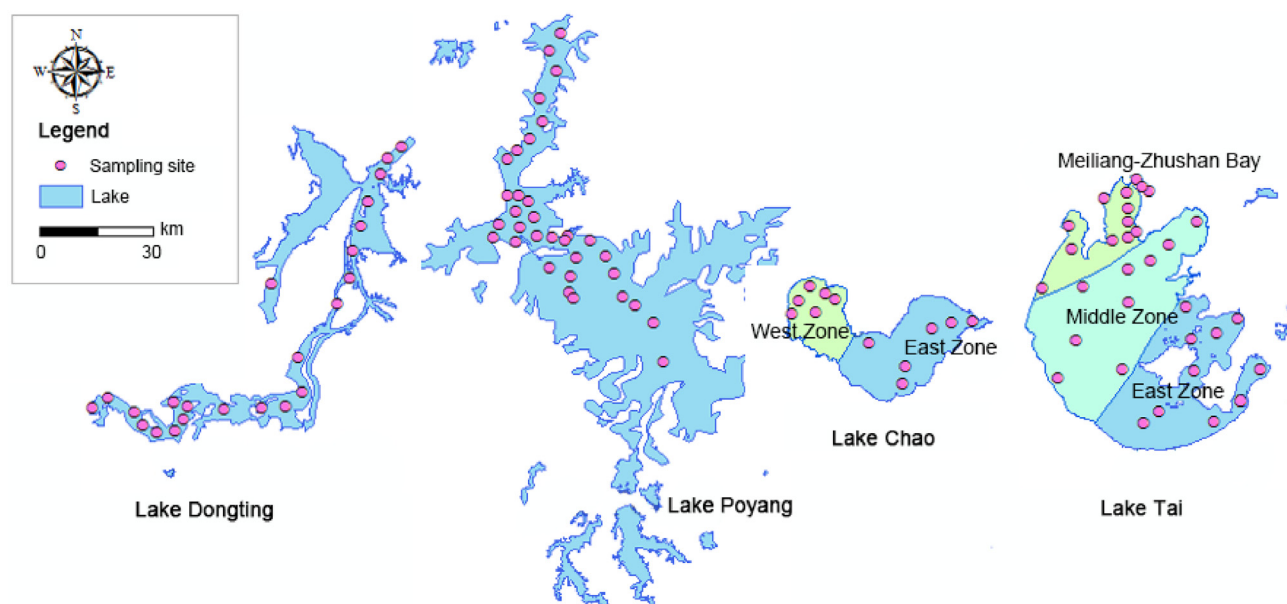


Fig. 1. The map showing the sample sites of the four lakes.

discharges from three tributaries, namely the Fengle River, the Hanbu River and the Nanfei River, accounting for more than half of the total inflow into the lake [22]. The east zone receives no discharges and functions as the lake's outlet, controlled by the Chaohu Dam on the Yuxi River; its water quality is better than that of the lake's west zone. Similarly, Lake Tai was subdivided into three zones labelled Meiliang-Zhushan Bay, the middle zone, and the east zone (Fig. 1). Meiliang-Zhushan Bay, which is located at the north end of the lake, is severely polluted and tends to receive algae from the other two zones during the summer due to the prevalent northeast wind. The middle zone receives direct discharges from several tributaries, accounting for one third of the total inflow into the lake, and has better water quality than Meiliang-Zhushan Bay. The east zone functions as the outlet of the

lake downstream into the Taipu River, and supplies drinking water to the city of Shanghai [23].

2.2. Data

Daily data on Chl-a for the four study lakes were obtained from the Chinese Research Academy of Environmental Sciences (CRAES) for the period from 2000 to 2010. Across each lake are several observational sites: 23 sites across Lake Dongting, 35 sites across Lake Poyang, 12 sites across Lake Chao, and 31 sites across Lake Tai (Fig. 1). Chl-a was extracted with a 90% acetone solution and the concentration was determined using a spectrophotometer-based method [24].

Daily data on water levels was obtained from the Ministry of Environmental Protection of the People's Republic of China

(MEPPRC) for the same record period, 2000 to 2010. This data was collected at the Chenglingji station on Lake Dongting, the Hukou station on Lake Poyang, the Chaohuzha station on Lake Chao, and the Wangting station on Lake Tai. Monthly data on wind speed, precipitation and temperature was obtained from CRAES, also for the same record period. This data was recorded at the Yueyang station on Lake Dongting, the Poyang station on Lake Poyang, the Chaohu station on Lake Chao, and the Wuxiandongshan station on Lake Tai. All data was checked for accuracy by experts in the field following strict scientific procedures; the records were deemed complete and considered to be reliable for the purposes of this study.

2.3. Surrogates for selected factors affecting CyanoHABs

2.3.1. Surrogates for hydrologic factors

Water level fluctuations have an important impact on most tropical lakes and reservoirs, as they have a direct correlation with the size and depth of the lake system [25]. The hypothesis that the lake's productivity is driven by water level is based on the "flood pulse" concept, which suggests that seasonal flooding is a major driver of the biotic productivity of river-floodplain systems [26]. Since the pioneering study by [27] on Lake Bonneville, water level fluctuation in closed-basin lakes has been recognized as a useful indicator of Late Quaternary palaeoclimatic changes in arid and semi-arid regions [28]. demonstrated that the extent to which water level fluctuations influence the stability of lake ecosystems also depends on lake morphology, which is particularly true for shallow lakes or those with shallow margins. Therefore, this study used a "relative lake level fluctuation (RLLF)" index as a surrogate for both hydrologic and morphologic factors. According to [25]; RLLF is defined as:

$$RLLF = \frac{\text{lake level amplitude}}{\text{mean water depth}} \times 100 \quad (1)$$

2.3.2. Surrogates for climatic factors

This study selected four variables, namely wind speed, the ratio of wind speed to mean water depth, precipitation, and air temperature, as suitable surrogates for climatic factors in order to examine the effects of climate on CyanoHABs. Wind speed and the ratio of wind speed to mean water depth are selected as variables due to the properties of shallow lakes. Wind-driven water movement is the dominant force governing the formation of riptides and choppy waves in shallow lakes [29]. A persistent wind direction can concentrate algae and increase downwind Microcystis Chl-a concentrations in the water [30]. In addition, wind can induce shear stresses between different water depths, reducing the thickness of the diffusion boundary layers and thus enhancing the advection-diffusion transport of chemicals across the sediment-water interface [31]. Moreover, the ratio of wind speed to mean water depth can be used as a surrogate to take into account the effect of water depth on the vertical distribution of wind-induced shear stresses.

2.4. Analysis methods

For each of the four study lakes and each of the hydrologic years (September to August) from 2000 to 2010, the daily RLLF values were geometrically averaged to derive two time series: one monthly and one annual. Similarly, the daily Chl-a values were geometrically averaged to derive monthly and annual Chl-a

concentration time series. Daily data on wind speed, precipitation, and air temperature were each arithmetically averaged to derive a monthly time series for each variable. In total, seven time series were derived. The relation between annual Chl-a concentration and RLLF was analyzed for the four lakes. The monthly Chl-a concentration versus the wind speed to water depth ratio and precipitation were analyzed for each lake separately. In addition, the relationship between monthly Chl-a values and air temperature was examined in each lake and in each different zone in Lake Chao and Lake Tai.

2.5. Statistical analysis

At both the annual and monthly scales, scatter and box plots were generated in OriginLab®Origin 8.5 to show how RLLF, wind speed, precipitation, and temperature affect Chl-a concentration. For each of the time series for RLLF, wind speed, precipitation, and temperature (hereinafter referred to as "categorical variables"), the gross average was computed and used to split the corresponding Chl-a time series into two datasets: one for the categorical variables with values less than the gross average and the other for the categorical variables with values greater than the gross average, producing four paired datasets. For each paired dataset, a t-test was conducted to test the null hypothesis that the mean Chl-a concentration was independent of the categorical variable at a significance level of $\alpha = 0.05$.

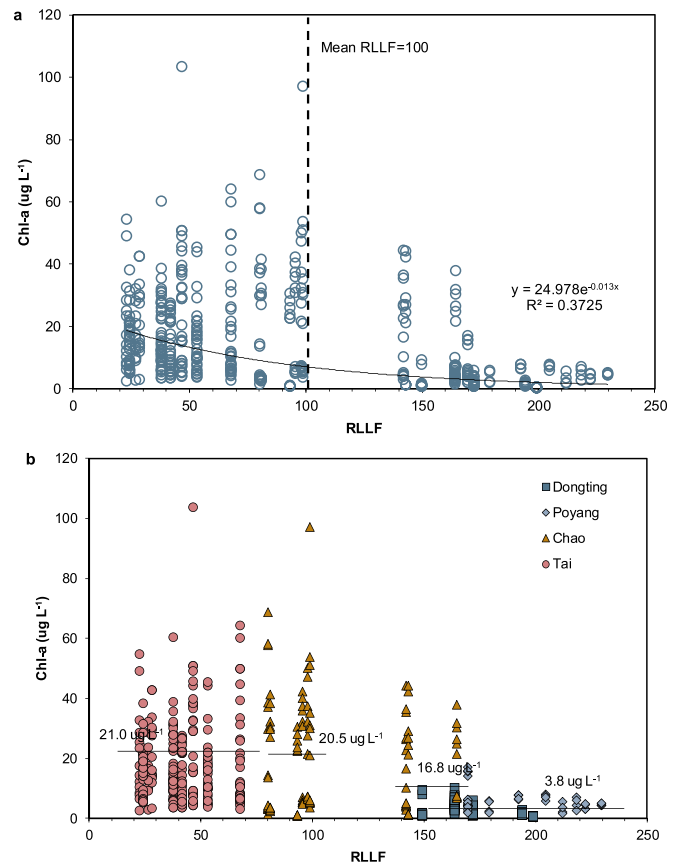


Fig. 2. Plots showing observed annual chlorophyll-a (Chl-a) concentration versus relative lake level fluctuation (RLLF): (a) for the four lakes combined; and (b) for each individual lake.

3. Results and discussion

3.1. Effects of RLLF

For all four lakes, the Chl-a concentration tended to decrease exponentially with increasing RLLF at the annual scale (Fig. 2a). Chl-a concentration in lakes with RLLF less than 100 was significantly higher compared to lakes with RLLF greater than 100 (Fig. 3). The mean Chl-a concentration for the lakes with RLLF less than 100 was $18.73 \mu\text{g L}^{-1}$, while the mean Chl-a concentration for the lakes with RLLF greater than 100 was $5.71 \mu\text{g L}^{-1}$. Across the four lakes, Lake Poyang and Dongting had RLLFs greater than Lake Tai and Chao, and hence also lower Chl-a concentrations (Fig. 2b and Table 1). The Chl-a concentrations in Lake Tai and Chao were almost ten times that in Lake Dongting and three times that in Lake Poyang. Traveling from upstream to downstream along the Yangtze River, the water level of the four lakes decreased from 26.9 m in Lake Dongting to 3.3 m in Lake Tai, but the Chl-a concentration increased from $2.0 \mu\text{g}$ per liter in Lake Dongting to $21 \mu\text{g}$ per liter in Lake Tai (Table 1).

The annual Chl-a concentrations in Lake Dongting and Poyang clearly decreased with RLLF greater than 100, whereas there was no change apparent for either Lake Chao or Tai with RLLF less than 100 (Fig. 2b). The lakes with RLLF greater than 100 have better hydrological connectivity with the Yangtze River than the lakes with RLLF less than 100. The Chl-a concentrations in the Yangtze-connected lakes are better than the isolated lakes due to this natural hydrological connectivity which brings higher water level fluctuations, deeper water depth, and shorter hydraulic retention times. The water level amplitudes for Lake Dongting and Poyang were about 11 and 10 m, respectively, whereas the amplitudes for Lake Chao and Tai were only 3 and 1 m, respectively (Table 1). The retention times for Lake Dongting and Poyang were correspondingly short at just 18 days and 20 days, respectively, whereas the retention times for Lake Chao and Tai were much longer, at about 210 days and 310 days, respectively. Additionally, the mean water depths for Lake Dongting and Poyang were around 6.4 and 5.1 m, respectively, while the maximum water depths for these two lakes were 23.5 and 19.5 m, respectively. In contrast, the mean depths for Lake Chao

and Tai were around 2.7 and 2.1 m, respectively, and their maximum depths 3.8 and 3.3 m, respectively (Table 1).

CyanoHABs are also likely to break out more easily in stagnant water with shallow water depths and smaller fluctuations in the water level, the conditions typically found in Lake Chao and Tai. There is much less chance of CyanoHABs breaking out in swift running water with deeper water depths and greater fluctuations in the water level, as in Lake Dongting and Poyang. In general, Chl-a concentrations seem to decrease with increased instability (increased RLLF). Our results indicate that the Chl-a concentration in a lake with RLLF less than 100 will likely be significantly higher than that in a lake with RLLF greater than 100 (p -value = 0) (Fig. 3). In contrast, the four largest lakes in Africa (Victoria, Malawi, Tanganyika and Kivu) are all hydrologically stable, with RLLF values of less than 100 [25], but the water quality in the African lakes is markedly better than in the four study lakes. Similarly, the RLLF values of the Laurentian Great Lakes (Lakes Superior, Erie, Michigan, Huron and Ontario) in North America are also less than 100, but their water quality is again better than that in the study lakes [32]. This is primarily because the water depths of the African lakes and the Great Lakes are all far greater than those of the study lakes to the point that they are not on the same order of magnitude. The mean depths of the four largest lakes in Africa range from 40 m to 580 m which is 19 times to 90 times the depths of the four Chinese lakes in this study [25]. The mean depths of the Laurentian Great Lakes are 9 times to 23 times the depths of the studied lakes in China based on a depth of 19 m in Lake Erie and 150 m in Lake Superior [33]. Thus, the study shows that the RLLF index is more appropriate for shallow lakes with mean depths less than 10 m.

3.2. Effects of precipitation

For the four lakes as a whole, a negative correlation was found between the Chl-a concentration and precipitation, with the Chl-a concentration decreasing exponentially with increasing precipitation at the monthly scale (Fig. 4a). The Chl-a concentration in lakes with precipitation less than 210 mm was significantly higher than that in lakes with precipitation greater than 210 mm (p -value = 0). The mean Chl-a concentration in the lakes with precipitation less than 210 mm was $15.68 \mu\text{g L}^{-1}$, whereas the mean Chl-a concentration in the lakes with precipitation greater than 210 mm was $8.39 \mu\text{g L}^{-1}$ (Fig. 3). Across the four lakes, Lake Poyang (292 mm) and Dongting (313 mm) received more precipitation than Chao (191 mm) and Tai (94 mm), and thus also had lower Chl-a concentrations (Fig. 4b). The overall pattern seems to be that, along the Yangtze River, the downstream lakes received less precipitation than the upstream lakes. The mean precipitation decreased from the 313 mm received by Lake Dongting to the 94 mm received by Lake Tai, while the Chl-a concentration increased significantly from $3.8 \mu\text{g L}^{-1}$ in Lake Dongting to $21 \mu\text{g L}^{-1}$ in Lake Tai.

These results indicate that Chl-a concentrations exhibit a downward trend with increasing precipitation (Fig. 4b). A similar result has been found in Lake Escondido, where cyanobacteria increased during periods with decreased precipitation [34]. This may be because heavy rainfall processes create surface water turbulence due to large volume inflows and associated strong wind events, which both diminish cyanobacterial bloom intensity and reduce the probability of their occurrence [35]. Our results revealed that the effects of precipitation on Lake Dongting and Poyang were greater than on either of the other two lakes (Fig. 5). The mean precipitation levels for both Lake Dongting and Poyang, located in the middle reaches of the Yangtze River, were about 1.5 and 3 times those of Lake Chao and Tai, respectively, which are located in the lower reaches of the river. Water inputs or outputs and water levels that fluctuate dynamically are affected by precipitation. For

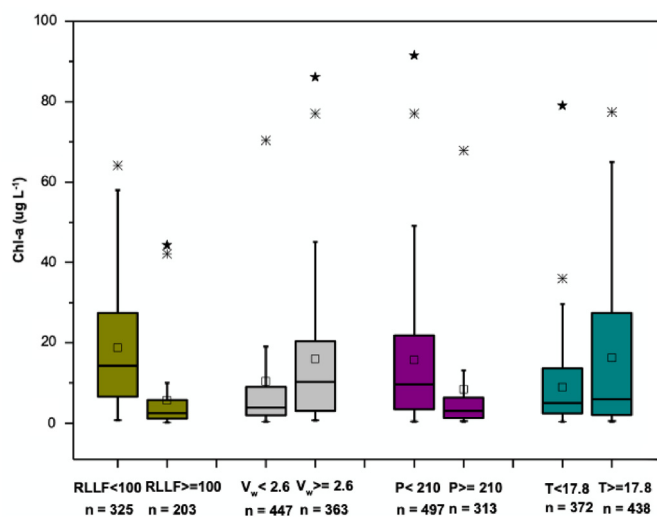


Fig. 3. Boxplot showing chlorophyll-a (Chl-a) concentrations categorized by the means (as subdivides) of relative lake level fluctuation (RLLF), wind speed (V_w), precipitation (P), and air temperature (T) for the four lakes. Pentagram: maximum; dash: minimum; asterisk: upper 99% percentile; open square: mean. For a given categorical variable, the two subsets of Chl-a concentrations are significantly different (p -value = 0).

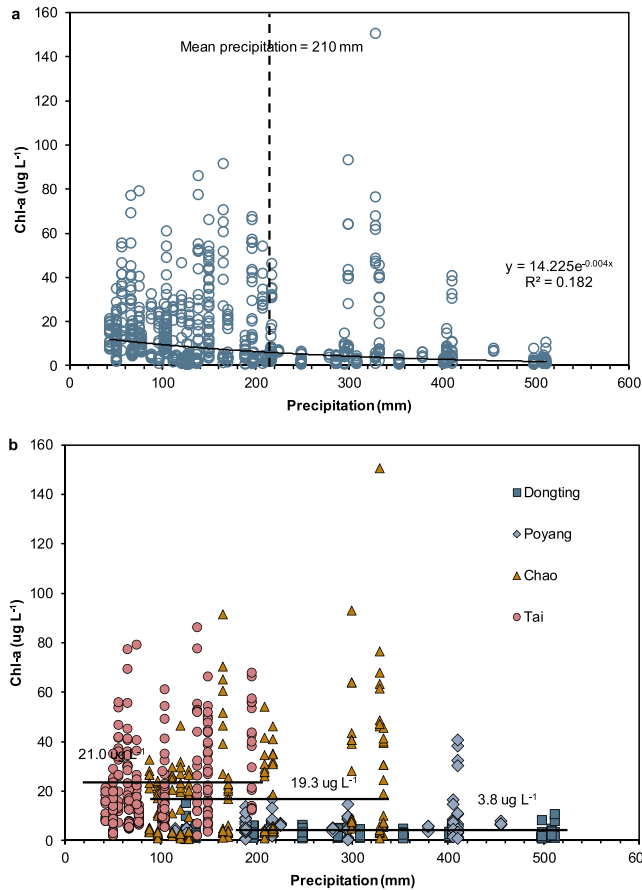


Fig. 4. Plot showing observed monthly Chl-a concentration versus precipitation: (a) for the four lakes combined; and (b) lake by lake.

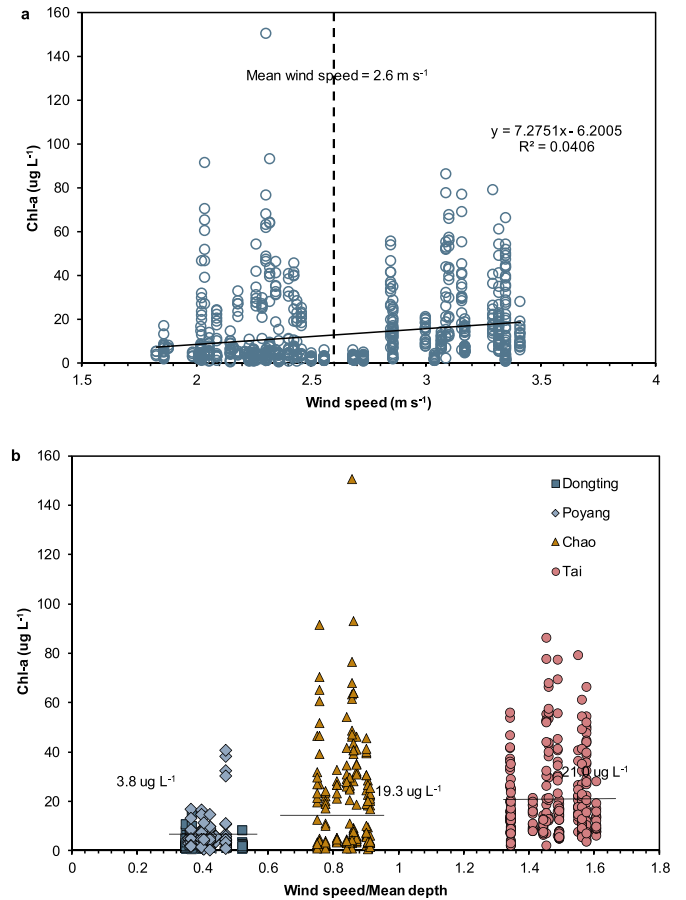


Fig. 6. Plot showing observed monthly Chl-a versus: (a) wind speed for the four lakes combined; and (b) ratio of wind speed to mean water depth.

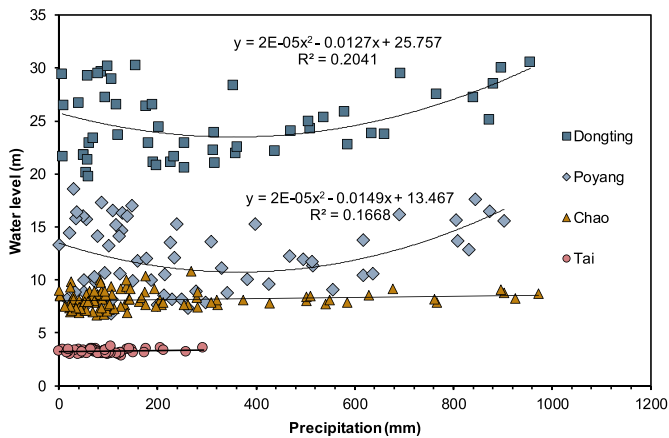


Fig. 5. Plot showing monthly average lake water level versus monthly precipitation for the four study lakes.

example, water levels in Lake Dongting and Poyang increased due to higher precipitation (Fig. 5) and their water level amplitudes also varied greatly between the wet and dry seasons. This was not the case for Lake Chao and Tai, whose natural hydraulic conditions have been disconnected from their local river systems by control gates and/or dams, leading to longer residence times, more stable water levels and better conditions for algal growth. Thus, both hydrological and meteorological conditions are vital to consider for

efforts to control CyanoHABs. The data indicates that the probability of CyanoHABs occurring is lower in lakes with higher precipitation and larger fluctuations in water level amplitude.

3.3. Effect of wind speed and its ratio with mean water depth

For the four lakes as a whole, the monthly Chl-a concentration was found to have a weak positive correlation with wind speed (Fig. 6a). The Chl-a concentrations in the lakes with wind speed less than 2.6 m s^{-1} ($10.4 \mu\text{g L}^{-1}$) were significantly lower than those in the lakes with wind speed greater than 2.6 m s^{-1} ($15.9 \mu\text{g L}^{-1}$) (p-value = 0) (Fig. 3). This result indicates that the Chl-a concentration may increase with wind speed.

Across the four lakes, the ratio of wind speed to mean water depth was found to positively affect the Chl-a concentration at a monthly scale (Fig. 6b). The ratios for Lake Poyang and Lake Dongting were much smaller than those for Lake Tai and Lake Chao, while the mean Chl-a concentrations in Lake Poyang and Dongting were almost one sixth of those for Lake Tai and Chao. Among the four lakes, Lake Tai had the highest mean wind speed of 3.15 m s^{-1} but the shallowest mean water depth at 2.12 m. The effect of wind speed on CyanoHABs in Lake Tai was thus the greatest.

Cyanobacteria can be buoyant, and in combination with wind this can result in an accumulation of cyanobacteria at specific locations during a bloom. Wind may also indirectly influence nutrient availability through mixing processes in the water column [30]. [36] reported that wind speeds of at least $2\text{--}3 \text{ m s}^{-1}$ are sufficient for mixing the upper half-meter of a water column. Harding also

found that wind speeds of greater than approximately 6 m s^{-1} are sufficient for mixing up to 1.9 m deep, the mean depth in Lake Zeekoevlei in South Africa. The mean wind speeds at each of the four Chinese lakes are all less than 4 m s^{-1} , which favors the accumulation of algae in the surface waters of the lakes [9].

Moreover, although the ratio of wind speed to mean water depth consistently had a strong positive correlation with the Chl-a concentrations (Fig. 6b), the concentrations in Lake Chao and Tai were markedly greater than in Lake Dongting and Poyang. One possible reason for this observation is that wind can produce greater shear stress in lakes with shallower water depth than in lakes with deeper water depths, thus enhancing the mass transport of chemicals across the sediment-water interface [31]. The values of the wind speed to mean water depth ratios for Lake Chao and Tai were over 2 times those for Lake Dongting and Poyang, and the corresponding Chl-a concentrations were over 4 times greater. Additionally, Lake Tai and Chao are closer to the Pacific coast, so their wind speeds are higher than those experienced at Lake Dongting and Poyang.

Of the four study lakes, CyanoHABs were the most serious in Lake Tai, largely because its mean wind speed was the highest and water depth the shallowest of all the lakes, as well as being the closest to the Pacific Ocean. Hence, the effect of wind speed on Lake Tai was greater than on any of the other three lakes.

3.4. Effects of air temperature

For all four lakes, the Chl-a concentrations were found to increase linearly with increasing air temperature at the monthly scale (Fig. 7a). The Chl-a concentrations in the lakes with air temperatures less than $17.8 \text{ }^\circ\text{C}$ were significantly lower than those in the lakes with air temperatures greater than $17.8 \text{ }^\circ\text{C}$ ($p\text{-value} = 0$). The mean Chl-a concentration for the lakes with air temperature less than $17.8 \text{ }^\circ\text{C}$ was $8.89 \mu\text{g L}^{-1}$, whereas the mean Chl-a concentration with air temperature greater than $17.8 \text{ }^\circ\text{C}$ was $16.24 \mu\text{g L}^{-1}$ (Fig. 3).

For every lake in the study, the Chl-a concentration tended to increase with increasing air temperature (Fig. 7b). Nevertheless, across the four lakes the Chl-a concentration exhibited a large spatial variability for the same air temperature. For example, the Chl-a concentration in the west zone of Lake Chao was significantly higher than that in the east zone ($p\text{-value} = 0$) and also more sensitive to air temperature (Figs. 7c and 8). Similarly, the Chl-a concentration in Meiliang-Zhushan Bay in Lake Tai was significantly higher than that in either the middle or east zone ($p\text{-value} = 0$). In Lake Tai, the Chl-a concentration in Meiliang-Zhushan Bay was most sensitive to air temperature, followed by the Chl-a concentration in the middle zone and then the east zone (Figs. 7d and 8). Comparatively, the Chl-a concentrations in Lake Poyang and Dongting were much less sensitive to air temperature.

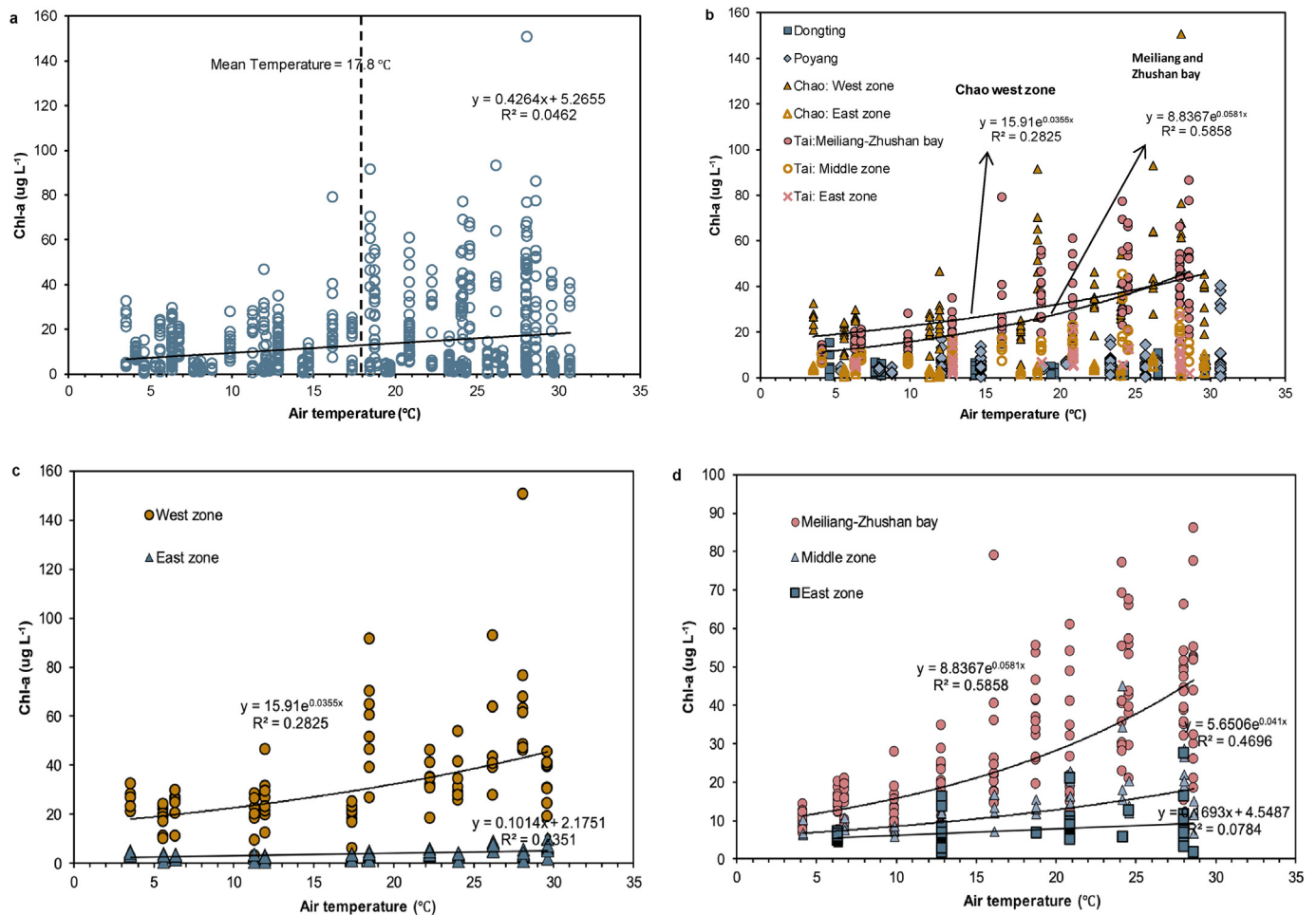


Fig. 7. Plot showing observed monthly Chl-a versus air temperature: (a) for the four lakes combined; (b) lake by lake; (c) in the two zones of Lake Chao; and (d) in the three zones of Lake Tai. The zones are illustrated in Fig. 1.

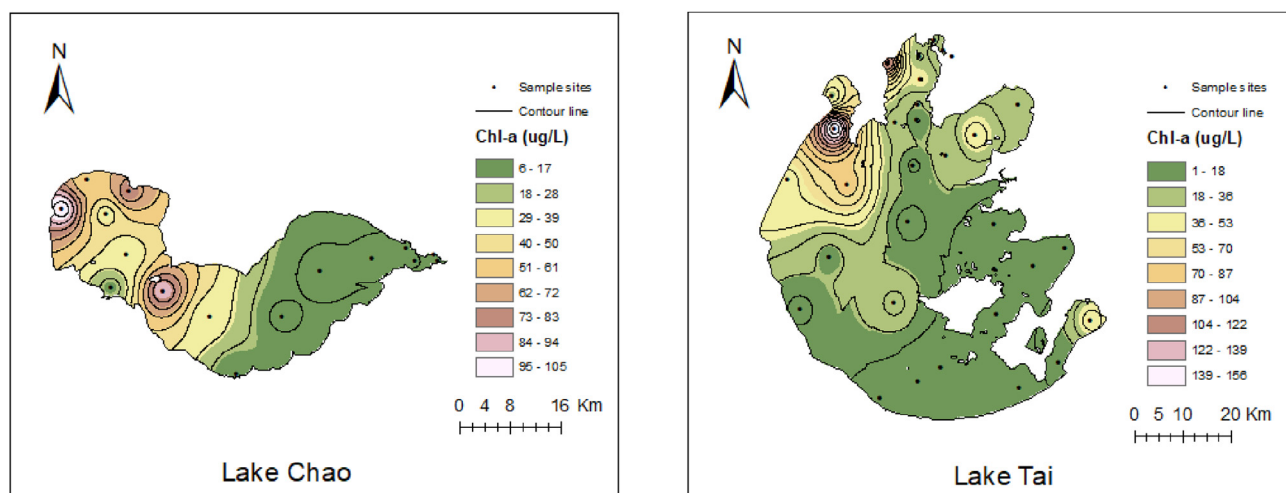


Fig. 8. Spatial distribution of Chl-a concentration in Lake Chao (August, 2012) and Tai (August, 2010).

The Chl-a concentrations in Meiliang-Zhushan Bay in Lake Tai ($28.24 \mu\text{g L}^{-1}$) and the west zone of Lake Chao ($34.62 \mu\text{g L}^{-1}$) were significantly higher than the overall mean Chl-a concentration in the four lakes ($13.73 \mu\text{g L}^{-1}$) (p -value = 0). In contrast, the Chl-a concentrations in Lake Poyang, Lake Dongting, the east zone of Lake Tai, and the east zone of Lake Chao were significantly lower than the overall mean (p -value = 0). Lastly, the Chl-a concentration in the middle zone of Lake Tai was statistically equal to the overall mean Chl-a concentration.

Chl-a concentrations in Meiliang-Zhushan Bay in Lake Tai and the west zone of Lake Chao were significantly higher than those in other areas of Lake Tai and Chao (p -value = 0) (Fig. 8). Similarly, blooms have been observed in Lake Erie's western basin [37], Lake Michigan's Green Bay [38] and Huron's Saginaw Bay [39] more frequently than other areas of the same lakes. This shows that CyanoHABs tend to break out easily and sharply with increasing air temperature, especially in the bays and near shore areas. One possible explanation is that cyanobacteria are easily pushed by summer monsoons into stagnant water areas such as bay areas and coves. It is also possible that large contaminant inflows into sensitive areas of lakes from polluted rivers lead to serious eutrophication via deposition and loading, making the lakes vulnerable to frequent CyanoHABs when temperatures rise. This contrasts markedly with the situation in the middle-east zone of Lake Tai and the east zone of Lake Chao, where there are far fewer CyanoHAB events. This is probably due to the open water conditions and ongoing water diversion projects in these areas. For example, in order to improve the water quality and counteract algal blooms, fresh water has been transferred from the Yangtze through Gonghu Bay and the Wangyu River downstream into Lake Tai from time to time since 2002 [23,40]. Similarly, fresh water began to be transferred from the Yangtze through the Baishitian and Zhao rivers into Lake Chao in 2006 to increase the lake's water recirculation and improve its water quality (An et al., 2009). Interestingly, the water quality in the middle-east zone of Lake Tai and the east zone of Lake Chao is very similar to that in Lake Poyang and Dongting, whereas the water quality in Meiliang-Zhushan Bay in Lake Tai and the west zone of Lake Chao is significantly worse than in Lake Dongting and Poyang (p -value = 0). Hence, it is important to ensure that water quality standards clearly distinguish between zones in the same lake that are polluted at different levels.

4. Conclusions

This study conducted a detailed analysis of the correlation between the Chl-a concentration and the hydrologic and meteorological variables in Yangtze-connected and Yangtze-isolated lakes. The results indicated that Chl-a concentrations were greatly affected by meteorological variables such as precipitation, wind and temperature. In the Yangtze-isolated lakes (Lake Chao and Tai), high Chl-a concentrations were due to more stagnant water, shallow water depths, smaller water level fluctuations, and high internal nutrients. The Chl-a concentrations of Yangtze-connected lakes (Lake Dongting and Poyang), however, were mitigated by meteorological variables and their naturally dynamic hydrologic conditions.

Moreover, relative lake level fluctuation (RLLF) and the ratio of wind speed to mean water depth could be innovative coupling factors, more useful in examining variation in the characteristics of CyanoHABs in shallow lakes than single factors. The RLLF was found to have a negative correlation with the Chl-a concentration, whereas the ratio of wind speed to mean water depth had a positive correlation with the Chl-a concentration. The lakes with RLLF greater than 100 have better hydrological connectivity with rivers than the lakes with RLLF less than 100. Additionally, the Chl-a concentrations in the bays and shore areas of shallow lakes are more susceptible to air temperature than in other areas, providing evidence for the observations that CyanoHABs break out more easily and sharply with increasing air temperature in these areas. At present, cyanobacteria blooms are still an important issue in Chinese lakes with increasing hydraulic constructions, including the four lakes of this study. Future research may need to explore mechanisms of cyanobacteria blooms and detect potential utilization of cyanobacteria for clean fuels and carbon capture.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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