

Evolving phytoplankton primary productivity patterns in typical Tibetan Plateau lake systems and associated driving mechanisms since the 2000s

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ABSTRACT

Phytoplankton primary productivity from the surface to the euphotic depth (PP_{eu}) is an important indicator for estimating the carbon (C) sequestration capacity of a lake system. Approximately 50% of China's lake systems are distributed throughout the Tibetan Plateau (TP), playing an important C neutrality role in China and beyond. Over the past 20 years, the PP_{eu} of TP lake systems may undergo dramatic spatial and temporal transformation under the significant influence of climate change and human activities. To reveal corresponding changing mechanisms, this study explored spatiotemporal PP_{eu} patterns in typical TP lake systems with MODIS observations during 2002–2020. Since the 2000s, results reveal that the annual mean PP_{eu} in TP lake systems ranges from 476.7 to 621.6 mg C/m²/d, with an average value of 553 ± 36.2 mg C/m²/d. Spatially, PP_{eu} was much higher on the northeastern boundary and in the south of the TP compared to its remaining northern regions. PP_{eu} trends in TP lake systems with higher salinity levels and those at higher altitudes were lower. Temporally, 48% of lakes on the TP exhibited a significant descending PP_{eu} trend, while 31% of lakes exhibited a significant ascending trend. PP_{eu} in TP lake systems may have mostly been influenced by day length (decimal hours), land surface temperature, and chlorophyll-*a* (Chl-*a*) content while being mainly limited by relative humidity (RHU). Additionally, PP_{eu} also showed a significant positive relationship with total N and P imported from wastewater in TP (especially in Tibet), indicating that anthropogenic emissions could have an important influence on PP_{eu} . Spatiotemporal pattern and driving mechanism results from this study can help us better understand the C sequestration capacity of TP lake systems.

1. Introduction

Gross primary production (GPP) quantified the carbon fixation rate of organic matter producers created from inorganic compounds, the energy from sunlight, and carbon dioxide (CO₂) (Lakshmi et al., 2014; Deines et al., 2015), which was one way of C

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neutrality. Phytoplankton generally contributes 50% of the GPP in aquatic ecosystems (Yang et al., 2018). GPP produced by Phytoplankton primarily occurs from the surface to the euphotic depth which can be shorted as PP_{eu} , extremely representing a fundamental property related to aquatic system C sequestration. Given the rapid growth of phytoplankton, it will respond quickly to changes in the surrounding environment (Kromkamp et al., 2017). Examples of potential changes are salinity (Huang et al., 2014; Liu et al., 2016), sunlight (Matsumoto et al., 2014; Tanabe et al., 2019), temperature, and precipitation (Park et al., 2004; Hillman et al., 2018). Certain studies have shown that changes in land-use and nutrient enrichment can increase primary production levels in many aquatic systems (Cloern, 2001; Underwood and Kromkamp, 1999). Contaminants (Buma et al., 2009; Komenda et al., 2000; Mason et al., 2003; Snel et al., 1998), such as anti-fouling hull paint (Buma et al., 2009; Jellali et al., 2013), have been shown to also influence primary production. Furthermore, anthropogenic activities can promote PP_{eu} by increasing nutrient content, such as nitrogen (N) (Hillman et al., 2018) and phosphorus (P) (Reeder, 2017). The calculation of PP_{eu} is critical to further explore its associated spatiotemporal and driving patterns, which will help us better understand C cycling and ecological environmental changes, particularly under a background of climate change and anthropogenic activities (Behrenfeld et al., 2005; Jia et al., 2021). Jia et al. (2022) found that fluctuance in different environmental factors (such as high water level, high temperature, strong solar radiation) in Poyang Lake stimulate comparatively lush phytoplankton growth and thus affect PP_{eu} during the rainy season. Deng et al. (2017) believed that different chlorophyll-a concentrations resulting from different nutrient concentrations mainly result in the spatiotemporal changes in the PP_{eu} of Taihu. Saberi (2017) found that different spatiotemporal global water flow and deposition would affect PP_{eu} .

Traditionally, PP_{eu} is measured in-situ through means of marine cruise sampling methods (i.e., via light/dark bottle oxygen measurements and the C isotope tracer method) (Ye et al., 2015), which are accurate but extremely time-consuming (Smith et al., 1989; Pi et al., 2021). Conversely, remote sensing is far more practical and economical compared to in-situ methods (Ye et al., 2015; Vollenweider et al., 1974; Kemili and Putri, 2014; Kromkamp et al., 2017). Satellite-based PP_{eu} measurements are typically combined with other models, such as the Talling Model (Talling, 1957), the Cadée Model (Colijn and Cadée, 2003), and the Vertically Generalized Productivity Model (VGPM) (Behrenfeld and Falkowski, 1997). The VGPM is the most widely used model to estimate PP_{eu} (Zeng et al., 2011; Jia et al., 2021; Deng et al., 2017; Yin et al., 2012), as it can be easily combined with remote sensing technology as its input parameters which was derived from satellite data (Zeng et al., 2011; Zhang et al., 2007, 2008; Yin et al., 2012; Jia et al., 2021).

The TP is the original source of many of Asia’s famous river systems, while also being the largest high-altitude inland lake region in the world (B. Wang et al., 2020). The lake systems distributed throughout the TP account for approximately 49% of all lake area in China (Ma et al., 2010). Over the past few decades, the TP, being an important “Asian Water Tower”, has undergone significant environmental changes (Liu and Chen, 2000; Xu et al., 2008; Qiu, 2008; Kuang and Jiao, 2016). Not only can the environment influence lake characteristics, but lake characteristics can also reflect environment change. Several TP lake system properties have been investigated, such as chlorophyll-a (Chl-a) content (Pi et al., 2021), water clarity (Pi et al., 2020; Liu et al., 2021a,b; S. Wang et al., 2020), and lake system PP_{eu} on the Qinghai–Tibet Plateau (QTP) (Jia et al., 2021).

However, being an important C sequestration indicator, systematic spatiotemporal PP_{eu} patterns in lake systems throughout the

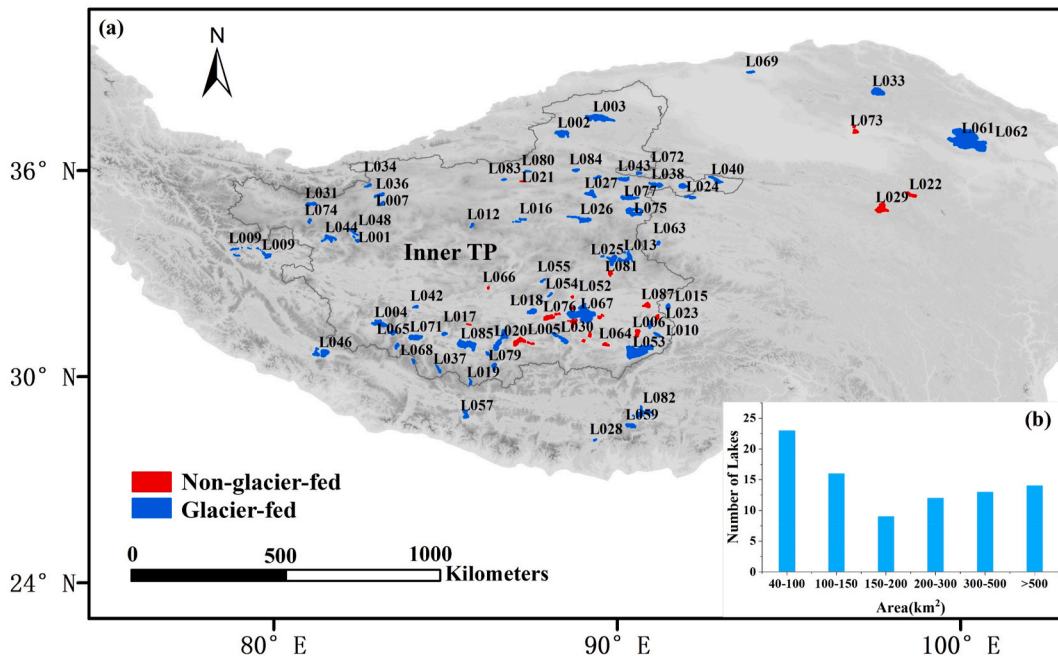


Fig. 1. a Locations of all TP 87 lake systems selected for this study. Lake systems in blue represent those fed by glacial meltwater while all remaining lake systems were not. Fig. 1b provides statistical information on lake size characteristics. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

entire TP as well as associated driving mechanisms have been largely disregarded. Accordingly, this study hypothesized that environmental and climate changes under natural altitude gradients drive geographical PP_{eu} patterns in TP lake systems. Therefore, the objectives of this study were as follows: (1) to analyze dynamic spatiotemporal patterns of lake PP_{eu} patterns on the TP since the 2000s; (2) to reveal the corresponding driving mechanisms of these associated spatiotemporal patterns.

2. Materials and methods

2.1. Study area

The TP is situated in Western China and Central Asia, within latitudes 26°00' N-39°47' N and longitudes 73°19' E-104°47' E (Lu et al., 2005), a vast place rich in mineral resources but poor in people and economy. Its mean elevation is greater than 4000 m, and its highest elevation is approximately 8804 m.a.s.l., being referred to as “the roof of the world”. Owing to its unique location, the climate of the TP is distinctive, governed by both the Asian monsoon system and the westerlies (Pi et al., 2021). The TP has attracted considerable attention from the hydrological, meteorological, and climatic communities (Wan et al., 2016). Being the source of all essential components within the TP’s hydrosphere, its lake systems play an important role in both regional and global biogeochemical processes (Liu et al., 2009). The TP is home to the densest distribution of lake systems globally, accounting for approximately 50% of all China’s lake systems (Luo et al., 2020), with total area more than 46500 KM². Surface runoff, precipitation, and glacial meltwater are the main water supplies of these lake systems (Wang et al., 2018). Most TP lakes are salt lake and saltwater lake systems, although it is also home to a few freshwater lake systems (Luo et al., 2020). For this study, 87 TP lake systems was selected based on data quality (i. e., greater than six effective satellite data per file and per lake system, where lake size is greater than 40 km²), including research group samples. Lake distribution is shown in Fig. 1a, and lake size is shown in Fig. 1b.

2.2. Vertically generalized production model

From 2002 to 2020, the PP_{eu} of the 87 TP lake systems was estimated using the VGPM obtained from Aqua/MODIS data. A simplified formula was selected (Behrenfeld and Falkowski, 1997):

$$PP_{eu} = 0.66125 \times P_{opt}^B \times \frac{E_0}{E_0 + 4.1} \times Z_{eu} \times C_{opt} \times Dirr \tag{1}$$

where P_{opt}^B is the maximum rate of C fixation within a water column (mg C/[mg Chl·h]); E_0 is the photosynthetically active radiation (PAR) of surface photosynthetic effective radiation of a lake system; Z_{eu} is the euphotic depth (m); C_{opt} is the Chl-*a* content where P_{opt}^B is located, which can be substituted by remotely sensed surface Chl-*a* data; and Dirr is day length in decimal hours.

Some parameters were calculated as follows:

$$P_{opt}^B = \begin{cases} 1.13 & (T \leq -1.0 \text{ } ^\circ\text{C}) \\ 4 & (T \geq 28.5 \text{ } ^\circ\text{C}) \\ P_{opt}^{B'} & (-1.0 < T < 28.5 \text{ } ^\circ\text{C}) \end{cases} \tag{2}$$

where

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

Additionally,

$$Z_{eu} = 4.605 / K_d; \text{ (Li et al., 2019)} \tag{4}$$

$$K_d = f / Z_{sd}; \text{ (Holmes, 1970)} \tag{5}$$

$$Z_{sd} = 0.032 \times Rrs_645^{-0.753}; \text{ (Pi, et al., 2020)} \tag{6}$$

where T is lake surface temperature (LST) (°C); Z_{sd} is water transparency (m); K_d is the diffuse attenuation coefficient (m⁻¹). For the TP, parameter f is 1.19 (Shang et al., 2018).

2.3. Satellite data

Many studies have combined VGPM with MODIS data to calculate PP_{eu} (Bergamino et al., 2010; Deng et al., 2017; Yin et al., 2012; Ye et al., 2015), in both lake and river systems. The Aqua satellite (which carries the MODIS instrument) orbits from south to north over the equator during daylight hours. Its maximum spatial resolution is 250 m (band 1 and band 2), having a very short revisit interval (1 image/day). This study selected Aqua/MODIS Level-2 ocean color data (1 km² resolution) from July 2002 to December 2020 to procure Chl-*a*, euphotic depth (Z_{eu}), PAR, and K_d parameters obtained from the NASA OceanColor Web archive (<https://oceancolor.gsfc.nasa.gov/>). LSTs between 2002 and 2020 derived from the MOD11A1 V6 product using the Google Earth Engine (GEE). The six months (January, February, March, April, February, and October) where in surface ice forms were not included in this study. For TP lake systems, where Chl-*a* values higher than 0.3 mg m⁻³ were predicted (Pi et al., 2021), the selected Chl-*a* content estimated using

the OCx algorithm, which was specially designed for Chl-a rich water (O'Reilly et al., 1998).

2.4. Related environmental and anthropogenic factor data

For this study, 20 factors were selected to explore PP_{eu} driving factors of the selected TP lake systems, which include environmental, meteorological, and anthropogenic factors. According to their associated relationships, PP_{eu} factor correlations greater than 0.1 were selected for analysis. Additionally, an adequate amount of in-situ data were selected for validation. Four environmental variables were selected for box plot figure analysis, including lake size, salinity, glacier meltwater (or not), and water level. Lake size and glacial meltwater (or not) data was collected from Lakes of China (Wang and Dou, 1998) and Hydro-lake dataset (Messenger et al., 2016). Salinity data derived from in-situ data by Liu et al. (2021), for which only 57 out of 87 lake systems had valid data. Additionally, 2010–2018 long-term water level (WL) data was derived from Cryosat-2 by Liao et al. (2020). Apart from the seven environmental and meteorological variables (i.e., Dirr, Chl-a, LST, Z_{eul} , PAR, particulate inorganic carbon [PIC], and particulate organic carbon [POC]), five other meteorological factors (i.e., evaporation [EVP], precipitation [PRE], relative humidity [RHU], air pressure [PRS], and wind speed) were selected for correlation analysis. These factors were obtained from the China Meteorological Data Network (<http://data.cma.cn/>), and inverse distance weighting (IDW) was used to interpolate the data from each lake system. For anthropogenic factor data, annual total N and P between 2011 and 2017 and annual chemical oxygen demands (COD) between 2003 and 2017 discharged from Tibet and Qinghai Province wastewater were collected to determine their influence on lake PP_{eu} . These data were obtained from the

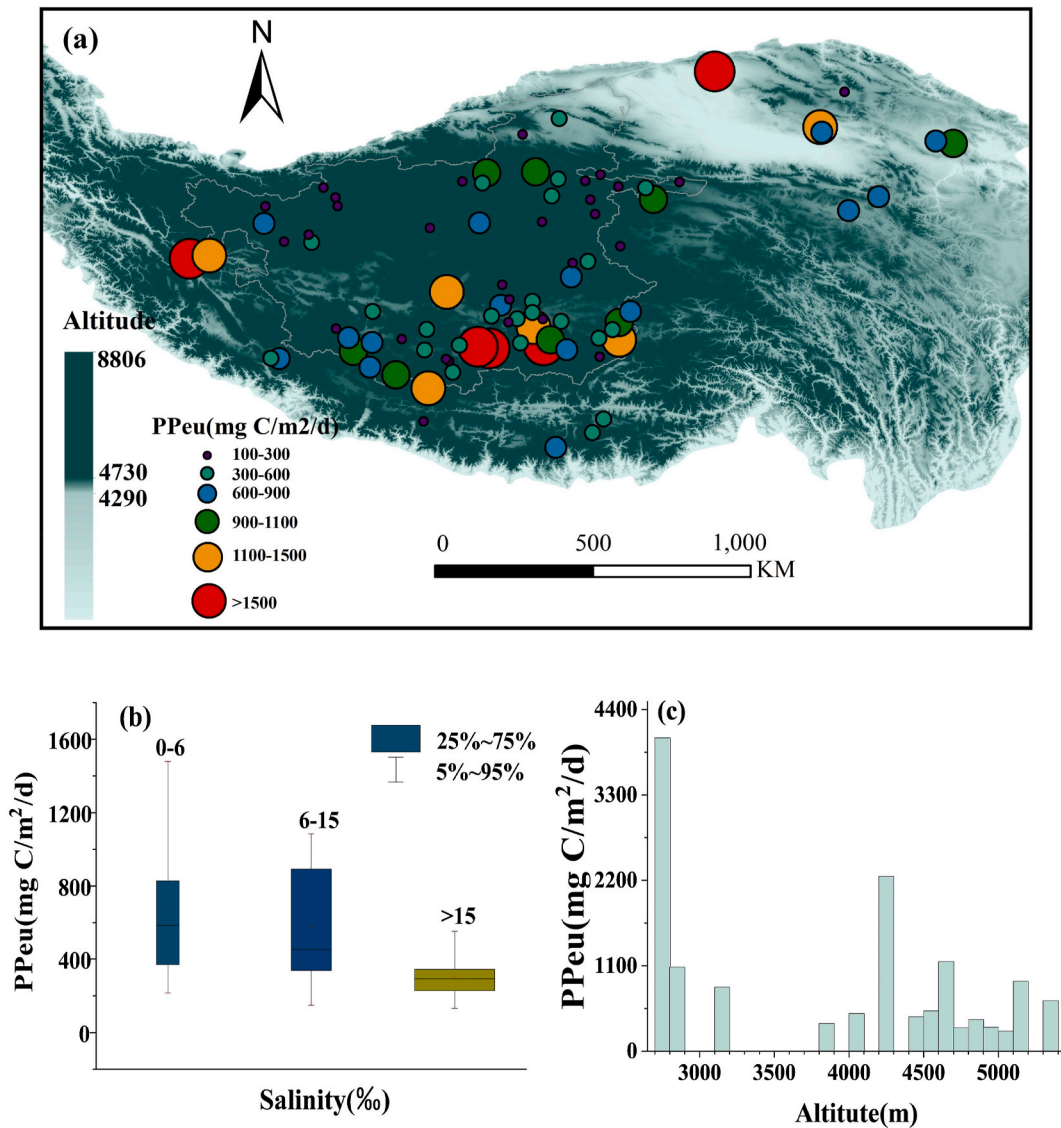


Fig. 2. (a) Spatial distribution of long-term annual mean PP_{eu} in TP lake systems since the 2000s. (b) Distribution boxplot of lake system salinity levels on the in TP. (c) 100 interval histogram representation of the lake systems investigated for this study.

online version of the China Statistical Yearbook (<http://www.stats.gov.cn/tjsj/ndsj/>).

2.5. Data analysis

Due to data quality and quantity, not all downloaded files were used in this study. The following pretreatment steps were conducted to filter the valid data. First, through means of combining information obtained from the study region, unusable data was discarded including invalid data and off-repeated means \pm standard deviation data values that exceeded the three-sigma rule. Second, files with six or less valid data points within one day were discarded from all lake systems, while lake systems with five or less years of data were also disregarded. For climate data, only the first pretreatment step was necessary. After these steps, a total of 87 suitable lake systems passed our criterion test. Following data selection, monthly and annual mean PP_{eu} values between 2002 and 2020 were estimated in all 87 TP lake systems. For each lake system, long-term mean PP_{eu} was calculated as the average of all annual mean PP_{eu} values during the study period. Unless otherwise specified, annual means in this study are mean PP_{eu} values between May and October. This was because of the absence of data resulting from surface ice cover during the other months. Linear regression was also conducted on each lake system to calculate average changing rates (in percentage/year or $\%/yr^{-1}$, denoted as the slope of PP_{eu} changing trends divided by long-term mean PP_{eu} values). Moreover, The Mann-Kendall (MK) test (Hirsch and Slack, 1984) was applied on our lake system PP_{eu} results. To assess the validity of satellite derived PP_{eu} , coefficients of determination (R^2) and scatter plots were used to compare the $PP_{eu-vgpm}$ derived from remote sensing to the $PP_{eu-vgpm}$ reported by Jia et al. (2021), deriving from Liu's data (2021).

2.6. Uncertainty

Our PP_{eu} estimations can result in potential uncertainty. First, parameters that derived from remote sensing data (Chl-*a*, *T*, Z_{eul} , and PAR) could result in uncertainty. Second, data gaps owing to unfavorable measurement conditions (i.e., surface ice period) could also result in uncertainty. Third, there is small part of phytoplankton primary production under euphotic depth, however it can be ignored as photosynthesize under euphotic layer is generally rather weak. Under cloud cover, stray light, sun glint, and imperfect solar/viewing angle conditions, the validity of PP_{eu} retrieval will decrease considerably and will be typically discarded according to the corresponding effective data range. As a result, data are not evenly distributed among lake systems; thus, such data do not represent lake conditions within the entire region. Another type of uncertainty may be induced by VGPM parameters, where certain parameters derive from the empirical model without a direct data source.

3. Results

3.1. Spatial PP_{eu} distribution

Annual mean PP_{eu} results from all 87 lake systems since the 2000s are shown in Fig. 2 and Table S. Lake PP_{eu} values ranged from 65.7 to 9000 mg C/m²/d, and annual mean PP_{eu} values ranged from 476.7 to 621.6 mg C/m²/d (at a level of 553.1 ± 36.2 mg C/m²/d). Maidong Co, a saltwater lake situated at the westernmost boundary of the TP, yielded the maximum annual mean PP_{eu} value (5597.7

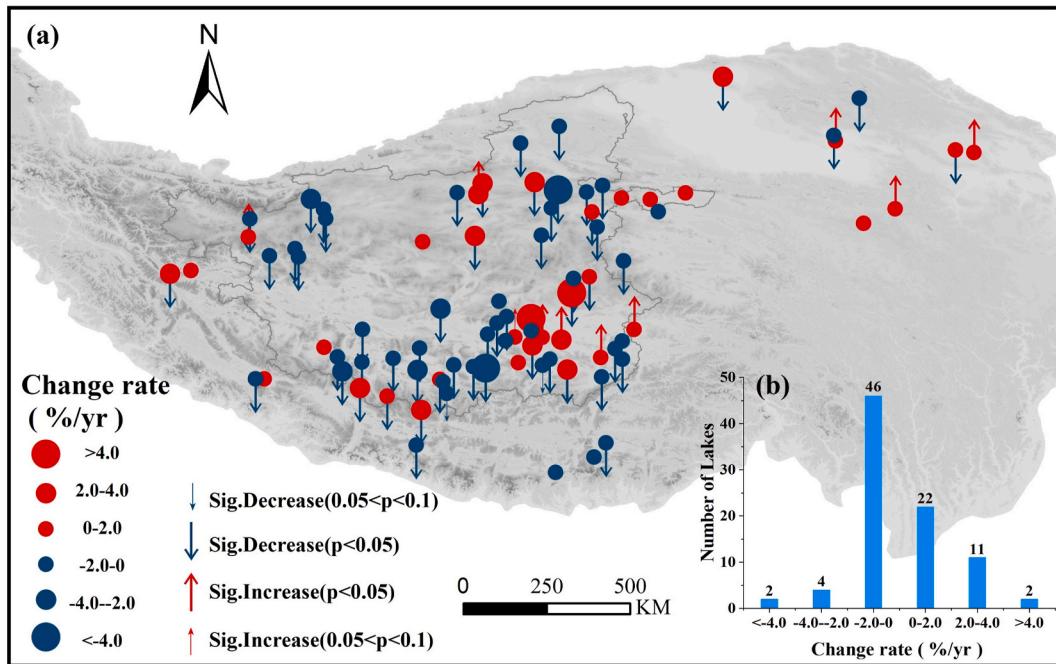


Fig. 3. a Distribution of annual PP_{eu} changing rates in TP lake systems since the 2000s. Lake systems with statistically significant change rates are annotated with “↑” and “↓”. Fig. 3b The number of lake systems characterized by different PP_{eu} change rate values.

mg C/m²/d, altitude 4291 m) while Monco Bunnyi, situated in the southern inner TP basin region, yielded the minimum *PP_{eu}* value (106.0 mg C/m²/d, altitude 4685 m). Specifically, mean *PP_{eu}* values for 80% of all the selected lake systems were lower than 900 mg C/m²/d (see Fig. 2), while greater than half of the lake systems yielded mean *PP_{eu}* values less than 600 mg C/m²/d. Only five lake systems yielded annual mean *PP_{eu}* values greater than 1500 mg C/m²/d (see Table A1). Annual *PP_{eu}* values of lake systems greater than 1000 km² were all less than 900 mg C/m²/d. Most lake systems with higher *PP_{eu}* values were in the southern inner TP basin region. Only a few lake systems with *PP_{eu}* values above the mean (i.e., 553.1 mg C/m²/d) were in the western inner TP basin region.

As shown in Fig. 2b and c, there was a trend in higher *PP_{eu}* values for lake systems at lower altitudes or with lower salinity levels. Mean *PP_{eu}* values for lake systems with salinity levels between 0 and 6‰ were higher (averaging 695.9 ± 442.9 mg C/m²/d) than lakes

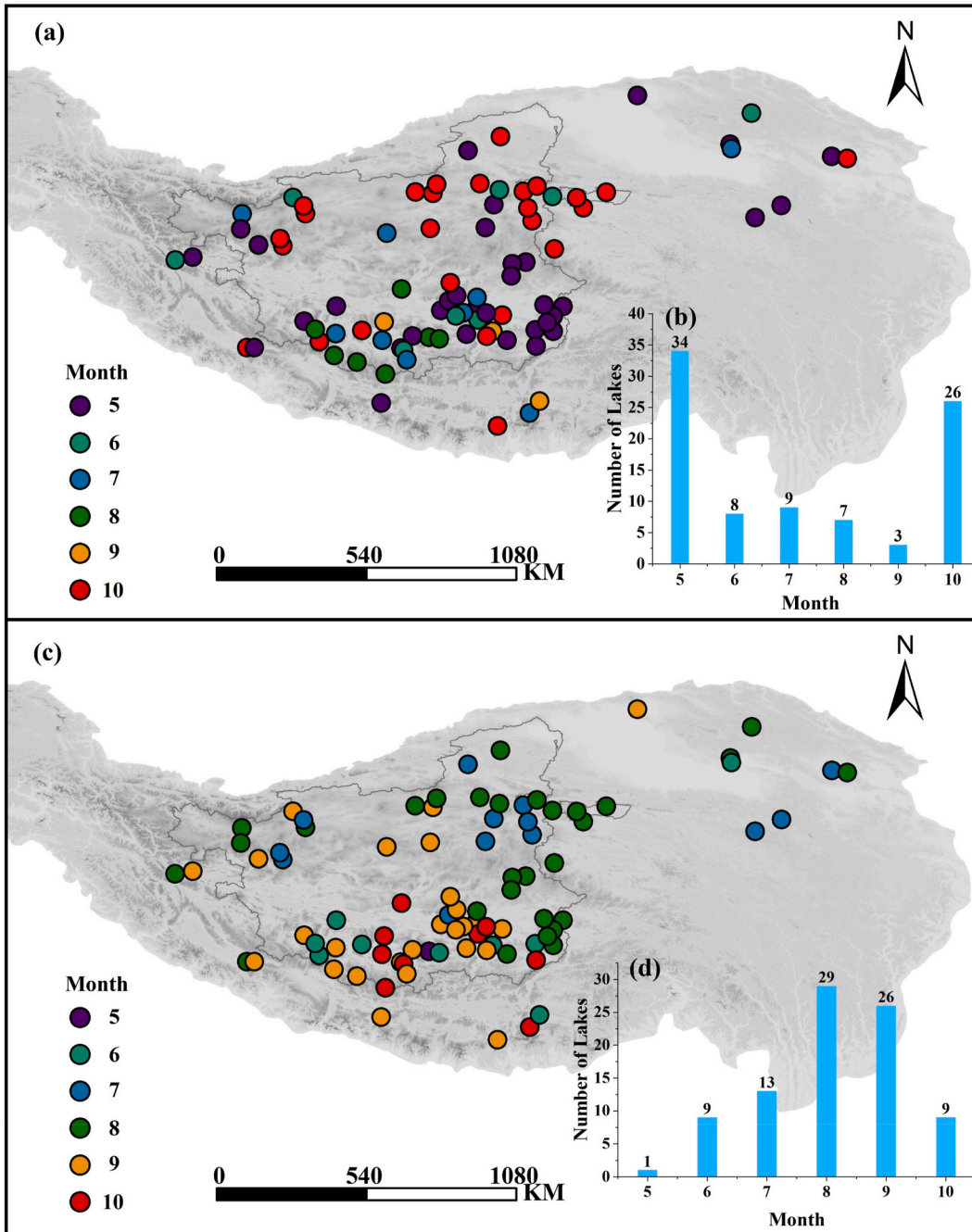


Fig. 4. (a) Maximum number of months with the lowest mean *PP_{eu}* values by frequency throughout all months. (c) Maximum number of months with the highest mean *PP_{eu}* values by frequency throughout all months. Note that (b) and (d) in the corresponding histograms of the number of lake systems throughout all months are shown in (a) and (c).

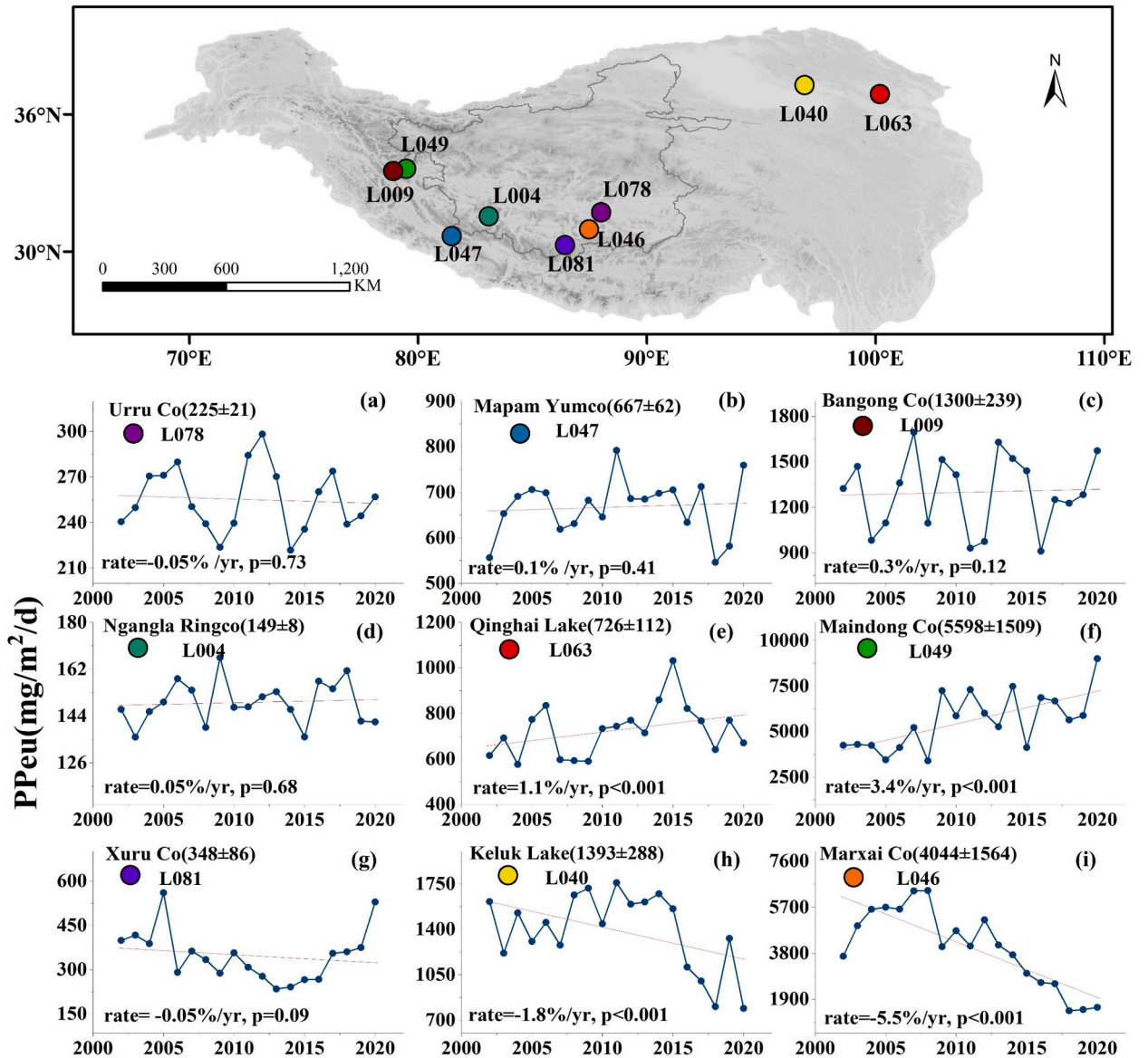


Fig. 5. Long-term interannual PP_{eu} curves of typical TP lake systems throughout 2002–2020. Lake systems are labeled by different colored circles and marked in the map; red lines represent the linear regression trend line. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Note: Since the 2000s, annual PP_{eu} changing rates in Urru Co (225 ± 21 mg C/m²/d, altitude 4554 m), Mapam Yumco (667 ± 62 mg C/m²/d, altitude 4585 m), and Bangong Co (1300 ± 239 mg C/m²/d, altitude 4669 m) remained fairly low ($-0.05\%/yr^{-1}$, $0.1\%/yr$, and $0.3\%/yr$, respectively). Ngangla Ringco (149 ± 8 mg C/m²/d, altitude 4716 m), Qinghai Lake (726 ± 112 mg C/m²/d, altitude 3194 m), and Maindong Co (5598 ± 1509 mg C/m²/d, altitude 4291 m) exhibited a significant increasing trend with changing PP_{eu} rates of $0.05\%/yr^{-1}$, $1.1\%/yr$, and $3.4\%/yr$, respectively, promoting an increased in eutrophication. Xuru Co (348 ± 86 mg C/m²/d, altitude 4714 m), Keluk Lake (1393 ± 288 mg C/m²/d, altitude 2814 m), and Marxai Co (4044 ± 1564 mg C/m²/d, altitude 4692 m) exhibited significant decreasing trends with changing PP_{eu} rates of $-0.05\%/yr^{-1}$, $-1.8\%/yr$, and $-5.5\%/yr$, respectively, indicating a deterioration in environment conditions.

between 6‰ and 15‰ (averaging 576.7 ± 335.2 mg C/m²/d), and higher than lakes with salinity levels greater than 15‰ (averaging 299.4 ± 106.1 mg C/m²/d), which is consistent with findings from Jia et al. (2021). Moreover, as shown in our 100 interval histogram representation (Fig. 2c), higher PP_{eu} values (i.e., greater than 3600 mg C/m²/d) were mainly observed at lower altitudes (i.e., no higher than 2800 m), while lower PP_{eu} values (less than 450 mg C/m²/d) were observed at altitudes above 4700 m.

3.2. Interannual PP_{eu} variation in TP lake systems

As shown in Fig. 3, mean PP_{eu} values in lake systems throughout the entire TP generally fluctuated between 500 and 600 mg C/m²/d, while PP_{eu} values in most lake systems exhibited a significantly decreasing trend over time, especially for those located in the inner TP basin and the southern TP region. Greater than half (72%) of all the lake systems exhibited a decreasing trend over time. Most lake systems exhibiting significantly increasing PP_{eu} values were mainly located in the southeastern inner TP basin and the northeastern TP

region. For lake systems exhibiting significant changes ($p < 0.0001$), those with altitudes below 4600 m mostly exhibited a descending PP_{eu} trend between $-2\%/yr$ and $0\%/yr$. And lakes between 5000 and 5100 m (i.e., the northern region of Lake Heishi, Gozha Co, and Palung Co) all exhibited decreasing PP_{eu} trends with rates no greater than $4\%/yr$. Lake systems with altitudes greater than 5100 m (i.e., Daggayai Co and Gyesar Co) exhibited significantly increasing PP_{eu} trends with rates no greater than $4\%/yr$.

Lake systems with altitudes between 4600 and 5100 m, namely, those with the most rapid decreasing and increasing PP_{eu} values, exhibited far more complex PP_{eu} changing rates (mainly from $-2\%–0\%/yr$). Lake systems with significant changing rates (i.e., greater than $\pm 2.5\%/yr$) were almost exclusively those with areas between 0 and 200 km^2 . Moreover, PP_{eu} values of almost all lake systems between 200 and 1000 km^2 showed significant decreasing trends (i.e., with rates no greater than $2.5\%/yr$). Compared to smaller lake systems, those with areas greater than 2000 km^2 all exhibited less significant change. It is noteworthy that Qinghai Lake, China's largest lake system (i.e., greater than 4000 km^2), situated at the easternmost edge of the TP (with an altitude of 3194 m), has experienced an increasing changing PP_{eu} rate (i.e., $1\%/yr$).

3.3. Monthly PP_{eu} variation

Monthly spatial PP_{eu} variation patterns in TP lake systems were consistent with annual results (Fig. S1). However, there were seasonal discrepancies. For example, there were a lower number of lake systems with PP_{eu} values $< 300\text{ mg C/m}^2/\text{d}$ and a higher number with PP_{eu} values $> 900\text{ mg C/m}^2/\text{d}$ in September. Conversely, the opposite was true for May and October. Additionally, Fig. S1 shows that monthly coefficients of variation (CV) during the same period also revealed monthly variations. The CV map clearly shows that monthly variations in lake systems within the northern TP region were higher than its southern region, where greater than three-quarters of lake systems in the former had CV values $> 20\%$, while CV values of the majority of lake systems in the eastern TP region were $< 20\%$.

As shown in Fig. 4a, the lowest PP_{eu} values mostly occurred in May and October in lake systems in the northern and southern regions of the inner TP basin, respectively. Anomalously, lake systems in the southwestern TP region primarily yielded the lowest PP_{eu} values in either July or August. The highest lake system PP_{eu} values were observed in August, which were mostly concentrated in the northern and eastern TP regions (Fig. 4b). As shown in Fig. 4, peak PP_{eu} values in most TP lake systems occurred later in the south (compared to the north). However, one lake system in the southern region (i.e., Ngangzi Co) had the lowest PP_{eu} value in August and the highest in May.

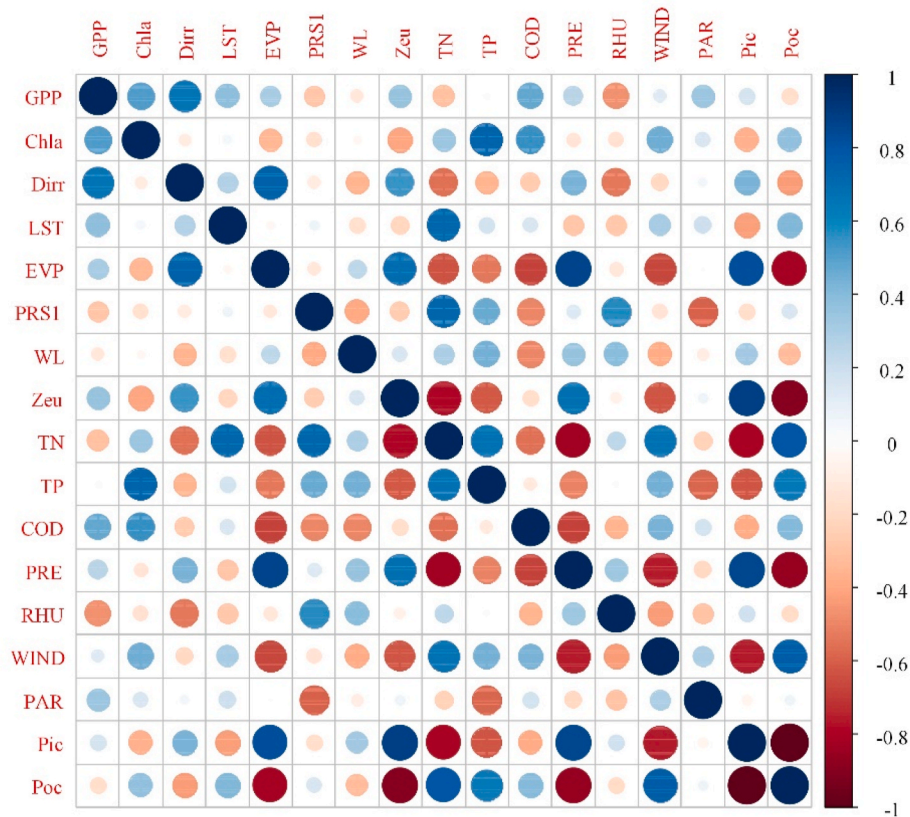


Fig. 6. Annual correlations between environment factors and phytoplankton primary production in TP lake systems since the 2000s. Note: Blue dots represent positive correlations and red dots represent negative correlations. Dot size and color represent the value size.

4. Discussion

4.1. Phytoplankton PP in lake systems

In Fig. 5, long-term interannual lake system PP_{eu} curves are shown at low (0–400 mg C/m²/d), mid (400–2000 mg C/m²/d), and high (greater than 2000 mg C/m²/d) PP_{eu} ranges, whose absolute PP_{eu} changing rate trends are typically characteristic at low ($\leq 0.05\%/yr^{-1}$), mid (from $0.05\%/yr^{-1}$ to $3\%/yr^{-1}$), and high ($> 3\%/yr^{-1}$) change rates.

This showed that PP_{eu} values in some lake systems underwent a sudden decrease (i.e., Marxai Co), which may have resulted from a decrease in precipitation. Meanwhile, some lake systems continued to increase with little seasonal fluctuation (i.e., Maindong Co and Qinghai Lake). The main reasons for these observed fluctuations of increasing trends in Qinghai Lake were overgrazing and the rapid

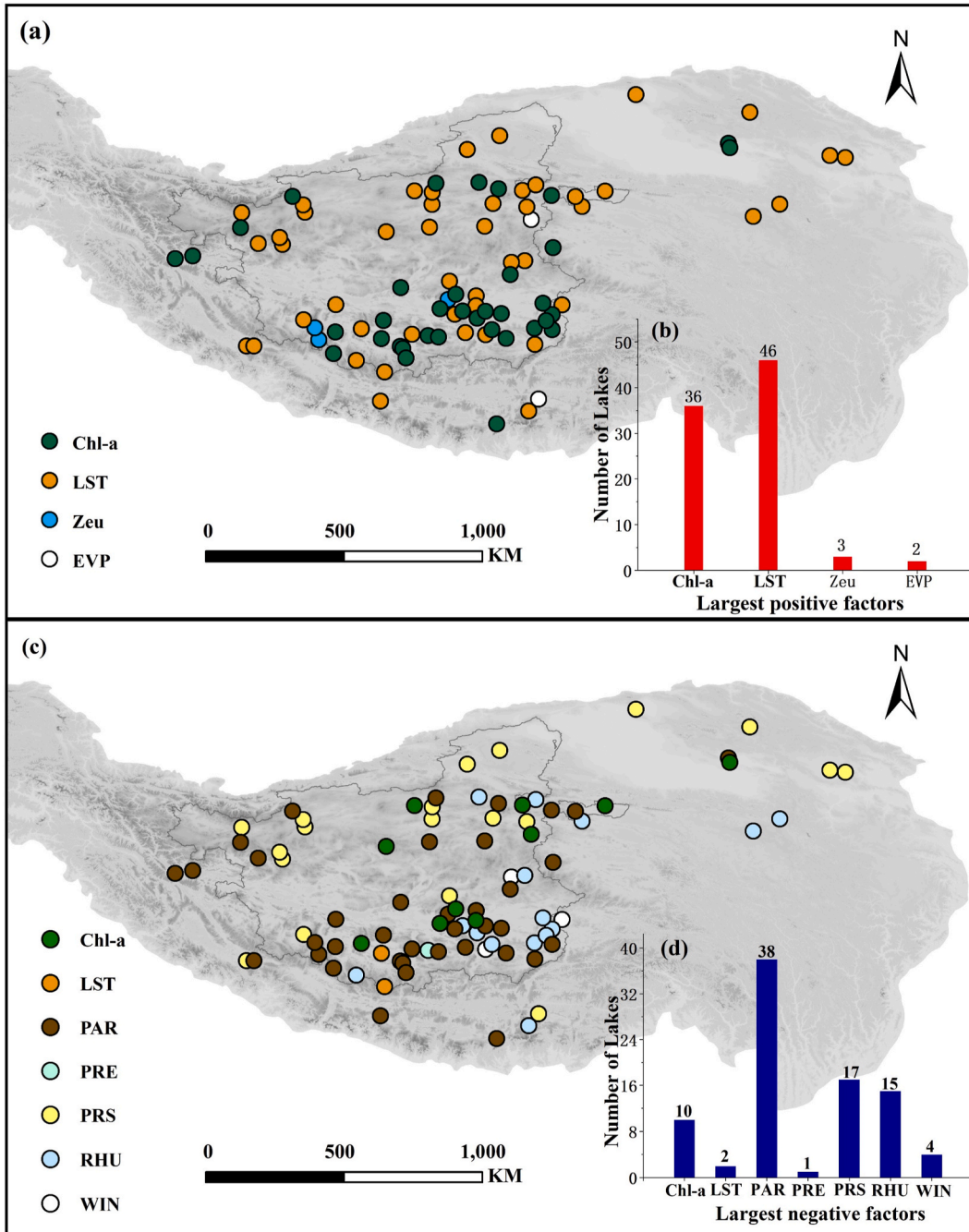


Fig. 7. Environmental factors where lake system PP_{eu} values (a) yielded the highest positive correlations and (c) yielded the highest negative correlations throughout 2002–2020 as well as (b) and (d), which show the corresponding histograms representing the number of different driving factors.

development of the tourism industry, which resulted in the deterioration of lake water quality while contributing to its eutrophication (Ao et al., 2014; Li et al., 2018). However, this differed for Maindong Co and Bangong Co at the Chinese-Indian border. For a long time, troops have been stationed within the vicinity of these two lake systems at both sides of the border. Therefore, resultant anthropogenic activities in this region may have caused eutrophication to occur in these lake systems, subsequently improving PP_{eu} values. More details and results from the MK test are provided in Fig. S3 in the online supplementary materials version of the article.

4.2. Environmental factors affecting PP_{eu}

Previous studies have reported that phytoplankton biomass is the main driving factor for changes in PP_{eu} (Bergamino et al., 2010; Feng et al., 2016; Deng et al., 2017; Huang et al., 2019). As shown in Figs. 6 and 7, correlation analysis between environmental factors and PP_{eu} demonstrated that Drrr, LST, PAR, and Z_{eu} (as reactive conditions) and Chl-*a* (as a reactive medium) both strongly and positively correlated to PP_{eu} values throughout the TP, subsequently causing the PP_{eu} distribution patterns. According to our analysis of monthly variations (shown above) as well as that from another study (Deng et al., 2017), seasonal discrepancies exist, which is consistent with the result showing that LST and Chl_a strongly and positively correlated to PP_{eu} . Spatially, lake systems for which Chl_a

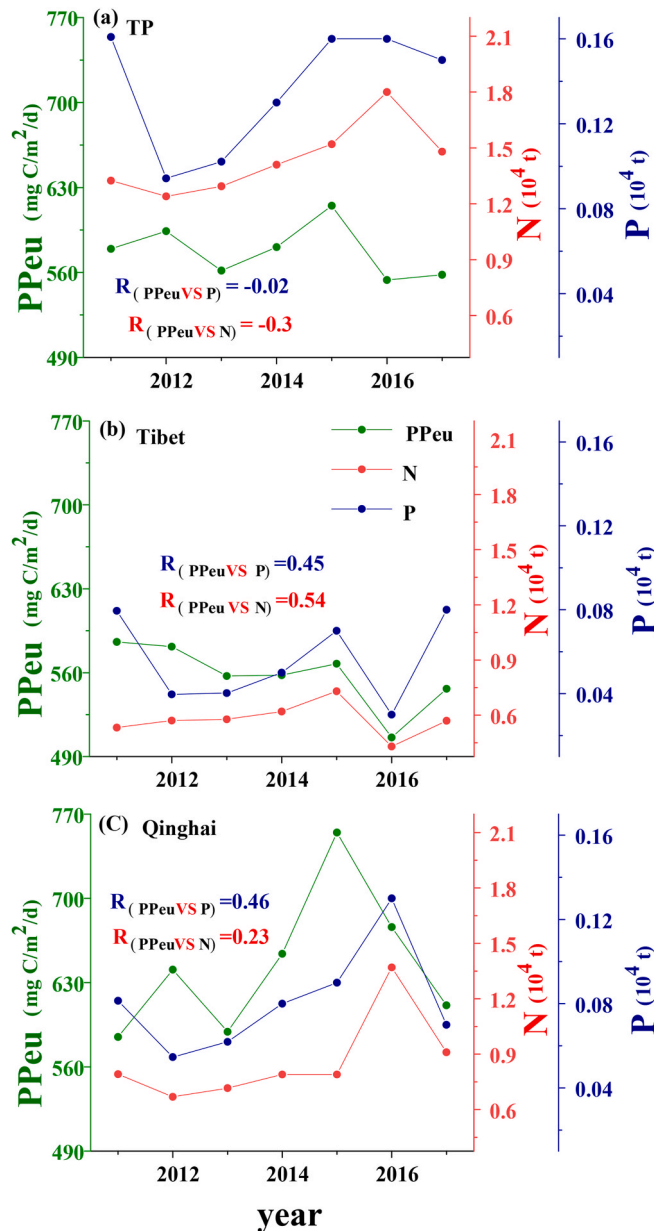


Fig. 8. Correlations between PP_{eu} and nitrogen (N) and phosphorus (P) in wastewater discharge. TP, Tibet, and Qinghai denote lake systems throughout the entire TP, those in Tibet Province, and those in Qinghai Province, respectively.

was the dominant driving factor were mostly distributed in the southern region of the inner TP basin. This could potentially have been caused by an increase in air temperature and downward longwave radiation that effectually drove lake system warming in the southern region of the inner TP basin (Huang et al., 2019), subsequently promoting food chain transmission efficiency coupled with a decrease in lake salinity levels, which consequently increased biodiversity (Zhu et al., 2019) and then promoted PP_{eu} . Additionally, other environmental factors, such as EVP, PRE, and WL, can also affect PP_{eu} change by transporting a greater amount of extraneous surface material (i.e., nutrients) into lake systems (Song et al., 2021). Decreasing evaporation and increasing rainfall will result in a greater amount of surface material (i.e., nutrients) being transported into lake systems (Song et al., 2021), while wind may influence water turbidity and subsequently affect nutrient levels (Zhu et al., 2014). Indeed, the impacts of these environmental factors on lake PP_{eu} are complex, affecting PP_{eu} related changes in different ways. For instance, increasing evaporation may cause an increase in rainfall. Additionally, wind directly effects PP_{eu} while also affecting nutrients, which will subsequently influence phytoplankton growth nutrient statuses as well as PP_{eu} (Wang et al., 2021). Moreover, increasing POC content will have a detrimental effect on water quality, decreasing Z_{eu} and subsequently affecting PP_{eu} .

4.3. Potential anthropogenic factors affecting PP_{eu}

Through its effect on the environment, anthropogenic activity is the main factor that typically effects PP_{eu} indirectly (Chen and Zhuang, 2012; Yao et al., 2018). For this study, anthropogenic activity factors are major pollutants that are discharged into wastewater, representing a regulated and readily measurable source of pollutants (DEC, 2017), including N, P, and COD. As a lack of long-term monitoring data on the Qinghai-Tibet Plateau, the waste water wasn't the only anthropogenic activity identified but the most relevant and comprehensive long-term statistical data related to water quality found from the existing statistical data. The N, P, and COD will affect PP_{eu} in lake ecosystems through affecting the algal growth (Gao et al., 2019). The time series of these pollutants and their correlation to PP_{eu} are shown in Fig. 8 and Fig. S2.

The N, P, and COD that were discharged into wastewater positively correlated to PP_{eu} , promoting phytoplankton productivity functions, which is consistent with results from Sumatra and Nurdin (2020). It should be noted that compared to that in Qinghai Province, the N and P that were discharged into the Tibet Autonomous Region significantly correlated to PP_{eu} . This indicated that phytoplankton productivity in the Tibet Autonomous Region is more easily influenced by the N and P discharge via anthropogenic activities. It also should be noted that this difference may be caused by lower N and P conditions in the Tibet Autonomous Region compared to Qinghai Province (Li et al., 2018). However, discharged COD in the Tibet Autonomous Region differs from that in Qinghai Province, the former being more significantly correlated to PP_{eu} . This means that organic matter in water, which decomposes into inorganic matter (i.e., CO_2 and other such C sources) (Li et al., 2018), may contribute to phytoplankton productivity in Qinghai Province while adversely effecting phytoplankton productivity in the Tibet Autonomous Region.

The N and P discharged into water exhibited an increasing general trend; however, a sudden decrease was observed in the Tibet Autonomous Region in 2016. The following reason may have been caused this phenomenon to occur. According to the agriculture and animal husbandry development plan of the Tibet Autonomous Region during the 13th Five-Year Plan, China encouraged the use of organic fertilizers and biological pesticides (Development and Reform Commission of Tibet Autonomous Region, 2015). Therefore, the input and usage of inorganic fertilizers decreased sharply in 2016. When the input and usage of organic fertilizers was later deemed insufficient, the N and P content that decreased up to 2017 increased once again when organic fertilizers were put back into usage. Therefore, government policy may indirectly affect phytoplankton productivity. Based on the above analysis, people may have an indirect effect on PP_{eu} in the TP, which differs from findings that suggested that anthropogenic activities have little effect on TP lake systems (Luo et al., 2020; Qiu, 2008; Kuang and Jiao, 2016), which is a finding in support of government regulation decision-making policies.

4.4. Potential impacts from other driving forces

Except for the environmental factors analyzed above, other environmental factors are difficult to quantify (i.e., owing to a lack of data) but may also exert a significant influence on the PP of phytoplankton (Jia et al., 2021; Pi et al., 2021), including lake size, glacial meltwater, etc. The influence of glacial meltwater is very complex, which could introduce water along with nutrients into lake systems while reducing LST and Dirr, which can influence changes in PP_{eu} (Pi et al., 2021). To analysis the influence of glacial meltwater, lake systems selected for this study were divided into glaciated and non-glaciated lake systems. As shown in Fig. 9a, compared to non-glaciated lake systems, those replenished by glacial meltwater had lower overall mean PP_{eu} values (i.e., 988 mg C/m²/d for non-glaciated lake systems and 604 mg C/m²/d for glaciated lake systems) and median overall PP_{eu} values (i.e., 787 mg C/m²/d for non-glaciated lake systems and 328 mg C/m²/d for glaciated lake systems). That may because Glacier melting will lead to the decrease of nutrient concentration in the lake and affect the growth of phytoplankton, resulting in lower PP_{eu} . Accounting for the changing trends in PP_{eu} values (Fig. 9c), non-glaciated lake systems exhibited greater variation in increasing and decreasing PP_{eu} rates compared to glaciated lake systems, while no significant difference was observed between the two groups, indicating that glacier field or not wasn't the main driving factors for annual change but may for seasonal change. Overall, results suggest that glacial meltwater had a potential negative impact on PP_{eu} rates in the TP region.

Lake size also can potentially influence environmental factors. Indeed, the expansion or shrinkage of lake systems may lead to changes in the aquatic environment, impacting lake PP_{eu} values. To investigate the impact of lake size, the lake systems selected for this study were divided into two groups, namely, lake systems whose area did not exceed 200 km² and lake systems whose area exceeded 200 km². By comparing the two groups (as shown in Fig. 9b), the latter group (i.e., those that exceeded 200 km²) exhibited lower mean and median PP_{eu} values. That may also because lake expansion will lead to the decrease of nutrient concentration, resulting in lower PP_{eu} . Regarding changing trends (Fig. 9d), both groups showed little different too.

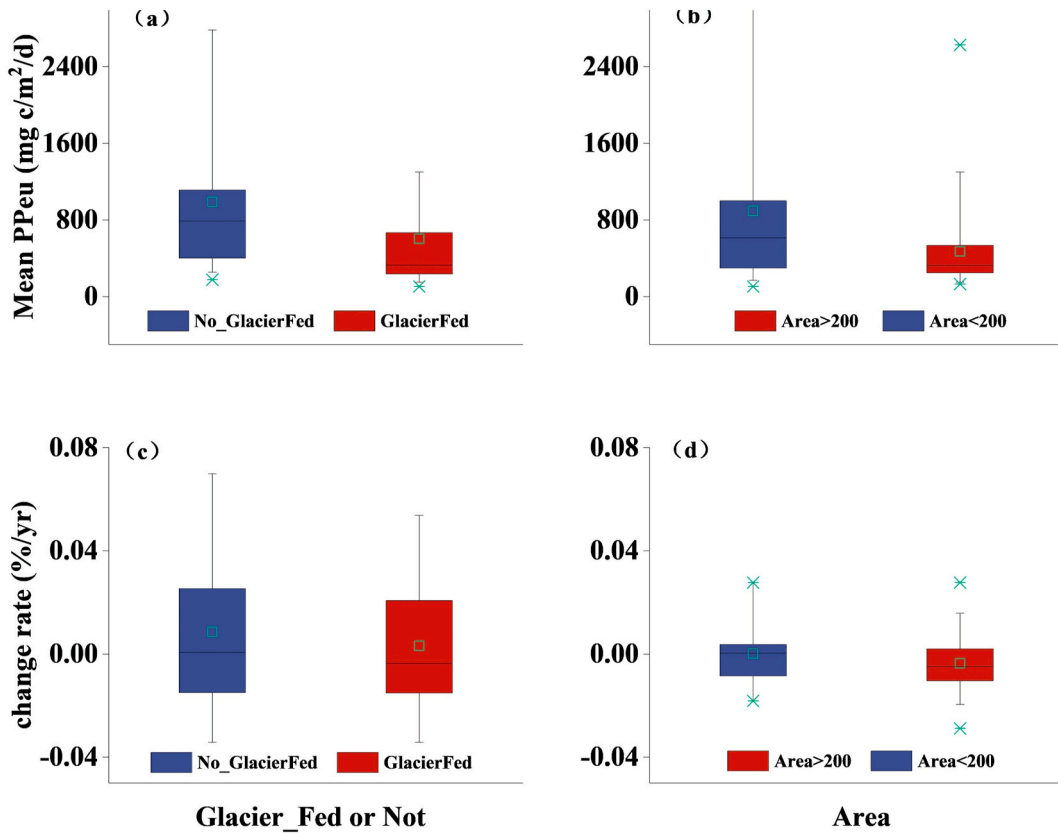


Fig. 9. Boxplots representing impacts of (a) glacial meltwater and (b) lake area on lake system PP_{eu} .

4.5. Factors driving comprehensively

Apart from a series of single factors were significantly correlated to PP_{eu} (i.e., Dirr, Chl-*a*, RHU, LST, TN, and TP). It is important to note that synergistic interactions among these lake systems could further amplify their associative response. Such as a cooperative response may exist like LST may potentially increase overland runoff through glacial meltwater while increasing the response of evaporation and rainfall, namely, transporting more surface matter (i.e., nutrients) generated by environmental or anthropogenic effects into lake systems, subsequently increasing overall PP_{eu} values.

4.6. Validity of remotely sensed PP_{eu}

In this study, PP_{eu} was firstly estimated by combining VGPM with measured lake system water quality parameters (Liu et al., 2021a, b). These estimated PP_{eu} values were then matched with data calculated from remote sensing data. Data intervals were less than four days for each pair. Finally, 28 data pairs were matched and their correlations were calculated. The PP_{eu} ($PP_{eu_{liu}}$) calculated by Liu et al. (2021a,b) correlated well with the PP_{eu} ($PP_{eu_{rs}}$) calculated in our study (0.28; significant at a level of $p = 0.1$). Relationships between their calculated Z_{eu} and lake temperature were 0.89 and 0.85 (both at a level of $p < 0.01$), respectively. Compared to Z_{eu} and lake temperature, these two Chl-*a* data sources did not correlate well. This may be due to the limited point sampling used in Liu's study, which does not reflect actual averaged chlorophyll lake concentrations. On the other hand, remotely sensed chlorophyll concentrations are the average of a wide planar range.

Seven pairs were matched to data reported by Jia et al. (2021). Our PP_{eu} data also showed a good correlation to that from Jia's study (i.e., 0.34). Correlations and scatter plot points from Jia's study are provided in Fig. 10. Generally, the PP_{eu} from our study was in good linear agreement with the data selected from other relevant studies, which to some extent confirms the reliability of our results. $PP_{eu_{rs}}$ was noticeably higher than $PP_{eu_{jia}}$, which may be because Jia's study mainly took samples from the lakeside, and lakeside water is relatively turbulent and mixed, resulting in the low transparency of measured water and the low PP_{eu} calculated. However, in our study, the lake vector was reduced by 1 km to avoid any terrestrial impacts. $PP_{eu_{liu}}$ was lower than $PP_{eu_{rs}}$, which may be due to the limited sampling points of Liu's study. Moreover, the sensor used in Liu's study was located approximately 10–20 cm below the lake surface, which does not match remote sensing sensors with respect to irradiation measurements and the larger scale involved. However, the photosynthetic rate of the surface layer always decreased due to photoinhibition, and the maximum value appeared in the subsurface layer (Falkowski and Woodhead, 2013).

The PP_{eu} data derived from Aqua/MODIS data were highly consistent with Liu's and Jia's in-situ data, indicative of the validity of results in revealing spatiotemporal variations and changing trends in lake PP_{eu} throughout the TP. Besides, though a comparison of

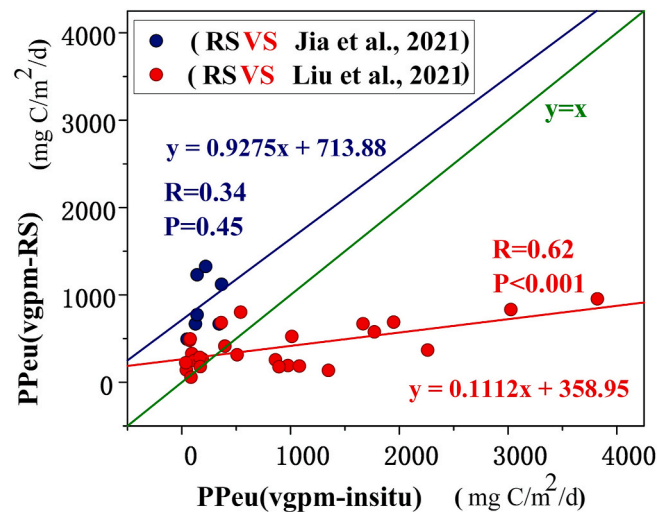


Fig. 10. Scatter plot points that correspond to phytoplankton productivity, applying remote sensing and measured lake data from different studies conducted on the TP, all based on the VGPM model.

changing Chl-*a* trends throughout 2003–2017 (Pi et al., 2021), changing PP_{eu} trends showed some inconsistency. In the TP, most changing trends in lake system PP_{eu} were significant, primarily decreasing. The consistency of changing PP_{eu} trends within the southern inner TP basin and the entire TP aligned more with Chl-*a*.

5. Conclusions

This study investigated the spatiotemporal patterns and driving mechanisms of typical lake systems throughout China's Tibetan Plateau (TP) since the 2000s by combining the Vertically Generalized Productivity Model (VGPM) with remotely sensed satellite data. Overall, although lake system PP_{eu} changed, it did not fluctuate significantly. Moreover, annual mean daily PP_{eu} values of the lake systems were low (553 ± 36.2 mg C/m²/d). Also, obvious spatiotemporal patterns was observed in long-term annual mean PP_{eu} . Spatially, PP_{eu} values of most lake systems (63%) were 100–600 mg C/m²/d. Lake systems with high PP_{eu} rates were mainly located on the northeastern boundary and the southern region of the TP. Those at higher altitudes and with higher salinity levels had lower PP_{eu} values. Temporally, greater than half of the lake systems experienced a downward trend, where the changing rates of most were between $-2.0\%/yr$ and $-0\%/yr$. Chl-*a*, Dirr, LST, and PAR were the main PP_{eu} driving factors. Anthropogenic activities affected PP_{eu} , which were more pronounced in the Tibet Autonomous Region than in Qinghai Province. According to our analysis, if no interventions were taken in 2015, PP_{eu} would have continued to slowly increase. Lastly, carbon (C) fixation processes closely correlated to changes in PP_{eu} . Therefore, it is recommended that C fixation effects should be continuously monitored and investigated on the TP.

Author contributions

Yang Gao: Conceptualization;
 Junjie Jia, Wanqian Deng, Xianrui Ha and Kun Sun: Resource and Data Curation;
 Wanqian Deng, Mingzhen Ma and Yao Lu: Writing - Original Draft;
 Wanqian Deng, Kun Sun, Shuoyue Wang and Zhaoxi Li: Writing - Review & Editing.

Ethical statement

It is stated that all ethical practices have been followed in relation to the development, writing, and publication of the article.

Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.rsase.2022.100825>.

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