Contents lists available at ScienceDirect

Earth-Science Reviews

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

Evolving geographical gross primary productivity patterns in global lake systems and controlling mechanisms of associated phytoplankton communities since the 1950s

Junjie Jia^{a,b}, Yang Gao^{a,b,*,1}, Boqiang Qin^c, Jennifer A.J. Dungait^d, Yong Liu^e, Yao Lu^{a,b}, Kun Shi^c, Guirui Yu^{a,b,1}

^a Key Laboratory of Ecosystem Network Observation and Modeling, Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, Beijing 100101, PR China

^b University of Chinese Academy of Sciences, Beijing 100049, PR China

c State Key Laboratory of Lake Science and Environment, Nanjing Institute of Geography and Limnology, Chinese Academy of Sciences, Nanjing 210008, PR China

^d Geography, CLES, Amory Building, University of Exeter, Rennes Drive, Exeter EX4 4RJ, UK

^e College of Environmental Sciences and Engineering, Peking University, Beijing 1008714, PR China

ARTICLE INFO

Keywords: Phytoplankton community Gross primary productivity Climate change Global lake systems Carbon cycle

ABSTRACT

In recent decades, anthropogenically-driven climate change has affected phytoplankton growth and has widened the differences observed among the gross primary productivity of waterbodies (WGPP) in global lake systems. Results from this study showed that the range of WGPP increased over time (from 1950 to 2020). However, the median WGPP of global inland lake systems has gradually and significantly decreased. On a geographical scale, the geographical distribution WGPP pattern was high in low- to mid-latitudinal regions and low in high-latitudinal regions. This study found that chrysophytes mainly control WGPP in high-latitudinal regions while diatoms, cyanobacteria, and chlorophytes are dominant in low-latitudinal regions. Additionally, dominant and sub-dominant phytoplankton communities contribute the most to WGPP. Under extreme environmental conditions, algae must strengthen its capacity to adapt to the burgeoning environmental conditions of global lake systems while gradually evolving to survive. Accordingly, regulating environmental conditions to promote phytoplankton community diversity and to accelerate community competition will play an important role in maintaining the ecological balance, environmental health and carbon cycle of global lake systems.

1. Introduction

Gross primary productivity of inland water bodies (WGPP) is the amount of organic carbon (C) fixed by autotrophic organisms including phytoplankton, macrophytes, and periphyton, etc. via photosynthesis per unit time and unit area (Hamdan et al., 2018; Murrell et al., 2018; Kazanjian et al., 2018). WGPP is the result of biological C sequestration processes that together with water and sediment C sequestration constituting C sequestration of inland water (Gao et al., 2021), and is also the basic link between the structure and function of aquatic food webs (Deng et al., 2017). WGPP determines the initial material and energy entering into aquatic ecosystems and constitutes the fundamental process of C sequestration and C cycle in inland water bodies. Additionally, WGPP also integrates C flows in other systems at regional and global scales, thus widely supporting life activities and facilitating biogeochemical cycle (Bogard et al., 2017). Worthwhile, phytoplankton in aquatic ecosystems contribute approximately half (50%) of the Earth's annual net primary production (Siegel et al., 2013). Thus, processes of producing WGPP by phytoplankton play significant roles in both global biogeochemical cycling and C cycling processes (Gao and Yu, 2020; Ma et al., 2017), it is therefore crucial to clarify regulation mechanisms of various phytoplankton on WGPP in global inland water systems.

At present, many observational studies on lake phytoplankton community characteristics have been conducted. Phytoplankton also constitute the primary producer group of lake systems, and different phytoplankton communities, including dominant species, sub-dominant

* Corresponding author at: Key Laboratory of Ecosystem Network Observation and Modeling, Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, Beijing 100101, PR China.

https://doi.org/10.1016/j.earscirev.2022.104221

Received 6 December 2021; Received in revised form 4 September 2022; Accepted 11 October 2022 Available online 15 October 2022 0012-8252/© 2022 Elsevier B.V. All rights reserved.







E-mail address: gaoyang@igsnrr.ac.cn (Y. Gao).

¹ Contribute equally.

species, and non-dominant species, effectuate disparate primary productivity outcomes. Different dominant phytoplankton communities inhabit various lake systems, such as Tahoe Lake (Paytan et al., 2010), Manzala Lake (Deyab et al., 2020), Tai Lake (Zhao et al., 2021), and Vitel Lake (Allende et al., 2009). It is critical to understand the community composition of primary producers and their corresponding production in C cycling and C neutrality research.

The development of anthropogenic activities has led to global warming with an increase in atmospheric carbon dioxide (CO₂) concentration and the discharge of nutrients and heavy metals (IPCC, 2021), so these environmental changes inevitably affect physiological activities and the primary production of phytoplankton in aquatic ecosystems (Winder and Sommer, 2012; Van de Waal and Litchman, 2020). Under global climate change, the CO₂, sunlight, and temperature affect the primary production and metabolism of phytoplankton through regulating C-concentrating mechanisms (CCMs) and material and energy redistribution (Ma and Wang, 2021; Barton et al., 2020). Nitrogen (N), phosphorus (P), silicon (Si), iron (Fe), and other biogenic elements participate in the biogeochemical cycle and influence significantly on the physiological and ecological processes and C production and metabolism of phytoplankton (Browning et al., 2017; Tagliabue et al., 2017; Moore et al., 2013). Water regimes such as water level (Dembowska and Kubiak-Wójcicka, 2017), water retention time (Schagerl et al., 2009), flow rate (Li et al., 2013), and water depth (Qin et al., 2020) indirectly influence phytoplankton community characteristics and primary productivity by regulating nutrients status (Wang et al., 2021). Transparency and turbidity also affect the absorption and scattering of light that penetrates into the water, thus affecting the primary productivity

(Ogbuagu and Ayoade, 2011). Additionally, more frequent and intensive droughts due to low precipitation may also drastically affect WGPP (Thompson et al., 2015; Winder and Sommer, 2012). Therefore, under the background of global change, it is of great significance to discuss the regulation of various environmental factors on the primary productivity for ecosystem C cycle and C sources/sinks.

For this study, our objective was to answer the three following scientific questions: 1) What is the geographical distribution WGPP pattern of global lake systems from 1950 to 2020? 2) Which phytoplankton communities control the WGPP pattern of global lake systems? 3) What factors determine the geographical WGPP pattern dominated by phytoplankton communities? To answer these questions, we collected WGPP and phytoplankton composition data from lake systems throughout the world to clarify geographical WGPP patterns and phytoplanktonic composition in global lake systems. This will enable us to integrate their phytoplanktonic regulation mechanisms and their associated contributions to the C cycling processes of inland aquatic systems, and to further promote our understanding of the C cycling of inland water bodies under the global climate change and anthropogenic activities.

2. Dataset and methods

2.1. Dataset collection and processing

This study collected WGPP data from 180, 270, and 242 global lake systems during 1950–1980, 1980–2000, and 2000–2020 (Fig. 1) (Appendix S1 in Supplementary Materials for details and references). Global



Fig. 1. Distribution of the global inland lake systems investigated during 1950–2020 (1950–1980 [n = 180], 1980–2020 [n = 270], 2000–2020[n = 242]). a. Part of America; b. Part of Europe; c. Part of China; d. The whole world.

lake area data were obtained from the Natural Earth Data website (htt p://www.naturalearthdata.com/), the Resource and Environment Data Cloud Platform, the Chinese Academy of Sciences (http://www.resdc. cn/), and a study by Wang and Dou (1998). WGPP unit conversion was conducted as follows: hour to day conversion was generally achieved by multiplying by daytime sunlight hours (10*h*) (Nurnberg and Shaw, 1998), while unit volume to unit area conversion was generally achieved by multiplying the unit volume by the euphotic (mean) depth (Morin et al., 1999; Patalas, 1980). Geographical WGPP patterns of global lake systems were obtained by means of the inverse distance weighted (IDW) spatial interpolation method (Arcmap 10.7).

In this study, we used SPSS (version 22) to classify and statistically compare datasets on a spatiotemporal scale. Non-parametric tests on the non-normal-distribution of lake area were conducted along longitude and latitude. Non-parametric tests on the non-normal-distribution of WGPP were conducted on hemispheric (i.e., Western Hemisphere and Eastern Hemisphere; Northern Hemisphere and Southern Hemisphere), continental (seven continents, including Oceania), area, and mean depth scales, using the same timescale. Nonparametric tests can be applied to data with non-normal distribution and inconsistent sample size to minimize the impact of inconsistent sample data of different groups on the statistical results. More detailed results can be found in Appendix S2 in Supplementary Materials. We collected phytoplankton biomass (biovolume) or abundance or composition data from 71 global lake systems and calculated the proportion of each taxonomic phytoplankton group to all groups (see Appendix S3 in Supplementary Materials for details and references).

2.2. Relationships among biomass and WGPP represented by dominant phytoplankton communities

In this study, we hypothesized that the proportion of total phytoplankton biomass represented by the dominant phytoplankton community corresponded to the contribution rate of the dominant phytoplankton community to WGPP, and we used Poyang Lake, China as a case study to substantiate this scientific hypothesis. We calculated the WGPP produced by each phytoplankton group and its proportion to the total biomass according to the Eqs. (1)-(17) in Section 2.3 and data described in Appendix S4 in Supplementary Materials. More detailed methods and results referred to Jia et al. (2022). We found that the phytoplankton composition of Poyang Lake was consistent with that of most global lake systems, particularly because the dominant and subdominant algal communities were also diatoms, cvanobacteria, and chlorophytes. Additionally, the proportion of the dominant phytoplankton in Poyang Lake (29.75%-83.91%) was consistent with the proportion of dominant to total phytoplankton in most global lake systems. Moreover, we conducted a non-parametric test and found no significant differences in the proportion of dominant communities between Poyang Lake and the other 70 inland lake systems investigated (p =0.311, Table S14 in Appendix S5 in Supplementary Materials), which can be used to effectively explain phytoplankton composition and dominant community contribution of inland lake systems. We also conducted linear regression analysis on the proportion of total phytoplankton biomass represented by the dominant phytoplankton community and the contribution rate of the dominant phytoplankton community to the WGPP of Poyang Lake, and results showed a strong and significant positive correlation between the two $(R^2 = 0.85)$ (Fig. S2). This indicated that the proportion of total phytoplankton biomass represented by the dominant phytoplankton community could be characterized as the contribution of the dominant community to the WGPP.

2.3. Calculation methods

At present, most methods used for measuring or estimating phytoplankton primary productivity in inland lakes are based on an entire waterbody or an entire water column. For example, oxygen stable isotopes method (Bogard et al., 2017; Song et al., 2018), model estimation (Behrenfeld and Falkowski, 1997a, 1997b), light and dark bottle technique (Gaarder and Gran, 1927), and ¹⁴C method (Nielsen, 1952) are used to measure the overall primary productivity of phytoplankton communities in waterbodies. Although C isotopic techniques (Fernández et al., 2005; Sackett et al., 2016; Thomas et al., 1978) can also measure the primary productivity of individual algae species cultured in the laboratory, we proposed a method to systematically estimate the primary productivity of each individual phytoplankton taxonomic group in inland lakes. Compared with other methods, this model is an efficient method that can make up for the current gap in estimating the productivity of each phytoplanktonic taxonomic group in a natural water, although it needs further development (Jia et al., 2022).

A series of novel equations to estimate total phytoplankton WGPP, net primary productivity of waterbodies (WNPP), and WGPP of phytoplanktonic taxonomic groups at each sampling point in a specific lake are described below. In this study, phytoplanktonic taxonomic groups include diatoms, cyanobacteria, chlorophytes, cryptophytes, chrysophytes, euglenoids, dinoflagellates, and xanthophytes. More detailed methods referred to Jia et al. (2022).

2.3.1. Total phytoplankton WGPP

WGPP is estimated using the Vertically Generalized Production Model (VGPM) (Behrenfeld and Falkowski, 1997a, 1997b). VGPM is described as follows:

$$WGPP_{T} = 0.66125P^{B}_{opt} \bullet \frac{E_{0}}{E_{0} + 4.1} \cdot Z_{eu} \cdot C_{opt} \cdot D_{irr}$$
(1)

where $WGPP_T$ (mg C m⁻² d⁻¹) is the primary productivity of the euphotic zone in waterbodies; C_{opt} (mg m⁻³) is the Chlorophyll *a* (Chl a) content of surface water; E_0 (mol m⁻² d⁻¹) is the photosynthetically available radiation intensity of the water surface; D_{irr} (h) is the duration of sunshine.

 P_{opt}^{B} (mg C mg Chla⁻¹ h⁻¹) is the maximum photosynthesis rate of water, which is a function of temperature, calculated as follows:

$$P^{B}_{opt} = \begin{cases} 1.13 \ T \le -1.0 \\ 4.00 \ T \ge 28.5 \\ P^{B'}_{opt} - 1.0 < T < 28.5 \end{cases}$$
(2)

$$P_{opt}^{B'} = 1.2956 + 2.749 \times 10^{-1}T + 6.17 \times 10^{-2}T^2 - 2.05 \times 10^{-2}T^3 + 2.462 \times 10^{-3}T^4 - 1.348 \times 10^{-4}T^5 + 3.4132 \times 10^{-6}T^6 - 3.27 \times 10^{-8}T^7$$
(3)

where P_{opt}^{B} (mg C mg Chla⁻¹·h⁻¹) is the maximum photosynthesis rate of water; $P_{opt}^{B'}$ is the maximum photosynthesis rate of water, when -1.0 < T < 28.5; T (°C) is the temperature of the water surface.

Z_{eu} (m) is the euphotic depth (Kirk, 2011; Holmes, 1970).

$$Z_{eu} = \frac{4.605}{K_d}$$
(4)

$$K_d = f/SD \tag{5}$$

where K_d is the vertical attenuation coefficient for downward irradiance; *f* is 1.44 (Holmes, 1970); *SD* (m) is water transparency.

2.3.2. WNPP of phytoplanktonic taxonomic groups

In this study, WNPP indicates an increase in organic matter per unit time and area in waterbodies (Kleiber, 1975) and estimated by the growth rate model (Kirchman, 2002; Cloern et al., 2014; Malthus, 1798; Orefice et al., 2019).

$$WNPP_P = \mu WCB_P \tag{6}$$

$$\mu = \frac{\ln(WB_t/WB_0)}{t} = \frac{\ln(WB_t/WB_0)}{(t_1 - t_0 - 1)}$$
(7)

where $WNPP_P$ (mg C m⁻³ d⁻¹) is production of each phytoplanktonic taxonomic group in waterbodies, which represents an increase in biomass over time in the absence of mortality (i.e., the NPP of each phytoplanktonic taxonomic group under the assumption of that no mortality has taken place); μ (d⁻¹) is the growth rate and the production capacity per unit biomass; WB_0 (mg L⁻¹) is the initial biomass of each phytoplankton taxonomic group at time *t* at a certain sampling point in waterbodies; WB_t (mg L⁻¹) is the biomass of each phytoplankton taxonomic group at the next sampling time at the same sampling point in waterbodies; t_0 is the order of the initial sampling time at a certain sampling point in a year; t_1 is the order of the next sampling time at the same sampling point in a year; t (d) is growth time, namely the time interval between two samplings. The phytoplankton sampling time is used to estimate the phytoplankton growth time interval, μ and WNPP. Each phytoplankton taxonomic group at each sampling point during each hydrological period has a corresponding growth rate.

 WCB_P (mg C L⁻¹) is the C biomass of each phytoplanktonic taxonomic group (a sum of all of the species-taxa-based estimates) in waterbodies at sampling times, estimated by Eqs. (8)–(11) (Eppley et al., 1970; Menden-Deuer and Lessard, 2000; Eppley et al., 1970).

$$WCB_P = \sum_{i=1}^{n} WCB_{Pi} = \sum_{i=1}^{n} WA_{Pi} \times WCB_C$$
(8)

Diatoms : $log_{10}WCB_C = 0.76(log_{10}V) - 0.352$ (9)

Dinoflagellates : $log_{10}WCB_C = 0.819(log_{10}V) - 0.119$ (10)

Other phytoplankton :
$$log_{10}WCB_C = 0.94(log_{10}V) - 0.600$$
 (11)

where WCB_{Pi} (pg C L⁻¹) is the C biomass of each phytoplankton species in waterbodies; WA_{Pi} (cells L⁻¹) is the cell abundance of each phytoplankton species in waterbodies; WCB_C (pg C cell⁻¹) is the carbon content of each cell of each phytoplankton species in waterbodies; *n* is phytoplankton species number. *V* (µm³) is the cell volume.

2.3.3. WGPP of phytoplanktonic taxonomic groups

The model relies on a series of assumptions, which include: (1) WGPP = WNPP + WR, there is no diffusion and convection flow of the phytoplankton, as well as no consumption of phytoplankton by other species in waterbodies; (2) $WR_P/WR_T = WB_P/WB_T$, there are no significant differences in respiration between phytoplankton species members per unit biomass due to they are in the same trophic level on a regional scale (May, 1973); (3) The growth rate of each phytoplankton taxanomic group reaches the maximum between two sampling periods according to Malthusian growth model.

$$WNPP_T = \sum_{i=1}^{n} WNPP_P \tag{12}$$

where $WNPP_T$ (mg C m⁻² d⁻¹) is the total NPP at each sampling point in waterbodies, which is estimated by a sum of WNPP of phytoplankton taxonomic groups; $WNPP_P$ (mg C m⁻² d⁻¹) is the NPP of each phytoplankton taxonomic group at each sampling point in waterbodies, estimated using Eqs. (6)–(11), while $WNPP_P$ per unit area is converted by $WNPP_P$ per unit volume multiplied by the eutrophic depth (Z_{eu}); n is phytoplankton taxonomic groups number.

$$WR_T = WGPP_T - WNPP_T \tag{13}$$

where $WGPP_T$ (mg C m⁻² d⁻¹) is the total phytoplankton GPP at each sampling point in waterbodies, estimated by Eqs. (1)–(5); WR_T (mg C m⁻² d⁻¹) is total phytoplankton respiration at each sampling point in waterbodies, calculated by $WGPP_T$ subtracted by $WNPP_T$.

$$WR_P = \frac{WR_T \times WB_P}{WB_T} \tag{14}$$

where WR_P (mg C m⁻² d⁻¹) is the C consumed through phytoplankton respiration for each taxonomic group at each sampling point in waterbodies, is estimated by the ratio of the biomass of each phytoplankton taxonomic group to the total biomass; WB_P (mg L⁻¹) is the phytoplankton biomass of each taxonomic group at each sampling point in waterbodies; WB_T (mg L⁻¹) is the total biomass of phytoplankton, i.e., the sum of WB_P at each sampling point in waterbodies.

WGPP of phytoplankton taxonomic groups is estimated based on the definition, namely NPP is the result of autotrophic respiration sub-tracted from the GPP of autotrophs in waterbodies.

$$WGPP_P = WNPP_P + WR_P \tag{15}$$

where $WGPP_P$ (mg C m⁻² d⁻¹) is the GPP of each phytoplankton taxonomic group at each sampling point in waterbodies. $WNPP_P$ (mg C m⁻² d⁻¹) is the NPP of each phytoplankton taxonomic group at each sampling point in waterbodies.

2.3.4. Contribution rate of phytoplankton community to WGPP

$$Contribution \ rate = \frac{WGPP_P}{WGPP_T} \times 100\%$$
(16)

where *Contribution rate* (%) is the contribution rate of phytoplankton community to WGPP. *WGPP*_P (mg C m⁻² d⁻¹) is the GPP of each phytoplankton taxonomic group in waterbodies. *WGPP*_T is the GPP of total phytoplankton communities in waterbodies.

2.3.5. Proportion of each phytoplankton community in total phytoplankton biomass

$$Proportion = \frac{WB_P}{WB_T} \times 100\%$$
(17)

where *Proportion* (%) is the proportion of total phytoplankton biomass represented by each phytoplankton community; WB_P (mg L⁻¹) is the phytoplankton biomass of each taxonomic group in waterbodies; WB_T (mg L⁻¹) is the total biomass of phytoplankton at each sampling point in waterbodies and the sum of WB_P .

3. Distribution characteristics of global lake systems

Global lake systems investigated exhibited considerable spatial distribution differences. Fig. 2 shows the number and area distribution characteristics of global inland lake systems investigated along longitude and latitude. Results showed that from 1950 to 2020, global lake systems investigated covered the area from 78°S to 82°N and 160°W to 177°E. The collected lake area ranged from 2.0×10^{-3} km² to 8.2×10^{4} km², which can effectively represent the global lake system. According to the number of lakes distributed at different latitudes and longitudes, >60% of global lake systems investigated were primarily distributed in the mid-latitudinal regions of the Northern Hemisphere (30°N–60°N). From 1950 to 1980, the lakes studied were mainly distributed in the areas of 45°W–135°W and 0°E–45°E. After 1980, the lakes studied have focused on the areas of 45°W–90°W, 0°E–45°E, and 90°E–135°E. Additionally, >50% of global lake systems had an area of <10 km². >20% of global lake systems covered an area of 10 km² to 100 km².

During different periods, significant spatial differences occurred in lake area. From 1950 to 1980, the area of lake systems at mid-highlatitudes of the Northern Hemisphere $(30^{\circ}\text{N}-90^{\circ}\text{N})$ was significantly lower than that at low latitudes $(30^{\circ}\text{S}-30^{\circ}\text{N})$. The lake area in the regions of $0^{\circ}\text{E}-45^{\circ}\text{E}$ was significantly higher than that in the Western Hemisphere. From 1980 to 2000, the lake area at low latitudes in the Southern Hemisphere $(0^{\circ}\text{S}-30^{\circ}\text{S})$ was significantly different from that in



Fig. 2. Number and area distribution characteristics of the global inland lake systems investigated along longitude (a) and latitude (b). (The English letters is that significance (p) difference of Mann-Whitney test for the lake area along longitude and latitude.)

the Northern Hemisphere. The lake area in the regions of $90^{\circ}E-135^{\circ}E$ was significantly greater than that in the Western Hemisphere. From 2000 to 2020, in the Northern Hemisphere, the area of lake systems at low latitudes was significantly higher than that at mid-high-latitudes, and the area of lake systems in the regions of $90^{\circ}E-135^{\circ}E$ was significantly higher than other regions.

4. WGPP patterns of global lake systems

Based on WGPP data collected for this study, the WGPP of global lake systems have fluctuated within a range of 0–22 g C m⁻² d⁻¹ from 1950 to 2020 (Fig. 3). Moreover, the WGPP range of global inland lake systems increased over time. This changing WGPP pattern generally occurred from 2000 to 2020 (0–22 g C m⁻² d⁻¹), which was considerably higher than that from 1980 to 2000 and from 1950 to 1980 (0–8 g C m⁻² d⁻¹) (Fig. 4). However, we observed significant temporal differences in the median WGPP of global inland lake systems (0.41 g C m⁻² d⁻¹ from 2000 to 2020, < 0.56 g C m⁻² d⁻¹ from 1980 to 2000, and < 0.71 g C m⁻² d⁻¹ from 1950 to 1980) (Fig. 5a and Table S4). This indicates that the median WGPP of global inland lake systems decreased significantly from 1950 to 2020. At the same time, this decreasing trend was also reflected in the WGPP distribution pattern of lake systems in the Northern Hemisphere (Table S4).

On a geographical scale, the geographical distribution WGPP pattern was high in low- to mid-latitudinal regions and low in high-latitudinal regions. Compared to the Southern Hemisphere, inland lake systems in the Northern Hemisphere were more densely distributed, and WGPP subsequently fluctuated more significantly (Fig. 4); however, the median WGPP between the two equatorial divides did not significantly differ (Fig. 5a and Table S5). The longitudinal distribution of inland lake systems (i.e., the Eastern Hemisphere and the Western Hemisphere) was balanced overall, but their WGPP varied widely. The median WGPP of the Eastern Hemisphere (0.89 g C m⁻² d⁻¹) was only significantly higher from 1950 to 1980 compared to the Western Hemisphere (0.60 g C m⁻² d⁻¹).

On a continental scale, no significant temporal differences were found between the median WGPP of inland lake systems except for Oceania (here regarded as a continent) and North America (Fig. 5b and Table S6). The median WGPP of lake systems in Oceania from 1950 to 1980 was significantly lower compared to the other two periods. The median WGPP of lake systems in all seven continents showed significant spatial differences during all three periods (Fig. 5b and Table S7). The median WGPP of Antarctic lake systems was significantly lower during all three time periods compared to the other six continents. After 1950, significant spatial differences were observed in the median WGPP of African lake systems compared to lake systems in the Northern Hemisphere, except for lake systems in Asia from 1950 to 1980, which were not generally significant. From 1950 to 1980 and from 2000 to 2020, the WGPP of lake systems in North America was significantly higher compared to all other continents except for Asia.

Lake WGPP was divided into five groups according to area $(0-1 \text{ km}^2)$ $1-10 \text{ km}^2$, $10-100 \text{ km}^2$, $100-1000 \text{ km}^2$, and $> 1000 \text{ km}^2$) and four groups according to depth (0–1 m, 1–10 m, 10–100 m, and > 100 m). Pertaining to area and depth characteristics, the WGPP of lake systems generally decreased with an increase in area and depth (Fig. 6). Using the same timescale, this study found significant differences in the median WGPP of lake systems with different areas and depths (Table S8 and S10), but no significant temporal differences were found (see Table S9 and S11). From 1950 to 1980, significant differences were found in the median WGPP of lake systems with depths <1 m and >100 m. From 1950 to 2000, the median WGPP of lake systems with an area $< 1 \text{ km}^2$ differed significantly from lake systems with an area $> 1000 \text{ km}^2$. From 2000 to 2020, the median WGPP of lake systems with an area between 1 and 10 km^2 (0.79 g C m⁻² d⁻¹) was significantly higher compared to lake systems with areas between 0 and 1 km² (0.37 g C m⁻² d⁻¹) and 10–100 km² (0.33 g C m⁻² d⁻¹).

5. Phytoplankton composition in global lake systems

Fig. 7 shows the biomass (or biovolume or abundance) proportion of phytoplankton groups to total phytoplankton of global inland lake systems. These lake systems included those in Asia, Europe, North America, South America, Antarctica, Oceania, and Africa. Results showed that phytoplankton communities in global lake systems mainly included diatoms, dinoflagellates, xanthophytes, chrysophytes, euglenoids, cryptophytes, cyanobacteria, and chlorophytes. Cyanobacteria, diatoms, and chlorophytes were dominant in most lake systems (90.14% of the 71 lake systems) (Fig. 7a). Among these 71 lake systems, 31 (43.66%) were dominated by cyanobacteria, while diatoms were the dominant algae in 20 (28.17%). Chlorophytes were the dominant phytoplankton group in global lake systems (18.31%), but dinoflagellates formed the dominant group in Kinneret Lake (i.e., the Sea of Galilee), Israel. Chrysophytes were the dominant community in only six lake systems near polar regions (Fig. 7b).

Phytoplankton composition consisted of at least four algal taxonomic groups in all seven continents. Similar dominant (cyanobacteria) and sub-dominant (diatoms, chlorophytes and cryptophytes) phytoplankton communities were found in all continents except for Antarctica, where chrysophytes were dominant (Fig. S3). Dominant and sub-dominant phytoplankton communities accounted for 53.00%–98.14% of all phytoplankton communities found in all the lake systems investigated,



Fig. 3. WGPP (g C m⁻² d⁻¹) pattern in global lake systems from 1950 to 2020. a. 1950–1980; b. 1980–2000; c. 2000–2020.

with an average of $76.63\% \pm 12.30\%$ (mean \pm standard deviation). Based on their corresponding relationship, this was also used as the contribution rate of dominant phytoplankton communities to total WGPP of the global lake systems investigated (Fig. S2).

6. Control mechanisms of geographical WGPP patterns in global lake systems

From 1950 to 2020, the trend in the geographical distribution WGPP pattern of global inland lake systems was a decrease from low-latitudinal regions (the equator) to high-latitudinal regions (the poles) (Fig. 3). Chrysophytes were the dominant algae community in high-latitudinal regions, and cyanobacteria, diatoms, and chlorophytes contributed the most to WGPP in low-mid latitudinal regions (Fig. 7). Additionally, the range of WGPP increased over time (Fig. 4). However, the median WGPP of global inland lake systems exhibited a significant decrease from 1950 to 2020 (Table S4). Potential reasons for this phenomenon can vary (Fig. 8). Fundamentally, WGPP that derives from lake system phytoplankton can be defined as the amount of organic carbon produced by phytoplankton utilizing CO₂ and H₂O during photosynthesis (Gao et al., 2021), thus, phytoplankton, sunlight, and CO₂ are the main influencing factors of WGPP.

Sunlight: Being a key determinant of primary productivity, the geographical pattern of sunlight is consistent with the distribution trend of WGPP. Because the earth is a sphere, sunlight illuminates the surface at different angles. While the azimuth of equatorial sunlight is vertical and fully illuminates the surface, sunlight is more oblique near the poles (Fig. 8). Therefore, compared to high-latitudinal regions, the solar elevation angle (i.e., the altitude angle) is broader in low-latitudinal regions, providing greater overall sunshine hours and solar radiation (Cloern et al., 2014), which also results in stronger photosynthetic intensity and subsequently greater WGPP. Additionally, photoinhibition during the phytoplanktonic photosynthesis process also reduces the photosynthetic rate (non-maximum) of phytoplankton under light saturation conditions (Kehoe et al., 2015). Multi-decadal in situ observational records of surface solar radiation has shown a widespread decline between the 1950s and the 1980s ("global dimming") and a partial recovery thereafter ("brightening") (IPCC, 2021). Moreover, this may have caused the supersaturation of sunlight, subsequently limiting phytoplankton-based photosynthesis after 1980, which would have also led to a significant decrease in the median WGPP from 1950 to 2020 (Table S4).

 CO_2 : Being a photosynthetic reactant, CO_2 is bound to have a potential impact on the WGPP of aquatic ecosystems. To overcome the



Fig. 4. WGPP (g C $m^{-2}\ d^{-1})$ of global lake systems along longitude (a) and latitude (b) from 1950 to 2020.



Fig. 6. The WGPP (g C $m^{-2} \ d^{-1})$ of global lake systems by area (a) and by depth (b).



Fig. 5. Changes in WGPP (g C $m^{-2} d^{-1}$) in different spatiotemporal scales. a. WGPP at different regional scales; b. WGPP at different continental scales. (IQR: interquartile range; The English letters labeled on the column is that significance (p) of Mann-Whitney test in different spatial scales on the same temporal scale; The Greek alphabets labeled on the column is that significance (p) of Mann-Whitney test in different temporal scales on the same spatial scale. The numbers were significance (p) of Median test in different temporal scales on the same spatial scale. Table S4-S7 in Supplementary Materials for details.)



Fig. 7. Phytoplankton composition proportion of global lake systems. a. from the west longitude to the east longitude; b. from the north latitude to the south latitude.



Fig. 8. Regulation mechanism of temporal and spatial pattern of WGPP and phytoplankton in global lake systems from 1950 to 2020. (The size of the earth indicates the range of WGPP; the position of the earth indicates the median WGPP; the arrow color indicates of the indexes (temperature, solar radiation, CO₂, nutrient and metal, and precipitation), and the dark color corresponds to the high value; the change trend of the indexes referred to IPCC (2021).)

limitation of low CO₂ concentration in waterbodies, the phytoplankton communities have evolved CCMs to maintain relatively high photosynthesis (Reinfelder, 2011). Pertaining to timescale, under a continuous increase in global atmospheric CO2 (IPCC, 2021) (Fig. 8), phytoplankton will reduce the cost of absorbing HCO₃⁻ energy by downregulating the high-efficiency CCMs for N and P absorption, cellular material redistribution, electron transfer and energy reuse, and phytoplankton growth (Ma and Wang, 2021; Luo et al., 2019). Elevated CO₂ improves algal growth and increases the biomass (Ma and Wang, 2021), which may be one reason for the increasing changes observed in the range of WGPP. However, most inland lake systems are averagely supersaturation (Cole et al., 1994), CO₂ may not have a significant effect on WGPP under a supersaturated state (Vogt et al., 2017). Additionally, metabolic respiration may cause lake systems to act as C sources (Raymond et al., 2013). The trend in the spatial distribution of CO_2 emissions from global lake systems was high in the Western Hemisphere and the Northern Hemisphere and low in the Eastern Hemisphere and Southern Hemisphere (Raymond et al., 2013), which was due to strong respiratory consumption, weak photosynthesis and inherently lower WGPP of the Western Hemisphere and the Northern Hemisphere, which also confirms the geographical distribution of WGPP, namely, it was high in the Eastern Hemisphere and the Southern Hemisphere but low in the Western Hemisphere and the Northern Hemisphere (Fig. 3 and Table S5).

Phytoplankton: Phytoplankton plays a key role in the primary production of photosynthesis. Generally, the dominant phytoplankton community mainly controls WGPP distribution of global lake systems (Fig. S2). In high-latitudinal regions, chrysophytes mainly control WGPP, while in low- and mid-latitudinal regions, diatoms, cyanobacteria, and chlorophytes dominate (Fig. 7). The upper water body with sufficient sunlight and suitable temperature often becomes the main gathering area for phytoplankton (Fernandez-Gonzalez et al., 2020). And phytoplankton rely on their own unique physiological structure to absorb various nutrients from the surrounding environment and

maintain normal physiological metabolic processes (Van de Waal and Litchman, 2020). However, phytoplankton growth is limited by environmental conditions (Biogeochem et al., 2011). Different algal species have different requirements for habitats, and competition for abiotic resources among algal species determines the changes between dominant species and other species (Tilman et al., 1981; Grover, 1990), which also causes differences in phytoplankton community distribution and biomass among different water bodies. In fact, different algal species also have different C sequestration capacities in different water environments. Under large and complex hydrological environment changes, rare phytoplankton communities (opportunists) have high net C sequestration potential, while under stable water environment, dominant communities (gleaners) have great contributions to C sequestration (Jia et al., 2022). Algae growth is determined by a variety of environmental factors, such as underwater light condition (Cloern et al., 2014; Winder and Sommer, 2012), temperature (Celewicz and Gołdyn, 2021; Weisse et al., 2016), nutrient (Anderson et al., 2020; Kumar et al., 2018), heavy metal (Jia et al., 2020a; Pinedo-González et al., 2015), salinity (Diego et al., 2015; Jia et al., 2021), pH (Beklioglu and Moss, 2010; Chakraborty et al., 2011; Unrein et al., 2009), turbidity (Cloern, 1987; Guenther and Bozelli, 2004), etc. Here, we describe the living habits and growth of phytoplankton under different sunlight, temperature, nutrients and metals levels, as well as precipitation and hydrological factors.

Light limitation: Incident solar irradiance, turbidity, and mixed layer depth together determine underwater light conditions and hence influence the phytoplankton growth rate (Cloern et al., 2014). Phytoplankton production within lake systems in high latitudinal regions is restricted by a short growth season. This is because solar irradiance cannot breach ice that covers the water surface in winter (Cloern et al., 2014), which leads to lower phytoplankton biomass and WGPP in these regions. Different algae also prefer different light environments. For instance, flagellates use several survival strategies, such as mixotrophy as a nutritional strategy (Waibel et al., 2019), reducing their metabolic rates, producing resting spores, or using stored energy reserves to

survive under darkened conditions (Celewicz and Goldyn, 2021; McMinn and Martin, 2013; Walter et al., 2017). Cyanobacteria can also survive under a large range of light intensities, while chlorophytes and diatoms prefer an environment with sufficient light (Wu et al., 2013). Thus, this may also constitute the geographical pattern of dominant phytoplankton communities in global lake systems. Additionally, the distribution of dominant algal species is also associated with the hydrological mobility of a lake system. Cyanobacteria are more likely to grow in static water (Park et al., 2012), while diatoms prefer flowing water (Zhang and Prepas, 1996). Variation in the mixed layer depth also affects the growth of phytoplankton by influencing light intensity (Cloern et al., 2014). Generally, sunlight cannot easily penetrate deeper water layers of lake systems; thus, phytoplankton growth is limited by light (Matsumoto et al., 2014). Fig. 6b also confirms this point, namely, that global lake system WGPP decreases with an increase in the mean depth of lakes.

Temperature: Low-latitudinal regions are characterized by strong sunlight and high temperatures. These climate characteristics are more likely to lead to the rapid growth and propagation of phytoplankton in lake systems within these regions. Algal communities respond differently to temperature. Cyanobacteria blooms will consistently occur in waterbodies under high temperatures (from 24 to 26 °C) (Kehoe et al., 2015; Park et al., 2012). Relatively higher temperatures are also suitable for the growth of chlorophytes (15–25 $^{\circ}$ C) and diatoms (< 15 $^{\circ}$ C) (Cho et al., 2007). Low temperatures are more suitable for the growth of different flagellate groups (chrysophytes and dinoflagellates) (Celewicz and Goldyn, 2021). Therefore, temperature is also a key factor affecting phytoplankton diversity and biomass. In recent decades, temperatures have gradually increased under global warming (IPCC, 2021). An increase in temperature may strengthen nutrient absorption, increase protein abundance, and promote growth and primary production by down-regulating CCMs and reducing the energy and material costs of phytoplankton metabolism (Winder and Sommer, 2012, Van de Waal and Litchman, 2020). However, respiration is always more dependent on temperature compared to photosynthesis, and rising temperature will also accelerate the respiratory consumption of organic carbon and change the ratio of primary production to respiration (Barton et al., 2020); thus, the median WGPP decreases significantly from 1950 to 2020.

Nutrients and metals: The supply of nutrients and metals from anthropogenic activities is another key factor that must be considered. Dam construction, industrial and agricultural activities, and changes in hydrological circulation will lead to differences in the ambient conditions of global lake systems, especially in developed and developing countries in low- and mid-latitudinal regions (Liu et al., 2015; Maavara et al., 2020a; Maavara et al., 2020b). For instance, the damming of the Yangtze River in China resulted in the backflow of water into Poyang Lake, subsequently causing nutrients to accumulate in the lake (Maavara et al., 2020b). Although the impact of the resultant nutrients and pollutants from this backflow on phytoplankton growth has not been clarified; it stands to reason that this must affect both dominant species and WGPP regulation (Jia et al., 2020a; Jia et al., 2020b). Nutrient inputs are also often an important factor in promoting the rapid propagation of algae. Cyanobacteria preferentially favors high P and low N/P conditions (Grossman et al., 1970; Jones and Brett, 2014; Park et al., 2012; Zhang and Prepas, 1996). Relatively low nutrients primarily drive diatom growth (Costa and Anil, 2010; Li et al., 2018). However, high heavy metal concentrations can poison algae through toxification and inactivating the enzyme system, severely affecting photosynthesis and WGPP (Jia et al., 2020a). Since 1950, anthropogenic activities have gradually increased (IPCC, 2021), the resultant increase in nutrients and heavy metals derived from anthropogenic inputs has also led to a gradual increase in WGPP variability (Figs. 3 and 4).

Precipitation and hydrological factors: Since the late 1970s, the frequency of extreme precipitation and severe drought has increased (IPCC, 2021), which leads to the evolution of hydrological cycles in

aquatic ecosystems in a more extreme direction. In such changing systems, phytoplankton also responds to climate change, for example, within regions that are wet or getting wetter, increasing rainfall is likely to increase WGPP, whereas in dry or drying ecosystems, algal abundances decrease (Thompson et al., 2015). This may also be another reason why the range of WGPP gradually increased from 1950 to 2020. The changing dry-wet cycles caused by extreme rainfall have the potential to increase C and N losses as well as P availability of nutrient runoff from terrestrial sources, thus affecting the availability of nutrients by phytoplankton in water bodies (Winder and Sommer, 2012; Reverey et al., 2016). Nutrient pulse by precipitation also promotes the generation of phytoplankton primary productivity (Meng et al., 2015). Simultaneously, increases in wind speed accompanied by heavy rainfall typically deepen the mixed layer, which can reduce light availability but increase nutrients mixing (Kim et al., 2014). Additionally, rainfall causes changes in hydrological factors, such as water level, water retention time, flow rate, and water depth (Germer et al., 2011). These factors affect nutrients status in aquatic ecosystems (Qin et al., 2020), thereby affecting the uptake and utilization of nutrients by phytoplankton, and thus leading to variability in phytoplankton biomass, species composition, and WGPP (Wang et al., 2021; Jia et al., 2022).

At global scales, sunlight is the dominant factor determining the geographical pattern of WGPP, and the temporal trend of WGPP is driven by temperature and CO₂ concentrations. At basin scales, the main factors controlling the spatiotemporal distribution pattern of WGPP in different lakes are differentiated. For example, in Poyang Lake in China, a floodplain lake with strong hydrological mobility, has a greater impact on WGPP by water level (Jia et al., 2022). In relative static water systems (e.g., Taihu Lake in China), P and temperature mainly control phytoplankton biomass (Huang et al., 2019). In plateau lake systems, solar radiation, salinity, and nutrient contents under altitude gradients are the main drivers of lake primary productivity (Jia et al., 2021). At urban scales, N, P, and Si dynamics caused by anthropogenic disturbance drive the seasonal periodicity of phytoplankton species (Silva, 2005), and ion concentrations, especially sodium and magnesium, have more significant effects on phytoplankton community structure (Lu et al., 2017). In practical terms, climate change driven by anthropogenic activities (IPCC, 2021) controls the geographical distribution pattern and longterm trend of WGPP in global lake systems. It is therefore critical to determine which factors will play a more significant role in WGPP variability into the future, which researchers and stakeholders will have to resolve.

7. Implications

7.1. Implications for global water environment management

Primary productivity provides an energy source for biological activities, is the basis of the biological food chain, and the starting point of ecosystem energy flow (Gao et al., 2021). Multiple ecological ramifications are also accomplished by increasing WGPP through biological carbon sequestration. On the one hand, increasing WGPP can improve ecosystem efficiency, promote water fertility and the ability to support biological resources, which is more conducive to fisheries, aquaculture and human development (Jia et al., 2022; Gao et al., 2021). On the other hand, the emergence of higher WGPP may also be accompanied by many negative ecological impacts, such as algal blooms, eutrophication, decreased species diversity, water quality deterioration, serious water environment pollution, and threats to drinking water safety (Feng et al., 2021; Ho et al., 2019). Therefore, even though understanding WGPP controls is critical in maximizing primary productivity, it is equally important to quantify its trophic fate while maintaining the ecological balance and environmental health.

In recent decades, anthropogenic-driven climate change has affected phytoplankton growth and expanded the scope of WGPP. High WGPP is particularly prevalent in inland water systems worldwide (Tonetta et al.,

2015). On a global scale, anthropogenic-derived nutrients cause excessive enrichment of aquatic and terrestrial ecosystems (Dokulil, 2014), which leads to proliferation of phytoplankton, elevated primary productivity, and an increase in the distribution and frequency of hypoxia, many waterbodies are gradually erupting water blooms and becoming eutrophic (Feng et al., 2021; Ho et al., 2019). Moreover, the increased frequency of extreme environmental conditions caused by climate change may be more detrimental to algae development in global lake systems. Under extreme environmental conditions, algae will have to strengthen its capacity to adapt to the burgeoning environmental conditions of global lake systems while gradually evolving to survive. Generally, algae blooms are caused by a single dominant algal species during its aggressive, explosive growth stages (Kumar et al., 2018). During such stages, the measures taken by governments or managerial departments typically involve the removal of algae to control algae blooms but such practices do not consider broad ecological goals, namely, encouraging the flow of WGPP into water systems. In fact, the control of environmental conditions is critical in preventing and controlling algal blooms. Therefore, effective measures cannot only maximize WGPP but must also effectively prevent algae bloom occurrences, a strategy that should urgently be applied to water-based environment management policies. The critical question is how to regulate environmental conditions to allow for the survival of a variety of algae species without promoting algal bloom occurrences, which is expected to be the main difficulty and focus of future research.

At present, a more natural and mutual beneficial strategy to combat algae blooms would be to reduce the density of dominant species and also promote phytoplankton community diversity as well as inhibit single species outbreaks. Therefore, for different lake systems, promoting phytoplankton community diversity and accelerating community competition by regulating controllable and primary environmental factors will play an important role in maintaining the ecological balance and environmental health of global lake systems. In a eutrophic lake in mid-latitudinal regions, the community competition and succession of phytoplankton is controlled by regulating Fe elements and underwater light conditions (Yuan et al., 2021). The proliferation of phytoplankton is more restricted by nutrients in waters less affected by anthropogenic activities, however, phytoplankton abundance in surface waters increases with an increase in anthropogenic activity intensity, especially in concentrated agricultural areas, which requires priority prevention and control (Zhao et al., 2019). And water level fluctuations can be used to regulate the community structure of phytoplankton and WGPP in a subtropical floodplain lake system (Wang et al., 2021). In Antarctic nutrient-poor small lakes, changing the light energy availability of phytoplankton is also an important measure to control WGPP (Tanabe et al., 2019). Therefore, for different types of lakes, we had better adjust environmental factors according to local conditions to prevent and control algal blooms and maximize WGPP. In conclusion, an in-depth understanding of the geographical pattern and long-term changes in global WGPP and its corresponding regulatory mechanism provides a significant scientific basis for responding to climate change and predicting phytoplankton community succession direction and the development trend of global WGPP in the future.

7.2. Implications for accurate quantification of lake primary productivity

Differences in understanding of lake C sequestration processes have led to a variety of quantitative methods for lake primary productivity. It is common to measure the primary productivity of autotrophs in aquatic ecosystems by using the equilibrium metabolism of oxygen, such as the diurnal dissolved oxygen kinetic model (Song et al., 2018), Odum's open water method (Murrell et al., 2018), the dark and light bottle technique (Gaarder and Gran, 1927), etc. Murrell et al. (2018) used Odum's open water method to study the seasonal dynamics of primary production in the estuarine water column based on dissolved oxygen time series. Bogard et al. (2017) used the ¹⁸O stable isotope method to analyze lake

primary productivity and sediment metabolism process. The ¹⁴C isotope method has also been used to measure carbohydrate production in surface waters (Nielsen, 1952). And constructing a water temperatureproductivity model by remote sensing techniques is also a common method to characterize the primary productivity of surface water bodies (Whitehead et al., 2010). However, the research objects of different methods are slightly different. Although most studies measure the phytoplankton GPP of surface water bodies for a lake, there are also studies that measure phytoplankton and aquatic plants (emergent macrophytes, floating plants, submerged plants) to characterize the primary productivity of the entire lake (Kazanjian et al., 2018). Here, we only consider phytoplankton GPP as the WGPP of global lake systems. Based on the total global lake area of 2.74×10^6 km² (Raymond et al., 2013) and the median WGPP in this study, we found that the gross C sequestration potential of global lake systems has reached 0.41 Pg C yr⁻¹ in the past 20 years. However, if the estimation of the primary productivity of aquatic plants is also incorporated into the assessment of the lake C sequestration process, the C sequestration potential of global lake systems should be overestimated. Therefore, how to determine the key process of lake C sequestration and accurately quantify the rate and potential of lake C sequestration are also key issues to be solved urgently in the future.

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.

Data availability

Data will be made available on request.

Acknowledgments

The authors of this study would like to thank all anonymous reviewers for their helpful remarks. We thank Brian Doonan (McGill University, Canada), Hans W. Paerl (The University of North Carolina at Chapel Hill) and Ping Xie (Institute of Hydrobiology, Chinese Academy of Sciences) for his help in writing this paper and provide useful suggestions. This study was financially supported by the National Natural Science Foundation of China (No. 42225103, 41871080 and 31988102).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.earscirev.2022.104221.

References

- Allende, L., Tell, G., Zagarese, H., Torremorell, A., Perez, G., Bustingorry, J., Escaray, R., Izaguirre, I., 2009. Phytoplankton and primary production in clear-vegetated, inorganic-turbid, and algal-turbid shallow lakes from the pampa plain (Argentina). Hydrobiologia 624 (1), 45–60.
- Anderson, N.J., Heathcote, A.J., Engstrom, D.R., Globocarb data contributors, 2020. Anthropogenic alteration of nutrient supply increases the global freshwater carbon sink. Sci. Adv. 6 (16), 1–8.
- Barton, S., Jenkins, J., Buckling, A., Schaum, C.E., Smirnoff, N., Raven, J.A., Yvon-Durocher, G., 2020. Evolutionary temperature compensation of carbon fixation in marine phytoplankton. Ecol. Lett. 23 (4), 722–733.
- Behrenfeld, M.J., Falkowski, P.G., 1997a. A consumer's guide to phytoplankton primary production models. Limnol. Oceanogr. 42, 1479–1491.
- Behrenfeld, M.J., Falkowski, P.G., 1997b. Photosynthetic rates derived from satellitebased chlorophyll concentration. Limnol. Oceanogr. 42, 1–20.
- Beklioglu, M., Moss, B., 2010. The impact of pH on interactions among phytoplankton algae, zooplankton and perch (Perca fluviatilis) in a shallow, fertile lake. Freshw. Biol. 33 (3), 497–509.
- Bogard, M.J., Vachon, D., St.-Gelais, N.F., del Giorgio, P.A., 2017. Using oxygen stable isotopes to quantify ecosystem metabolism in northern lakes. Biogeochemistry 133 (3), 347–364.

Browning, T.J., Achterberg, E.P., Rapp, I., Engel, A., Bertrand, E.M., Tagliabue, A., Moore, C.M., 2017. Nutrient co-limitation at the boundary of an oceanic gyre. Nature 551 (7679), 242–246.

Celewicz, S., Gołdyn, B., 2021. Phytoplankton communities in temporary ponds under different climate scenarios. Sci. Rep. 11 (1), 17969.

- Chakraborty, P., Acharyya, T., Babu, P.R., Bandyopadhyay, D., 2011. Impact of salinity and pH on phytoplankton communities in a tropical freshwater system: an investigation with pigment analysis by HPLC. J. Environ. Monitor. 13 (3), 614–620.
- Cho, S.H., Ji, S.C., Song, Y.C., 2007. Optimum temperature and salinity conditions for growth of green algae Chlorella ellipsoidea and Nannochloris oculata. Fish. Sci. 73, 1050–1056.
- Cloern, J.E., 1987. Turbidity as a control on phytoplankton biomass and productivity in estuaries. Cont. Shelf Res. 7 (11–12), 1367–1381.
- Cloern, J.E., Foster, S.Q., Kleckner, A.E., 2014. Phytoplankton primary production in the world's estuarine-coastal ecosystems. Biogeosciences 11 (9), 2477–2501.
- Cole, J.J., Caraco, N.F., Kling, G.W., Kratz, T.K., 1994. Carbon dioxide supersaturation in the surface waters of lakes. Science 265, 1568–1570.
- Costa, P.M.D., Anil, A.C., 2010. Diatom community dynamics in a tropical, monsooninfluenced environment: west coast of India. Cont. Shelf Res. 30 (12), 1337.
- Dembowska, E.A., Kubiak-Wójcicka, K., 2017. Influence of water level fluctuations on phytoplankton communities in an oxbow lake. Fundam. Appl. Limnol. 190 (3), 221–233.
- Deng, Y.B., Zhang, Y.L., Li, D.P., Shi, K., Zhang, Y.B., 2017. Temporal and spatial dynamics of phytoplankton primary production in Lake Taihu derived from MODIS data. Remote Sens.Basel 9 (3), 195.
- Deyab, M., Abu Ahmed, S., Ward, F., 2020. Seasonal patterns in phytoplankton growth, composition, and predominance in relation to water quality at Northwest El-Manzala Lake Egypt. Water Supply 20 (8), 3341–3357.
- Diego, F., Yamila, B., Gisela, M., Patricia, M., 2015. Controlling factors in planktonic communities over a salinity gradient in high-altitude lakes. Ann. Limnol. - Int. J. Lim. 51, 261–272.
- Dokulil, M.T., 2014. Photoautotrophic Productivity in Eutrophic Ecosystems. Springer, Dordrecht.
- Biogeochem, R.B., Anselmo, T.P., Barbosa, A.B., Sommer, U., Galvão, H.M., 2011. Light as a driver of phytoplankton growth and production in the freshwater tidal zone of a turbid estuary. Estuar. Coast. Shelf S. 91 (4), 526–535.
- Eppley, R.W., Reid, F.M.H., Strickland, J.D.H., 1970. The ecology of the plankton off La Jolla, California, in the period April through September 1967. Bull. Scripps Inst. Oceanogr. 17, 33–42.
- Fernandez-Gonzalez, C., Perez-Lorenzo, M., Pratt, N., Moore, C.M., Bibby, T.S., Maranon, E., 2020. Effects of temperature and nutrient supply on resource allocation, photosynthetic strategy, and metabolic rates of Synechococcus sp. J. Phycol. 56 (3), 818–829.
- Fernández, I.C., Raimbault, P., Garcia, N., Rimmelin, P., 2005. An estimation of annual new production and carbon fluxes in the northeast Atlantic Ocean during 2001. J. Geophys. Res. 110, C07S13.
- Feng, L., Dai, Y., Hou, X., Xu, Y., Liu, J., Zheng, C., 2021. Concerns about phytoplankton bloom trends in global lakes. Nature 590 (7846), E35–E47.
- Gaarder, T., Gran, H.H., 1927. Investigations of the production of plankton in the Oslo Fjord. J. Cons. Permanent Int. Explor. Mer 42, 1–48.

Gao, Y., Jia, J.J., Lu, Y., Yang, T.T., Lyu, S.D., Shi, K., Zhou, F., Yu, G.R., 2021. Determining dominating control mechanisms of inland water carbon cycling processes and associated gross primary productivity on regional and global scales. Earth-Sci. Rev. 213, 103497.

- Gao, Y., Yu, G.R., 2020. Regional coupled C-N-H2O cycle processes and associated driving mechanisms. Sci. China Earth Sci. 63, 1227–1236.
- Germer, S., Kaiser, K., Bens, O., Hüttl, R.F., 2011. Water balance changes and responses of ecosystems and society in the Berlin-Brandenburg Region–a review. Erde 142, 65–95.
- Grossman, A.R., Schaefer, M.R., Chiang, G.G., Collier, J.L., 1970. The Responses of Cyanobacteria to Environmental Conditions: Light and Nutrients. Springer, Dordrecht.
- Grover, J.P., 1990. Resource competition in a variable environment: phytoplankton growing according to Monod's model. Am. Nat. 136 (6), 771–789.
- Guenther, M., Bozelli, R., 2004. Effects of inorganic turbidity on the phytoplankton of an amazonian Lake impacted by bauxite tailings. Hydrobiologia 511 (1), 151–159.
- Hamdan, M., Byström, P., Hotchkiss, E.R., Al-Haidarey, M.J., Ask, J., Karlsson, J., 2018. Carbon dioxide stimulates lake primary production. Sci. Rep. 8, 10878.
- Ho, J.C., Michalak, A.M., Pahlevan, N., 2019. Widespread global increase in intense lake phytoplankton blooms since the 1980s. Nature 574 (7780), 667–670.
- Holmes, R.W., 1970. The secchi disk in turbid coastal water. Limnol. Oceanogr. 15 (5), 688–694.
- Huang, C.C., Zhang, Y.L., Huang, T., Yang, H., Li, Y.M., Zhang, Z.G., He, M.Y., Hu, Z.J., Song, T., Zhu, A.X., 2019. Long-term variation of phytoplankton biomass and physiology in Taihu lake as observed via MODIS satellite. Water Res. 153, 187–199.
- IPCC, 2021. Summary for policymakers. In: Masson-Delmotte, V., Zhai, P., Pirani, A., Connors, S.L., Péan, C., Berger, S., Caud, N., Chen, Y., Goldfarb, L., Gomis, M.I., Huang, M., Leitzell, K., Lonnoy, E., Matthews, J.B.R., Maycock, T.K., Waterfield, T., Yelekçi, O., Yu, R., Zhou, B. (Eds.), Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the
- Intergovernmental Panel on Climate Change, Cambridge University Press. In Press. Jia, J.J., Gao, Y., Lu, Y., Shi, K., Li, Z.X., Wang, S.Y., 2020a. Trace metal effects on gross primary productivity and its associative environmental risk assessment in a subtropical lakeChina. Environ. Pollut. 259, 113848.

- Jia, J.J., Gao, Y., Zhou, F., Shi, K., Johnes, P.J., Dungait, J.A.J., Ma, M.Z., Lu, Y., 2020b. Identifying the main drivers of change of phytoplankton community structure and gross primary productivity in a river-lake system. J. Hydrol. 583, 124633.
- Jia, J.J., Wang, Y.F., Lu, Y., Sun, K., Lyu, S.D., Gao, Y., 2021. Driving mechanisms of gross primary productivity geographical patterns for Qinghai-Tibet Plateau lake systems. Sci. Total Environ. 791, 148286.
- Jia, J.J., Gao, Y., Sun, K., Lu, Y., Wang, J., Shi, K., 2022. Phytoplankton community composition, carbon sequestration, and associated regulatory mechanisms in a floodplain lake system. Environ. Pollut. 306, 119411.
- Jones, J., Brett, M.T., 2014. Lake Nutrients, Eutrophication, and Climate Change. Springer, Netherlands.
- Kazanjian, G., Flury, S., Attermeyer, K., Kalettka, T., Kleeberg, A., Premke, K., Köhler, J., Hilt, S., 2018. Primary production in nutrient-rich kettle holes and consequences for nutrient and carbon cycling. Hydrobiologia 806, 77–93.
- Kehoe, M., O'Brien, K.R., Grinham, A., Burford, M.A., 2015. Primary production of lake phytoplankton, dominated by the cyanobacterium Cylindrospermopsis raciborskii, in response to irradiance and temperature. Inland Waters 5 (2), 93–100.
- Kim, T.W., Najjar, R.G., Lee, K., 2014. Influence of precipitation events on phytoplankton biomass in coastal waters of the eastern United States. Glob. Biogeochem. Cy. 28 (1), 1–13.
- Kirchman, D.L., 2002. Calculating microbial growth rates from data on production and standing stocks. Mar. Ecol. Prog. Ser. 233, 303–306.
- Kirk, J.T.O., 2011. Light and Photosynthesis in Aquatic Ecosystems, 3rd. Cambridge University Press, New York.
- Kleiber, M., 1975. Metabolic turnover rate: a physiological meaning of the metabolic rate per unit body weight. J. Theor. Biol. 53, 199–204.
- Kumar, P.S., Kumaraswami, M., Rao, G.D., Ezhilarasan, P., Sivasankar, R., Rao, V.R., Ramu, K., 2018. Influence of nutrient fluxes on phytoplankton community and harmful algal blooms along the coastal waters of southeastern Arabian Sea. Cont. Shelf Res. 161, 20–28.
- Li, F., Zhang, H., Zhu, Y., Xiao, Y., Chen, L., 2013. Effect of flow velocity on phytoplankton biomass and composition in a freshwater lake. Sci. Total Environ. 447, 64–71.
- Li, R., Chen, G.J., Kang, W.G., Chen, L., Zhang, T., 2018. Spatio-temporal variations of diatom community and their relationship with water environment in Fuxian lake. J. Environ. Sci. 39 (7), 3168–3178 (in Chinese).
- Liu, X., Qian, K., Chen, Y., 2015. Effects of water level fluctuations on phytoplankton in a Changjiang River floodplain Lake (Poyang Lake): implications for dam operations. J. Great Lakes Res. 41 (3), 770–779.
- Lu, L., Wu, Y.X., Zhang, W.H., 2017. Distribution and succession pattern of phytoplankton communities in a small urban lake, sand lake in Wuhan cityChina. Acta Ecol. Sin. 37 (18), 5993–6004 (in Chinese).
- Luo, Y.W., Shi, D., Kranz, S.A., Hopkinson, B.M., Hong, H., Shen, R., Zhang, F., 2019. Reduced nitrogenase efficiency dominates response of the globally important nitrogenfixer Trichodesmium to ocean acidification. Nat. Commun. 10, 1521.
- Ma, S., Tao, Z., Yang, X.F., Yu, Y., Member, I., Zhou, X., Ma, W.T., Li, Z.W., 2017. Estimation of marine primary productivity from satellite-derived phytoplankton absorption data. IEEE J-STARS 7 (7), 3084–3092.
- Ma, J., Wang, P., 2021. Effects of rising atmospheric CO2 levels on physiological response of cyanobacteria and cyanobacterial bloom development: a review. Sci. Total Environ. 754, 141889.
- Maavara, T., Akbarzadeh, Z., Van Cappellen, P., 2020a. Global dam-driven changes to riverine N:P: Si ratios delivered to the coastal ocean. Geophys. Res. Lett. 47, e2020GL088288.
- Maavara, T., Chen, Q.W., Van Meter, K., Brown, L.E., Zhang, J.Y., Ni, J.R., Zarfl, C., 2020b. River dam impacts on biogeochemical cycling. Nat. Rev. Earth Environ. 1, 103–116.

Malthus, T.R., 1798. An Essay on the Principle of Population As It Affects the Future Improvement of Society, with Remarks on the Speculations of Mr. Goodwin, M. Condorcet and Other Writers, 1 ed. J. Johnson in St Paul's Church-yard, London.

- Matsumoto, K., Honda, M.C., Sasaoka, K., Wakita, M., Kawakami, H., Watanabe, S., 2014. Seasonal variability of primary production and phytoplankton biomass in the western Pacific subarctic gyre: Control by light availability within the mixed layer. J. Geophys. Res.Oceans 119 (9), 6523–6534.
- May, R.M., 1973. Mass and energy flow in closed ecosystems: a comment. J. Theor. Biol. 39, 155–163.
- McMinn, A., Martin, A., 2013. Dark survival in a warming world. Proc. R. Soc. B Biol. Sci. 280, 20122909.
- Menden-Deuer, S., Lessard, E.J., 2000. Carbon to volume relationships for dinoflagellates, diatoms, and other protist plankton. Limnol. Oceanogr. 45 (3), 569–579.
- Meng, P.J., Lee, H.J., Tew, K.S., Chen, C.C., 2015. Effect of a rainfall pulse on phytoplankton bloom succession in a hyper-eutrophic subtropical lagoon. Mar. Freshw. Res. 66 (1), 60–69.
- Moore, C.M., Mills, M.M., Arrigo, K.R., Berman-Frank, I., Bopp, L., Boyd, P.W., Galbraith, E.D., Geider, R.J., Guieu, C., Jaccard, S.L., Jickells, T.D., Roche, L.L., Lenton, T.M., Mahowald, N.M., Marañón, E., Marinov, I., Moore, J.K., Nakatsuka, T., Oschlies, A., Saito, M.A., Thingstad, T.F., Tsuda, A., Ulloa, O., 2013. Processes and patterns of oceanic nutrient limitation. Nat. Geosci. 6 (9), 701–710.
- Morin, A., Lamoureux, W., Busnarda, J., 1999. Empirical models predicting primary productivity from Chlorophyll a and water temperature for stream periphyton and lake and ocean phytoplankton. J. N. Am. Benthol. Soc. 18 (3), 299–307.
- Murrell, M.C., Caffrey, J.M., Marcovich, D.T., Beck, M.W., Jarvis, B.M., Hagy III, J.D., 2018. Seasonal oxygen dynamics in a warm temperate estuary: effects of hydrologic variability on measurements of primary production, respiration, and net metabolism. Estuar. Coast. 41, 690–707.

- Nielsen, S., 1952. The use of radio-active carbon (C14) for measuring organic production in the sea. Fuel Energy Abstr. 37 (5), 332.
- Nurnberg, G.K., Shaw, M., 1998. Productivity of clear and humic lakes: nutrients, phytoplankton, bacteria. Hydrobiologia 382, 97-112.
- Ogbuagu, D.H., Ayoade, A.A., 2011. Estimation of primary production along gradients of the middle course of Imo River in Etche, Nigeria. Int. J. Biosci. 1 (4), 68-73.
- Orefice, I., Musella, M., Smerilli, A., Sansone, C., Chandrasekaran, R., Corato, F Brunet, C., 2019. Role of nutrient concentrations and water movement on diatom's productivity in culture. Sci. Rep. 9 (1), 1-10.
- Park, K.H., Kim, B.S., Yun, H.J., Ryu, K.Y., Jin, Y.I., 2012. Characteristics of water quality at main streams and lake doam in Daegwallyeong area. Kor. J. Soil Sci. Fertil. 45 (6), 882-889
- Patalas, K., 1980. Comment on "A relation between lake morphometry and primary productivity and its use in interpreting whole-lake eutrophication experiments" (E. J. Fee). Limnol. Oceanogr. 25 (6), 1147–1149.
- Paytan, A., Mackey, K.R., Jiang, Y., Liston, A., Schladow, S.G., 2010. Impact of atmospheric deposition on algal growth in Lake Tahoe, CA. In: merican Geophysical Union Fall Meeting.
- Pinedo-González, P., Joshua West, A., Tovar-Sánchez, A., Duarte, C.M., Marañón, E., Cermeño, P., González, N., Sobrino, C., Huete-Ortega, M., Fernández, A., López-Sandoval, D.C., Vidal, M., Blasco, D., Estrada, M., Sañudo-Wilhelmy, S.A., 2015. Surface distribution of dissolved trace metals in the oligotrophic ocean and their influence on phytoplankton biomass and productivity. Glob. Biogeochem. Cy. 29 (10), 1763–1781.
- Qin, B.Q., Zhou, J., Elser, J.J., Gardner, W.S., Deng, J.M., Brookes, J.D., 2020. Water depth underpins the relative role and fates of nitrogen and phosphorus in lakes. Environ. Sci. Technol. 54 (6), 3191-3198.
- Raymond, P.A., Hartmann, J., Lauerwald, R., Sobek, S., McDonald, C., Hoover, M., Butman, D., Striegl, R., Mayorga, E., Humborg, C., Kortelainen, P., Durr, H., Meybeck, M., Ciais, P., Guth, P., 2013. Global carbon dioxide emissions from inland waters. Nature 503 (7476), 355-359.
- Reinfelder, J.R., 2011. Carbon concentrating mechanisms in eukaryotic marine phytoplankton. In: Carlson, C.A., Giovannoni, S.J. (Eds.), Annu. Rev. Mar. Sci, 3, pp. 291–315.
- Reverey, F., Grossart, H.P., Premke, K., Lischeid, G., 2016. Carbon and nutrient cycling in kettle hole sediments depending on hydrological dynamics: a review. Hydrobiologia 775. 1-20.
- Sackett, O., Petrou, K., Reedy, B., Hill, R., Doblin, M.A., Beardall, J., Ralph, P.J., Heraud, P., 2016. Snapshot prediction of carbon productivity, carbon and protein content in a Southern Ocean diatom using FTIR spectroscopy. ISME J. 10, 416-426.
- Schagerl, M., Drozdowski, I., Angeler, D.G., Hein, T., Preiner, S., 2009. Water age-a major factor controlling phytoplankton community structure in a reconnected dynamic floodplain (Danube, Regelsbrunn, Austria). J. Limnol. 68, 274-287.
- Siegel, D.A., Behrenfeld, M.J., Maritorena, S., McClain, C.R., Antoine, D., Bailey, S.W., Bontempi, P.S., Boss, E.S., Dierssen, H.M., Doney, S.C., Eplee Jr., R.E., Evans, R.H., Feldman, G.C., Fields, E., Franz, B.A., Kuring, N.A., Mengelt, C., Nelson, N.B., Patt, F. S., Robinson, W.D., Sarmiento, J.L., Swan, C.M., Werdell, P.J., Westberry, T.K., Wilding, J.G., Yoder, J.A., 2013. Regional to global assessments of phytoplankton dynamics from the Sea WiFS mission. Remote Sens. Environ. 135, 77-91.
- Silva, E., 2005. Phytoplankton characteristics, trophic evolution, and nutrient dynamics in an urban eutrophic lake: Kandy Lake in Sri Lanka. In: Science Publishers Inc., pp. 227–270
- Song, C., Dodds, W.K., Rüegg, J., Argerich, A., Baker, C.L., Bowden, W.B., Douglas, M.M., Farrell, K.J., Flinn, M.B., Garcia, E.A., Helton, A.M., Harms, T.K., Jia, S., Jones, J.B., Koenig, L.E., Kominoski, J.S., McDowell, W.H., McMaster, D., Parker, S.P., Rosemond, A.D., Ruffing, C.M., Sheehan, K.R., Trentman, M.T., Whiles, M.R., Wollheim, W.M., Ballantyne, F., 2018. Continental-scale decrease in net primary productivity in streams due to climate warming. Nat. Geosci. 11 (6), 415-420.

- Tagliabue, A., Bowie, A.R., Boyd, P.W., Buck, K.N., Johnson, K.S., Saito, M.A., 2017. The integral role of iron in ocean biogeochemistry. Nature 543, 51-59.
- Tanabe, Y., Hori, M., Mizuno, A.N., Osono, T., Uchida, M., Kudoh, S., Yamamuro, M., 2019. Light quality determines primary production in nutrient-poor small lakes. Sci. Rep. 9, 4639.
- Thomas, W.H., Dodson, A.N., Reid, F., 1978. Diatom productivity compared to other algae in natural marine phytoplanton assemblages. J. Phycol. 14 (3), 250-253.
- Thompson, P., O'brien, T., Paerl, H., Peierls, B., Harrison, P., Robb, M., 2015. Predicting the future by observing the past: precipitation and phytoplankton. In: The 52nd Australian Marine Science Association (AMSA) Annual Conference.
- Tilman, D., Mattson, M., Langer, S., 1981. Competition and nutrient kinetics along a temperature gradient: an experimental test of a mechanistic approach to niche theory. Limnol. Oceanogr. 26 (6), 1020-1033.
- Tonetta, D., Laudares-Silva, R., Petrucio, M.M., 2015. Planktonic production and respiration in a subtropical lake dominated by Cyanobacteria. Braz. J. Biol. 75 (2), 460-470.
- Unrein, F., O'Farrell, I., Izaguirre, I., Sinistro, R., dos Santos Afonso, M., Tell, G., 2009. Phytoplankton response to pH rise in a N-limited floodplain lake: relevance of N2fixing heterocystous cyanobacteria. Aquat. Sci. 72 (2), 179-190.
- Van de Waal, D.B., Litchman, E., 2020. Multiple global change stressor effects on phytoplankton nutrient acquisition in a future ocean. Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci. 375 (1798), 20190706.
- Vogt, R.J., St-Gelais, N.F., Bogard, M.J., Beisner, B.E., del Giorgio, P.A., 2017. Surface water CO2 concentration influences phytoplankton production but not community composition across boreal lakes. Ecol. Lett. 20 (11), 1395-1404.
- Waibel, A., Peter, H., Sommaruga, R., 2019. Importance of mixotrophic flagellates during the ice-free season in lakes located along an elevational gradient. Aquat. Sci. 81, 1–10.
- Walter, B., Peters, J., van Beusekom, J.E.E., 2017. The effect of constant darkness and short light periods on the survival and physiological fitness of two phytoplankton species and their growth potential after re-illumination. Aquat. Ecol. 51, 591-603.
- Wang, S.M., Dou, H.S., 1998. The Annals of Chinese lakes(Zhongguohupozhi). Science Press, Beijing (in Chinese).
- Wang, S.Y., Gao, Y., Jia, J.J., Sun, K., Lyu, S.D., Li, Z.X., Lu, Y., Wen, X.F., 2021. Water level as the key controlling regulator associated with nutrient and gross primary productivity changes in a large floodplain-lake system (Lake Poyang), China. J. Hydrol. 599, 126414.
- Weisse, T., Gröschl, B., Bergkemper, V., 2016. Phytoplankton response to short-term temperature and nutrient changes. Limnologica 59, 78-89.
- Whitehead, H., O'Brien, K., Worm, B., 2010. Diversity of deep-water cetaceans and
- primary productivity. Mar. Ecol. Prog. Ser. 408, 1–5. Winder, M., Sommer, U., 2012. Phytoplankton response to a changing climate. Hydrobiologia 698 (1), 5-16.
- Wu, Z.S., Cai, Y.J., Liu, X., Xu, C.P., Chen, Y.W., Zhang, L., 2013. Temporal and spatial variability of phytoplankton in Lake Poyang: the largest freshwater lake in China. J. Great Lakes Res. 39 (3), 476-483.
- Yuan, Y., Jiang, M., Zhu, X., Yu, H., Otte, M.L., 2021. Interactions between Fe and light strongly affect phytoplankton communities in a eutrophic lake. Ecol. Indic. 126, 107664.
- Zhang, Y., Prepas, E.E., 1996. Regulation of the dominance of planktonic diatoms and cyanobacteria in four eutrophic hardwater lakes by nutrients, water column stability, and temperature. Can. J. Fish. Aquat. Sci. 53 (3), 621-633.
- Zhao, C.S., Shao, N.F., Yang, S.T., Ren, H., Ge, Y.R., Zhang, Z.S., Feng, P., Liu, W.L., 2019. Quantitative assessment of the effects of human activities on phytoplankton communities in lakes and reservoirs. Sci. Total Environ. 665, 213-225.
- Zhao, K., Wang, L., You, Q., Pan, Y., Liu, T., Zhou, Y., Zhang, J., Pang, W., Wang, Q., 2021. Influence of cyanobacterial blooms and environmental variation on zooplankton and eukaryotic phytoplankton in a large, shallow, eutrophic lake in China. Sci. Total Environ. 773, 145421.