Harmful Algae 110 (2021) 102127

Contents lists available at ScienceDirect

Harmful Algae

journal homepage: www.elsevier.com/locate/hal

Environmental controls of harmful cyanobacterial blooms in Chinese inland waters

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ARTICLE INFO

Edited by

Key words:
Harmful cyanobacterial blooms
China
Inland waters
Nutrients
Climate change
Geography

ABSTRACT

Harmful cyanobacterial blooms (CyanoHABs) are expanding world-wide, adversely affecting aquatic food production, recreational and tourism activities and safe drinking water supplies. China's inland waters have been increasingly threatened by CyanoHABs during the past several decades. The environmental factors controlling CyanoHABs are highly variable in space and time in China due to significant variations in climate, geography, geological and geochemical conditions among its many regions. Here, we synthesize diverse examples among Chinese water bodies regarding interactive effects of anthropogenic, climatic and geographic drivers influencing CyanoHAB potentials and dynamics in lakes and reservoirs; in order to provide a perspective and integrative approach to mitigating CyanoHABs. In China's many shallow water bodies, water quality is highly susceptible to human activity and to changing climatic and hydrological conditions, when compared to deeper lakes. Rapid increases in population, economic activity, and wastewater have accelerated CyanoHABs in China since 1980s, especially in the heavily urbanized, agricultural and industrial regions in the middle and lower Yangtze River basins. Climatic changes have provided an additional catalyst for expansion of CyanoHABs. In particular, rising spring temperatures have accelerated the onset and proliferation of *Microcystis* spp, blooms in the middle and lower reaches of Yangtze River basin. Large hydroelectric and water supply projects, like the Three Gorges Reservoir (TGR), have altered hydrological regimes, and have led to an increase of CyanoHABs in reservoirs and tributaries due to increases in water residence times. Manipulating water level fluctuations in the TGR may prove useful for controlling CyanoHAB in its tributary bays. Overall,CyanoHAB mitigation strategies will have to incorporate both N and P input reductions in these shallow systems. Furthermore, nutrient reduction strategies must consider climate change-induced increases in extreme weather events, including more intense rainfall and protracted heat waves and droughts, which can extend the magnitudes and duration of CyanoHABs. Ensuring the maintenance of natural hydrologic connectivity between lakes and rivers is of utmost importance in mitigating CyanoHABs throughout China.

1. Introduction

Harmful cyanobacterial blooms (CyanoHABs) are intensifying globally in freshwater ecosystems (Huisman et al., 2018; Ho et al., 2019; Paerl et al., 2020 a, b). CyanoHABs adversely affect aquatic food production (fisheries and aquaculture), recreational and tourism activities and safe supplies of drinking and irrigation water (Huisman et al., 2018), due to the production of cyanotoxins, taste and odor compounds, the formation of nuisance surface scums, and dissolved oxygen depletion (Rabalais, et al. 2010; Merel et al., 2013). As a result, CyanoHABs have led to economic losses throughout developed and developing regions of the world (Bullerjahn et al., 2016; Kudela et al., 2015; Wagner and Adrian, 2009; Carey et al., 2012; Visser et al., 2016) and China is no exception (Stone, 2011; Qin et al., 2019). It is therefore essential to identify key drivers affecting CyanoHABs in freshwater for safeguarding current and future water quality (Paerl et al., 2019).

In the past several decades, extensive studies have been conducted to better understand mechanisms of CyanoHAB formation and

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https://doi.org/10.1016/j.hal.2021.102127
Received 27 June 2021; Received in revised form 19 October 2021; Accepted 30 October 2021

proliferation in inland waters. It is well established that elevated anthropogenic nutrient loading, together with climatic changes, particularly rising temperatures, increasing severity of storms and droughts, and altered hydrologic regimes will favor more frequent, intensive, and persistent CyanoHABs (Paerl and Huisman 2008, 2009; Huisman et al., 2018; Jöhnk et al., 2008; Merel et al., 2013). Furthermore, the geomorphological and hydrologic characteristics of freshwater ecosystems, including depth, vertical stratification and water residence time (i.e. flushing rates) play critical roles in mediating lake eutrophication and CyanoHAB potentials (Mitrovic et al., 2003; Huang et al., 2014; Paerl 2014; Qin et al., 2020; Zou et al., 2020). To what extent and how exactly CyanoHABs are influenced is water body specific, since local meteorological conditions, water quality, dominant bloom strain properties, and hydrology may synergistically impact the response of CyanoHABs to these factors (Brooks et al., 2016; Rastogi et al., 2015; Visser et al., 2016; Paerl and Otten, 2013). Therefore, understanding drivers and responses of CyanoHABs is a major challenge to ensuring protection and sustainability of affected waters (Havens and Paerl 2015; Paerl et al., 2020 a, b).

China is a vast country characterized by significant variations among regions in climate, geography, geological and geochemical conditions. The chemical characteristics, meteorology, and morphology of the lakes located in different regions vary widely, leading to regional variations in nutrient concentrations and trophic states. China has been severely threatened by freshwater eutrophication, exemplified by increasing CyanoHABs during the past several decades, especially in large lakes like Taihu (Qin et al., 2019), Chaohu (Huang et al., 2018) and Dianchi (Wu et al., 2017); all of which have been listed as a top priority for lake management since the 1990s, in large part due to continuing proliferating of CyanoHABs (Zhang et al., 2014). The causal relationships and mechanisms leading to CyanoHAB events have not been adequately investigated (Harris and Graham, 2017; Scholz et al., 2017), largely because the dynamic responses of phytoplankton to changes in environmental conditions resulting in blooms are highly variable in space and time and we are now increasingly faced with the interactive effects of excessive anthropogenic nutrient loading and climatic changes on CyanoHABs. Here, we synthesize diverse examples in China of individual and interactive effects of human, climatic and geographic drivers influencing CyanoHAB potential and dynamics in lakes and reservoirs, in order to provide a perspective and integrative approach to their management in China.

2. General description of lakes across China

China is endowed with many lakes. There are 2693 lakes with a surface area larger than 1 km^2, covering a total area of 81414.6 km^2 and accounting for 0.9% of China's land area (Ma et al., 2011; Yang and Lu, 2014). Geographic location is an important natural factor affecting the trophic status of lakes. China's landscape is characterized by three very different types of topography, including, the first, second and third topography laddersFig. 1). The first topography ladder is located at the highest elevation (average higher than 4000 m), mainly comprising the Qinghai–Tibetan Plateau and the Qaidam Basin. The second topography ladder ranges from approximately 2000 m to 1000 m, mainly comprising the Inner Mongolia Plateau, Loess Plateau, Yunnan–Guizhou Plateau, Junggar Basin, Tarim Basin, and Sichuan Basin. The third topography ladder is located at the lowest elevation (average lower than 500 m), mainly containing Daxinganling, Xiaoxinganling, Shandong Hills, the southeast hills, northeast plain, North China plain, and the Yangtze River plain. The chemical characteristics, meteorology, and morphology of the lakes located in these three types of topography are linked to regional variations in nutrient concentrations, trophic status, and phytoplankton nutrient utilization efficiency (Ding et al., 2015). Based on topography, dry/wet conditions and administrative provinces, China's lakes were categorized into five geographic lake zones (Ma et al., 2010), i.e., the Tibetan Plateau Lake Zone, the Yunnan-Guizhou

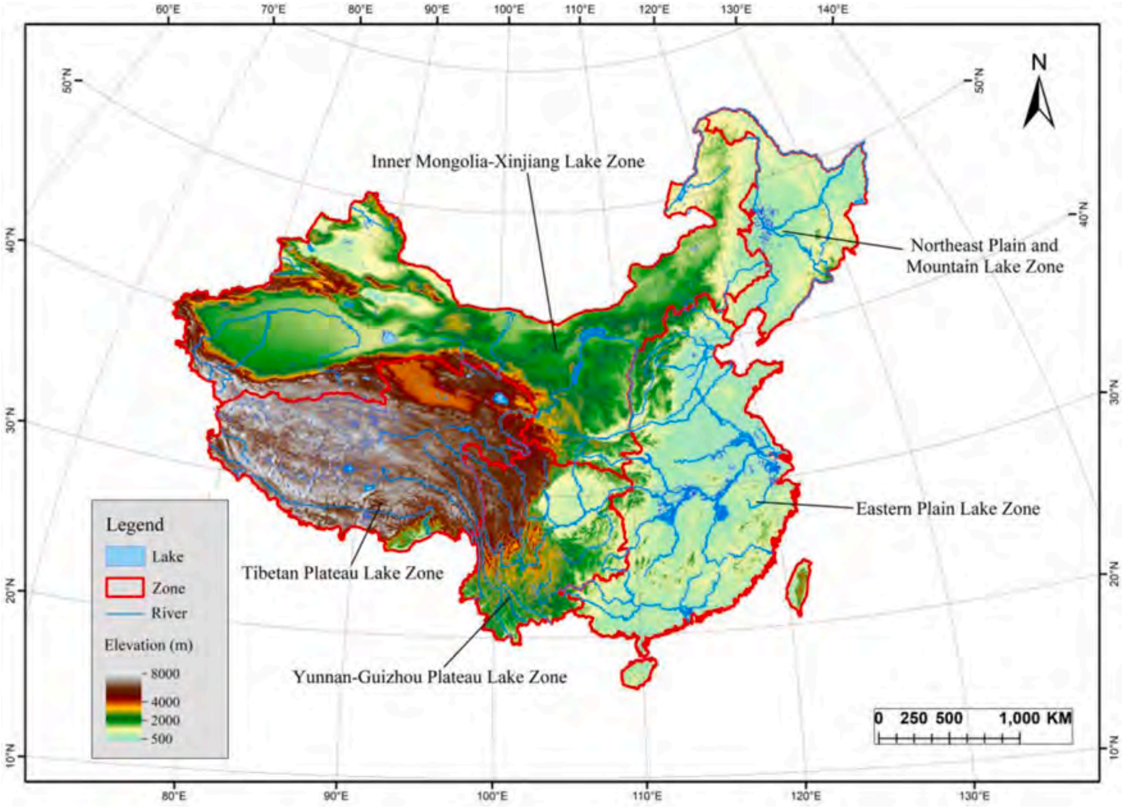

Fig. 1. Topography of China and spatial distribution of Chinese lakes. The first topography ladder is located at the highest elevation average higher than 4000 m, the second topography ladder ranges from approximately 2000 m to 1000 m and the third topography ladder is located at the lowest elevation average lower than 500 m.

Plateau Lake Zone, the Inner Mongolia-Xinjiang Lake Zone, the Northeast Plain and Mountain Lake Zone, and the Eastern Plain Lake Zone (Fig. 1). The Tibetan Plateau Lake Zone is located in the first topography ladder. Yunnan-Guizhou Plateau Lake Zone and the Inner Mongolia-Xinjiang Lake Zone are located in the second topography ladder. The Northeast Plain and Mountain Lake Zone, and the Eastern Plain Lake Zone are located in the third topography ladder.

The Tibetan Plateau Lake Zone has both the highest number of lakes (1055, 39%) and largest total lake area (41832 km^2, 51%). Moreover, the Tibetan Plateau has undergone expansion of existing lakes and formation of new lakes due to accelerating climate changes, such as more intense and higher amount rainfall and reduced pan evaporation and accelerated glacial melting (Zhang et al., 2019; Yang et al., 2014; Zhang et al., 2017; Mao et ., 2018). In contrast, the Eastern Plain Lake Zone and Inner Mongolia-Xinjiang Lake Zone account for a moderate share of water surface area (21053 km^2; 12590 km^2) and a moderate number of lakes (634; 514) (Ma et al., 2010). Lake shrinkage and disappearance have been observed in the arid regions (e.g., Inner Mongolia Plateau and part of the Xinjiang Uygur Autonomous Region) due to an arid climate with increased drought events and diversion irrigation (Zhang et al., 2019; Tao et al., 2015). The overall lake surface areas have decreased dramatically in the Eastern Plain region. Human activities such as water withdrawal and diversions are another cause of significant lake area decreases in this lake region. The Eastern Plain is China's economic and population center, with the middle and lower reaches of the Yangtze River as its core region. Almost all lakes in this region have been influenced by human activities through dam construction, river flow regulation and, in particular, empoldering-the process of converting lakes into croplands and urban lands (Ding et al., 2015). Empoldering was a major driver of lake area decrease in Lakes Dongting, Poyang and Taihu (Hou et al., 2020). The Three Gorges dam construction has also substantially changed lake and reservoir areas in the upstream and downstream regions of Yangtze River (Xie et al., 2017;Liu et al., 2020; Zhang et al., 2020; Zhou et al., 2020; Cai et al., 2016). The Northeast Plain and Mountain Lake Zone and Yunnan-Guizhou Plateau Lake Zone account for a relatively small share of water surface areas (4700 km^2; 1240 km^2) and a low number of lakes (425; 65) (Ma et al., 2010). The decreases in the lake area in the Northeast Plain and the Yun-Gui Plateau have been relatively small.

The Tibetan Plateau Lake Zone and Inner Mongolia-Xinjiang Lake Zone are generally considered parts of internal drainage systems with enclosed lagoons or salt lakes in arid or semiarid climates. The lakes in these two zones are mainly saline, including oligo- to mesohaline Lake Namco in Tibet and Lake Qinghai in Qinghai province, and euhaline lakes, such as Lakes Chaka and Chaerhan in Qinghai province, and Lake Balikun in Xinjiang province. The other three lake-zones are located in the Asian monsoon climate zone. They are strongly influenced by external drainage systems, characterized by abundant rainfall, and are readily-flushed .

There are numerous freshwater lakes in the Eastern Plain Lake Zone, most of them located within the middle and lower Yangtze River basins, accounting for ~ 54% of the freshwater resources in China (Ma et al., 2010; Wang et al., 2014). These lakes primarily originated due to sea-level rise during the last postglacial period when the water level of the Yangtze River increased, causing floods and persistent inundation of low-lying areas along the river banks. Hence, the lakes in the middle and lower Yangtze River basins are mostly shallow, with a water depth of less than 5 m (Yang et al., 2008); they include Lakes Poyang, Dongting, Taihu, and Chaohu, which are the first-, second-, third- and fifth-largest freshwater lakes in China, respectively (Fig. 2).

3. Lake trophic states and harmful cyanobacterial blooms along temporal and spatial scales

China, with its vast landmass and large population, is facing a major challenge with regard to eutrophication due to population growth and rapid economic development over the past 30 years (Fig. 3). Eutrophic lakes increased from 41% of total lakes in early 1980s to 61% in the late 1980s, and further increased to 77% by the late 1990s. Based on a survey of 145 lakes during 2002-2012, middle-eutrophic lakes accounted for 94.3% of total lakes, and oligotrophic lakes in China accounted for 5.7% of total lakes, including lakes Kanasi and Sailimu in Xinjiang Province, Lugu, Pindian and Fuxian in Yuannan Province (Cao et al., 2012). According to the latest Chinese national survey of the 138 lakes having a surface area greater than 10 km^2, 85% of lakes exceed the designation of eutrophic and 40% show advanced eutrophication (hypertrophic), with

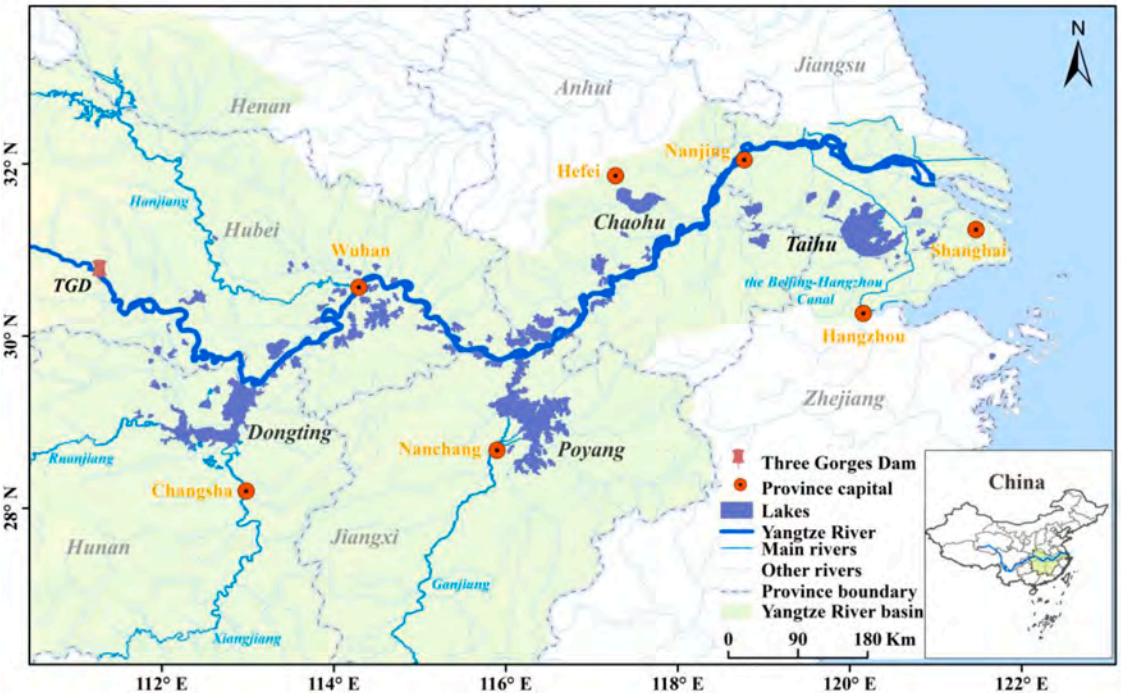

Fig. 2. The spatial distribution of lakes in the middle and lower Yangtze River basins .

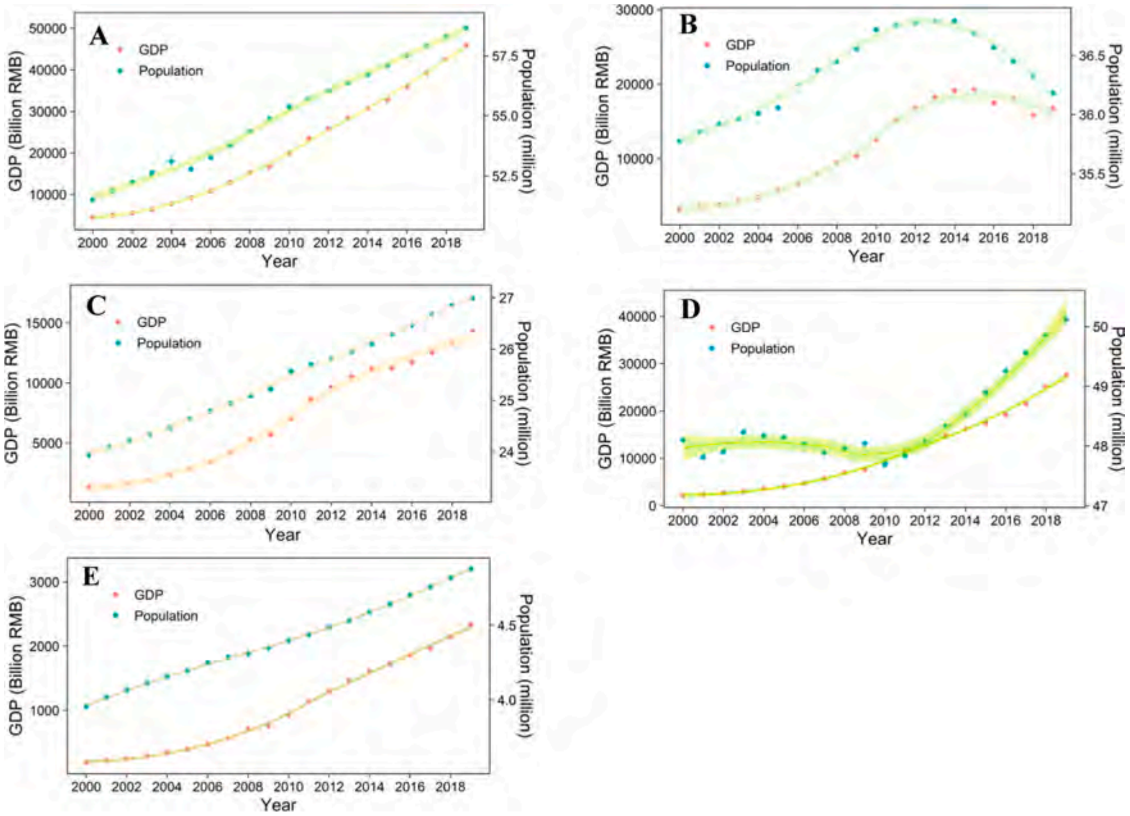

Fig. 3. Development of Gross Domestic Product (GDP) and population in Eastern Plain Lake Zone (A), The Northeast Plain Lake Zone (B), Inner Mongolia-Xinjiang Lake Zone (C), Yunnan-Guizhou Plateau Lake Zone (D) and Tibetan Plateau Lake Zone (E).

the total eutrophication area reaching more than 9000 km^2 (Trolle et al., 2011; Zhang et al., 2012).

Lake trophic status is affected not only by anthropogenic factors but also by natural factors, such as geographic location, lake morphology, and climate (Nõges, 2009; Liu et al., 2010). The oligotrophic lakes in China are mainly distributed at higher elevations (higher than 1000 m) and at far west longitudes (< 105° E); for example, most lakes on the Tibetan Plateau are oligotrophic with high water clarity, such as Lake Namco and Selinco (Li et al., 2016; Liu et al., 2017; Wang et al., 2018), because lakes in this region are fed by watersheds with low human population densities. This region is also mountainous, with a relatively harsh climate, including lengthy freezing periods with little precipitation (Yang et al., 2014; Zhang et al., 2017; Mao et al., 2018). In the Inner Mongolia-Xinjiang Lake Zone, the trophic states of lakes varied over a wide range, from oligotrophic (Lake Kanasi and Lake Sailimu) to highly eutrophic (Lake Bosten and Lake Hulun), indicating that the trophic levels of lakes of the same topography were also distinctly different. The trophic states of lakes on the Yun-Gui Plateau also varied widely, from oligotrophic (such as Lake Lugu and Lake Fuxian) to mesotrophic (Lake Erhai) and hyper- eutrophic (Lake Dianchi and Lake Xingyun) (Ding et al., 2015). Recently, many lakes on Yun-Gui Plateau have suffered from accelerating eutrophication (Zhou et al., 2016). In the Eastern Plain Lake Zone, the lowland topography and moderate climate is suitable for agricultural and industrial activities, which have contributed to the lakes being eutrophic (Ding et al., 2015). CyanoHABs are a troubling indicator of advanced eutrophication (Paerl et al., 2014; 2020), and in the Yangtze River Plain region, eutrophication has become the main environmental concern (Wang et al., 2018). Based on seasonal surveys in 27 large lakes and reservoirs of this region during 2017 to 2018, most of the lakes in the middle and lower reaches of Yangtze River were designated eutrophic, with significant increases in trophic state from 1988 to 1992, as indicated by increases in phytoplankton chlorophyll-a and total phosphorus (Zhu et al., 2019). In this region, Lakes Taihu, Chaohu, Poyang, and Dongting typify accelerating eutrophication in China (Chen et al., 2013; Shi et al., 2015; Wang et al., 2011; Liu et al., 2017b;).

CyanoHABs are occurring across China from north to south, but they are mainly concentrated in the central and coastal regions, especially the middle and lower reaches of the Yangtze River and Yun-Gui Plateau, such as Lakes Taihu, Chaohu, Poyang and Hongze in the middle and lower reaches of Yangtze River and Lakes Dianchi, Erhai and Xingyun in the Yun-Gui Plateau (Fig. 4) (Li et al., 2007; Xu et al., 2015; Zhang et al., 2015; Liu et al., 2016; Ren et al., 2014; Zhou et al., 2016; Tan et al., 2017). The yearly aerial coverage and frequency of cyanobacterial blooms in the middle and lower reaches of Yangtze River have increased since 1990 under the combined pressures of climate change and anthropogenic activities (Zong et al., 2019). The most severe CyanoHABs were found in Lakes Taihu, Dianchi and Chaohu with their contribution to the total CyanoHAB area varying from 62.6%-89.2% (Huang et al., 2019). Accordingly, these lakes have been listed as top three most severe CyanoHAB-impacted lakes in China (Wang et al., 2018). Using Landsat and MODIS satellite-based remote sensing, Duan et al. (2010, 2015) demonstrated that the occurrences of algal blooms in Lake Taihu became increasingly severe from 1987 to 2011, reflected largely by increased frequency, duration, and coverage. The same trend was observed for Lake Chaohu from 2000 to 2013 (Zhang et al., 2015). The history of CyanoHAB expansion in Lake Dianchi dates back to 1980s (Li et al., 2014). *Microcystis* spp.-dominated CyanoHABs can now be observed in the lake from early March and last ~300 days on a yearly basis (Jing, 2019). Lake Erhai is the second largest lake (ད250 km^2) on the Yun-Gui Plateau. The first onset of a *Aphanizomenon flos-aquae* bloom was observed in the southern lake in 1957 (Li et al., 1963). *A. flos-aquae* dominated blooms during1980s-1990s and dominant species shift from *A. flos-aquae* to *Anabaena* sp. in 1996, when the *Dolichospermum* bloom area reached 150 km^2 accounting for half of the lake surface area, while *Microcystis sp* dominated the phytoplankton after

Fig. 4. Cyanobacterial blooms in selected freshwater lakes and reservoirs of China. Photos of Lake Poyang, Lake Hongze, Xiangxi River (a tributary of Three Gorges Reservoir), and Yuqiao Reservoir are courtesy of Hans W. Paerl, Yuwei Chen, Yongjiu Cai, Jianrong Ma and Fan Ke; remaining photos are courtesy of Guangwei Zhu.

1999 (Wang et al., 2017). After 2002, both the bloom extent and the outbreak frequency have increased greatly (Tan et al., 2017). CyanoHABs have also expanded in numerous metropolitan drinking water reservoirs throughout China, such as Yuqiao reservoir in Tianjin (Yue et al., 2020) and Guanting reservoir in Beijing (Dai et al., 2008). CyanoHABs in the tributaries of the Three Gorges Reservoir also increased after impoundment of the Three Gorges Reservoir in 2003, such as the Xiangxi River (Wang et al., 2009) and Pengxi River (Zhang et al., 2020). Diatom blooms were observed more than nine times between 1992 and 2014 in the Han river – a tributary of Yangtze River (Xin et al., 2020).

4. Drivers of CyanoHABs

4.1. *Anthropogenic drivers*

There is broad agreement that anthropogenic nutrient over-enrichment of inland waters from urban, agricultural, and industrial sources has promoted CyanoHAB expansion and persistence globally (Glibert et al., 2010; Paerl and Otten, 2013; Paerl et al., 2020 a, b; Huisman et al., 2018), including China (Qin et al., 2019). The availability and composition of nitrogen (N) and phosphorus (P) compounds in these waters can control the production and composition of phytoplankton communities (Lewis et al., 2011; Paerl et al., 2011; Altman and Paerl, 2012; Wurtsbaugh et al., 2020.) Fertilizer application, agricultural and urban waste and wastewater discharge were identified as main routes by which anthropogenic activities export nutrients to surrounding water bodies (Schindler, 2012; Paerl et al., 2013; Huang et al., 2014). In China, most CyanoHABs prevail in lakes located in economically developed or developing regions. For example, the Yangtze River Plain has rapidly urbanized and become a global hotspot of human-environment interaction, with the population expanding from 160 million in 1953 to 340 million in 2018 (Cui et al., 2013; Xie et al., 2017). Lake Taihu is located in Jiangsu province, one of the most densely populated and rapidly growing regions of China. Rapid urbanization and agricultural expansion in the Taihu basin have lead to increased nutrient inputs from wastewater discharge, industries, and chemical fertilizer use (Qin et al. 2010). The nutrient concentrations and loadings in Lake Taihu have increased dramatically from the 1960s to 1980s. Since the turn of this century (2000), nutrient loads and concentrations have remained at high levels (TP: 0.09 ± 0.02 mg/L; TN: 2.63 ± 0.55 mg/L), and have exceeded cyanobacterial growth requirements in some lake regions (Qin et al., 2010; Xu et al., 2015). The Gross Domestic Product (GDP) is strongly correlated with the aerial extent and frequency of CyanoHAB coverage in lakes and the development of tertiary industries may also be related to the increase in CyanoHABs (Zou et al., 2019). The GDP has doubled in the major Taihu Basin cities Wuxi, Changzhou and Huzhou since 2007 (Qin et al., 2019). It is likely that the nutrient loads and cyanobacterial blooms would have increased even further under such intense development pressure without the initial investment in restoration measures. Similar to Lake Taihu, Lake Chaohu is experiencing accelerating eutrophication due to a rapid increase in population, economic activity, and wastewater generated in its catchment (Zhang et al., 2015a). The total human population living in the catchment increased from 3.1 million in 1950 to 7.4 million in 2013 (Kong et al., 2016). In the same period, the gross value of industrial output increased by approximately 5000-fold (from 31.44 million RMB in 1950 to 165 525 million RMB in 2013) (Zhang et al., 2015a). CyanoHABs have occurred from May to November since the 1980s. However, CyanoHAB coverage, frequency and duration have shown an increasing trend from 2000 to2013 (Zhang et al., 2015b). During this period, the average nutrient concentrations (TN: 2.20 ± 0.42 mg/L; TP: 0.18 ± 0.03mg/L) exceeded cyanobacterial growth requirements (Zhang et al., 2012; Xu et al., 2015). Lake Dianchi is the largest freshwater lake on Yunnan-Guizhou Plateau at an altitude of 1, 887.4 m, and lies southwest of the city of Kunming. Downstream of Kunming, $> 4.0 \times 10^8$ m^3 of advanced treated sewage from point sources flow into Lake Dianchi each year, together with large volumes of surface runoff carrying high concentrations of nutrients (Xu et al., 2016). The history of CyanoHABs in Lake Dianchi dates back to the 1980s (Li et al., 2014). *Microcystis* spp.-dominated CyanoHABs can now be observed in the lake from early March and last ~300 days on a yearly basis (Jiang, 2015). Despite costly and time-consuming efforts aimed at nutrient reduction, aquatic macrophyte restoration, sediment dredging, mechanical CyanoHAB biomass removal, major blooms still occur and persist in these lakes due to legacy nutrients (especially phosphorus) from a >40 year accumulation history of excessive nutrient loading (Qin et al., 2019; Zhang et al., 2012).

4.2. Climate change as an additional catalyst for expansion of Chinese CyanoHABs

Many studies have shown that, in addition to increasing nutrient loads, climate change, including rising global temperatures and changing precipitation patterns, have also affected the temporal-spatial dynamics of algal blooms (Paerl et al., 2012; 2020; Burford et al., 2020; Shi et al., 2019). Warmer temperatures favor surface bloom-forming cyanobacterial genera because they are well adapted to hot conditions and their maximal growth rates occur at relatively high temperatures when compared to eukaryotic algal taxa; often in excess of 25°C (Paerl et al., 2011; Paerl and Paul, 2012). Increasing temperatures also tend to increase vertical density stratification, which contributes to the surface accumulation of buoyant CyanoHAB taxa (Jöhnk et al., 2008; Paerl and Huisman 2008; 2009; O'Neil et al., 2012). Warming can result in either more or less precipitation, each of which can be beneficial to the development of blooms (Paerl et al. 2016 a). Global warming also induces low mean summer wind speeds (Wentz et al., 2007). Reduced wind speed promotes water stability and facilitates the gathering of cyanobacteria at the water surface to form blooms (Cao et al., 2006); a phenomenon observed in shallow, eutrophic lakes, including Taihu (Wu et al., 2015; Deng et al., 2018). Overall, global warming has the potential to change the initiation, magnitude, duration, and distribution of CyanoHABs (Paerl et al., 2016a; Paerl et al., 2020a; Kosten et al., 2012).

Yearly mean temperatures and extremely high temperatures in recent years may be linked with the increase in cyanobacterial blooms in lakes in the middle and lower reaches of Yangtze River (Zong et al., 2019; Zou et al., 2020). For example, Lake Taihu has experienced increasing rates of 0.36°C/decade and 0.37°C/decade for the yearly mean air and water temperatures, respectively during past 20 years (Zhang et al., 2018). Water temperature during May usually rises above 20°C in Lake Taihu, making it suitable for *Microcystis* spp. bloom development and proliferation (Deng et al., 2014). The onset of the *Microcystis* spp. growing season in Lake Taihu has advanced by nearly 20 days with increased temperatures in spring (Zhang et al., 2012; Deng et al., 2014). Lake Taihu is located in a subtropical zone and only rarely freezes over completely in winter, which facilitates cyanobacterial overwintering (Ma et al., 2015). As temperatures rise in spring, cyanobacterial biomass increases steadily, with *Microcystis* spp. becoming the dominant bloom-forming species by late spring-early summer. The relatively high earlier water temperatures in spring in 2017 rapidly increased the density of *Microcystis* spp. in Taihu, causing the largest bloom area since 2007 (Shi et al., 2019). Clearly, Taihu's cyanobacterial blooms are affected by warming as noted by increasing accumulated water temperature in spring (Deng et al., 2014). In addition, the annual mean wind speed at Taihu has shown a significant decreasing trend, with maximum continuous days with wind speed < 3 m/s increasing significantly from 1996 to 2017 (Deng et al., 2018). This enhanced water column stability and vertical stratification has enabled buoyant cyanobacterial genera *Microcystis* spp. and *Dolichospermum* spp. to accumulate at very high surface concentrations (Wu et al., 2015). As a result, decreasing mean wind speeds associated with climate change have favored an increase in buoyant cyanobacterial bloom taxa in Taihu (Deng et al., 2018). The distribution of the phytoplankton biomass has also expanded spatially towards the central lake region, and seasonally towards the autumn and winter due to the synergistic effect of declining wind speeds and increased water temperatures (Zhang et al., 2018). Qin et al. (2010) implied that the magnitude and duration of cyanobacterial blooms in Taihu are mainly controlled by water temperature, wind velocity, wind direction and irradiance, since nutrient loading is currently far exceeding the requirement for cyanobacterial growth. Furthermore, climate change-induced increases in heavier rainfall events followed by extensive summer droughts and heat waves, result in episodic nutrient inputs, which can extend the magnitudes and duration of CyanoHABs in Taihu (Yang et al., 2016) and elsewhere (Paerl et al., 2016a). This is also the case for Lake Chaohu located on the same eastern China plain and sharing a similar climate with Taihu (Zhang et al., 2015b). Lake Dianchi, located on Yunnan-Guizhou Plateau, has distinctly different meteorological conditions, as it lies in a region experiencing a subtropical monsoon climate, differentiating it from the other two plain-located lakes to the east, Taihu and Chaohu. Average water temperatures were 5°C higher in winter and spring in Lake Dianchi than that in Lakes Taihu and Chaohu, and yearly average temperature showed an increase of 0.48°C per decade (Wang et al., 2019), strongly favoring CyanoHAB formation (Liu et al., 2013; Sheng et al., 2012; Zhou et al., 2016). Therefore, the initial onset of bloom in Dianchi occurs earlier and last longer than observed in the lakes of eastern China plain (Wang et al., 2018; Wang et al., 2019).

4.3. Hydrological process influencing CyanoHABs

Hydrological processes affect nutrient loads, water retention time and stratification of lakes and reservoirs, and as such strong impact CyanoHAB dynamics in China. An important feature explaining the success of many bloom-forming cyanobacteria is buoyancy. Buoyancy allows cyanobacteria to remain in the upper illuminated water layer of a stratified lake and increase their total daily light dose, while other negatively buoyant phytoplankton taxa sink out of these layers and may experience light limitation (Ibelings et al., 1991; Zhu et al., 2014). Furthermore it is well-known that decreased stability of the water column and more readily mixed conditions can cause a shift in dominance from cyanobacteria to chlorophytes and diatoms (Visser et al., 1996; 2016).

The lakes located within the middle and lower Yangtze River basins are oxbow riverine types that were hydrologically connected with the Yangtze River and its major tributaries prior to the 1950s (Yang et al., 2002). The maintenance of natural hydrologic connectivity is of great importance to the ecological equilibrium of these lake ecosystems (Liu and Wang, 2010). However, most of the lakes in this area have become reservoirs due to modified (largely reduced) flows and damming, causing environmental and ecological problems, including a proliferation of CyanoHABs (Ding et al., 2019). The water quality of lakes hydraulically-connected with rivers was found to be markedly better than that of the isolated lakes. Hydrologically-connected lakes experience more frequent inflow and thus a shorter retention times. For example, Lake Poyang and Dongting, which are hydraulically connected with the Yangtze River, have average residence times of about 21 days and 20 days respectively, whereas Lake Taihu and Chaohu, which are isolated lakes, have average residence times of more than 220 days and 170 days respectively (Xu et al., 2015; Zhang et al., 2015b). In Taihu, efforts to reduce *Microcystis*-dominated blooms by flushing this large lake with nearby Yangtze River water reduced the overall residence time in the lake to less than 180 days, but have not had a significant impact on reducing bloom intensity or duration (Qin et al., 2010); most likely because, 1) the residence time was not reduced enough to overcome CyanoHAB growth rates, and 2) Yangtze River water is greatly enriched in soluble (as well as total) N and P, leading to increased external loading of N and P to Lake Taihu. A high rate of water flow with short retention times is a key factor preventing the accumulation of cyanobacteria in these eutrophic lakes. As evidence, the mean annual cyanobacterial biomass was significantly lower in the Yangtze-connected lakes (Poyang Lake, 1.01 mg l^{-1}; Dongting Lake, 1.71 mg l^{-1}) than in Taihu Lake at Meiliang Bay (13.54 mg l^{-1}) (Liu et al., 2016), demonstrating that hydrological conditions strongly dominate the accumulation of cyanobacterial blooms in the Yangtze-connected eutrophic lakes of eastern China. Lake Hongze is located in the east route of the South-to-North Water Diversion Project. CyanoHABs in Lake Hongze have not been as serious as those in Lake Taihu or other typical eutrophic lakes such as Lakes Dianchi and Chaohu (Huang et al. 2010). There have been periodic cyanobacterial blooms in Lake Hongze during warm periods in the recent decade (Wang et al., 2010; Ye et al., 2011), and the sites where these cyanobacterial blooms took place are characterized by restricted water exchange (Ren et al., 2014). It is well known that rapid water exchange (or flushing) can suppress large-scale accumulation of cyanobacterial blooms (Ye et al., 2011; Ren et al., 2014).

The development of water conservancy projects has also changed hydrological conditions, and in general has led to an increase of blooms in reservoirs and rivers; largely due to increases in water residence times (Liu et al., 2016). China has undergone a period of water conservancy development in recent decades. During this period, Three Gorges dam, Xiaolangdi, Gezhouba and other major water conservation projects have been completed and put into operation, bringing great social and economic benefits. However, these major projects have had an increasingly significant impact on the large-scale hydrological cycle in China's river basins and regions. Due to the influence of the upstream inflow and the periodic controlled changes of the water levels upstream from the dams, the river/reservoir morphology, flow regimes and flushing rates show periodic seasonal changes (Dai et al., 2015), which have a very significant impact on resident phytoplankton community structure (Li et al., 2016). For example, the completion of the Three Gorges Reservoir (TGR, China) on the Yangtze River in 2006 significantly elevated the water level and formed numerous reservoir bays in the upper tributaries. After the initial filling of the TGR, average flow velocity in the mainstream in front of the dam decreased from $2 m \bullet s^{-1}$ to $0.17 m \bullet s^{-1}$(Ji et al., 2012), and the flow velocity in some tributaries was generally less than 0.05 $m \bullet s^{-1}$ (Li et al., 2007). There is thermal stratification occurring in the tributaries which affected the algal growth and bloom potentials much more profoundly than in the mainstem where the relatively high flow, rapid transport conditions suppress algal bloom formation. Liu et al. (2016) found that after the impoundment of the Three Gorges Reservoir, stratified heterogeneous flows, influenced by the temperature differences of dry tributaries and differences in water density, occurred in the tributaries of the Xiangxi, Daning and the Shennong Rivers. The resultant stagnant, longer residence time conditions of tributary bays of the reservoir led to proliferation of seasonal algal blooms. Spring algal blooms have been observed in Xiangxi Bay since 2008, which is the nearest and largest tributary bay in the upper reach of TGR, 32 km from the Three Gorges Dam (Liu et al., 2012; Yang et al., 2014). The flow velocity of the Yangtze River was 0.2 – 0.3 m/s at the water impounding stage of the TGR. The flow velocity became nearly static in tributaries during the algal bloom period with a flow velocity generally smaller than 0.005 m/s (Li et al., 2018). The dominant phytoplankton species gradually changed from riverine types (dinoflagellate and diatoms) during the initial impoundment period to lacustrine types (cyanobacteria and chlorophytes) (Tian et al., 2014). In 2008, a *Microcystis aeruginosa* bloom in the Gaolan River, which is a tributary of the Xiangxi River, was the most severe of these events (Wang et al., 2009). At present, the seasonal succession of algal blooms in the tributary bays of the TGR is as follows; diatoms and dinoflagellates being dominant in spring, green algae and cyanobacteria dominant in summer, green algae, diatoms and dinoflagellates dominant in autumn, while diatoms and dinoflagellates are dominant in winter (Chuo et al., 2019).

5. Strategies for mitigating cyanoHABs

Despite considerable investment in external nutrient load reductions, CyanoHABs continue to persist in large Lakes Taihu, Chaohu and Dianchi, as well as many other, smaller lakes throughout China (Qin et al. 2019; Tong et al., 2020). This indicates that there is sufficient N and P available to support blooms on an annual basis. In freshwater ecosystems, P availability has traditionally been viewed as a key factor limiting HABs proliferation (Schindler et al., 2008). Accordingly, controlling P inputs has been the primary mitigation target for water quality managers. However, for shallow eutrophic lakes in China, legacy internal N and especially P supplies can satisfy nutrient demands of CyanoHABs (Wang et al., 2019; Liu et al., 2019; Xu et al., 2021). In deep, vertically stratified lakes, residual P is "trapped" as particles settles to and are often buried in bottom sediments (Qin et al., 2020).As temperatures increase, polymictic lakes are undergoing increased frequencies of water column stability that would promote anoxic conditions and P release that counter P burial efforts in deeper lakes (Ficker et al., 2017; Shatwell et al., 2019). The resultant released P can be used by phytoplankton onlyfollowing autumn turnover. However, in shallow well-mixed lakes, frequent hydrodynamic disturbances effectively resuspend P in surficial sediments into the water column, maintaining relatively high total P concentrations and P availability in the water column (Qin et al., 2020). This helps explain why some longstanding efforts to control lake eutrophication have resulted in frustratingly slow or modest effects in shallow productive lakes and why P-only reduction strategies are more effective in deep relatively oligotrophic lakes. Reduction in external N loading in eutrophic lakes will lead to a relatively rapid response of in-lake TN concentrations, because N loss by denitrification reduces internal N loading (Scott et al., 2019). Furthermore, recent work has shown that N_2 fixation does not compensate for N losses in many eutrophic lakes (Scott and McCarthy 2010; Shatwell and Köhler 2019; Yao et al., 2018). Therefore, reducing N inputs, along with P, will yield a more rapid and sustainable reversal of eutrophication and bloom potentials as opposed to reducing P inputs alone in these shallow system (Paerl et al., 2016a, b; Qin et al., 2020). Furthermore, nutrient reductions must also consider climate change-induced increases in extreme weather events, including more tense rainfall and protracted heat waves and droughts, which can extend the magnitudes and duration of CyanoHABs (Yang et al., 2016; Paerl and Huisman 2009; Paerl et al., 2016a). At the same time, the maintenance of natural hydrologic connectivity between lakes and rivers is of great importance for mitigating CyanoHABs and the water level fluctuations operation method of the TGR could effectively control the algal blooms by influencing thermal flushing and stratification. Table 1

Table 1
Lake morphology and hydrology parameters of the component basins of Lake Dianchi and the five largest freshwater lakes in China (from Wang et al., 2018).

Parameters	Poyang	Dongting	Taihu	Hongze	Chaohu	Dianchi
Surface area (km^2)	2933	2625	2440	1597	765	11 (Caohai) 299 (Waihai)
Lake storage (10^{8}m^3)	149.6	167	51.4	30.4	20.7	15.6
Residence time (day)	21	20	180	35	168	1460
Mean water depth (m)	5.1	6.4	2.1	1.9	2.7	2.5 (Caohai) 5.0 (Waihai)
Connectivity	Connected	Connected	Isolated	Connected	Isolated	Isolated

6. Conclusion and perspective

China's inland waters have been increasingly threatened by CyanoHABs during the past several decades. Investigating the dynamics of CyanoHABs and exploring the underlying driving mechanisms are important for water quality management in lakes and reservoirs. We found the synergistic combination of anthropogenic nutrient loading, rising temperatures, reduced wind speeds, enhanced vertical stratification, increased residence time and more extreme hydrological events (increasingly severe floods and droughts) overall will favor cyanobacterial dominance in a wide range of these aquatic ecosystems in China.The environmental factors controlling CyanoHABs are highly variable in space and time in China due to significant variations in climate, geography, geological and geochemical conditions among its many regions. The oligotrophic lakes in China are mainly distributed at higher elevations and at far west longitudes; especially in the Tibetan Plateau due to low human population densities and relatively harsh climate. Rapid increases in population, economic activity, and wastewater have accelerated CyanoHABs in China since 1980s, especially in the heavily urbanized, agricultural and industrial regions in the middle and lower Yangtze River basins. In addition to increasing nutrient loads, climate change, including rising global temperatures and changing precipitation patterns, have also affected the temporal-spatial dynamics of algal blooms. Lake warming, in addition to lowering the threshold for CyanoHAB formation and persistence, will likely result in stronger seasonal pulses of internal loading, creating conditions promoting persistence of CyanoHABs. Large hydroelectric and water supply projects, like the Three Gorges Reservoir (TGR), have altered hydrological regimes, and have led to an increase of CyanoHABs in reservoirs and tributary rivers due to increases in water residence times. To be most effective and expedient, nutrient mitigation strategies will have to incorporate both N and P input reductions. The magnitudes of these reductions will need to be system-specific and will likely need to be adjusted with changing nutrient-bloom thresholds brought about by climate change. Specifically, water quality managers will have to rethink the existing mitigation strategies in the restoration of China's eutrophic lakes and emphasize the potential interactions among lake warming, altered hydrology and external nutrient inputs as well as internal nutrient cycling dynamics.

Declaration of Competing Interest

The authors declare no conflict of interest.

Acknowledgments

This research was supported by the National Natural Science Foundation of China (41830757, 41621002), and US National Science Foundation Dimensions projects 1240851, 1831096 , 1803697, and National Institutes of Health (1P01ES028939-01). We thank Yuwei Chen, Jianrong Ma and Fan Ke for providing photos of cyanobacterial blooms for Lake Poyang, the Xiangxi River and Yuqiao Reservoir.

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