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The unprecedented 2022 extreme summer heatwaves increased harmful cyanobacteria blooms

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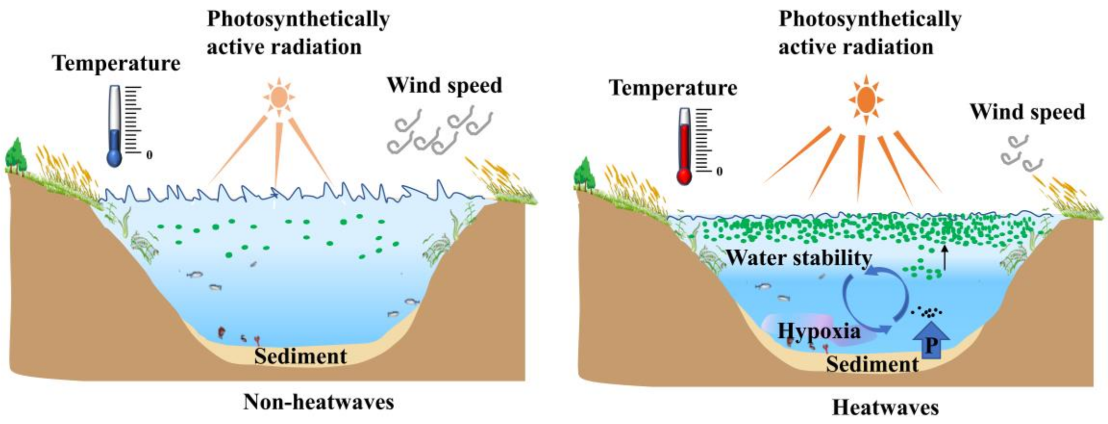
Highlights:

1 Lake Taihu experienced unprecedented heatwaves in the summer of 2022.

2. Three heatwaves with high Chl*a* concentrations and low wind speed were recorded.

3. Summer heatwaves significantly promoted harmful cyanobacteria blooms.

Graphical Abstract



Abstract

Heatwaves are increasing and expected to intensify in coming decades with global warming. However, direct evidence and knowledge of the mechanisms of the effects of heatwaves on harmful cyanobacteria blooms are limited and unclear. In 2022, we measured chlorophyll-a (Chl*a*) at 20-second intervals based on a novel ground-based proximal sensing system (GBPSs) in the shallow eutrophic Lake Taihu and combined *in situ* Chl*a* measurements with meteorological data to explore the impacts of heatwaves on cyanobacterial blooms and the potential relevant mechanisms. We found that three unprecedented summer heatwaves (July 4-15, July 22-August 16, and August 18-23) lasting a total of 44 days were observed with average maximum air temperatures (MATs) of 38.1 ± 1.9 ℃, 38.7 ± 1.9 ℃, and 40.2 ± 2.1 ℃, respectively, and that these heatwaves were characterized by high air temperature, strong PAR, low wind speed and rainfall. The daily Chl*a* significantly increased with increasing MAT and photosynthetically active radiation (PAR) and decreasing wind speed, revealing a clear promotion effect on harmful cyanobacteria blooms from the heatwaves. Moreover, the combined effects of high temperature, high PAR and low wind, enhanced the stability of the water column, the light availability and the phosphorus release from the sediment which ultimately boosted cyanobacteria blooms. The projected increase in heatwave occurrence under future climate change underscores the urgency of reducing nutrient input to eutrophic lakes to combat cyanobacteria growth and of improving early warning systems to ensure secure water management.

Keywords: Extreme heatwaves; harmful cyanobacteria blooms; chlorophyll *a*; eutrophic lake; wind speed; Lake Taihu

1 Introduction

Increasing surface air temperature is one of the most recognized consequences of anthropogenic climate change, with robust evidence of warming during at least the last century (Hansen et al., 2002; Li et al., 2020). Future climate model projections suggest that in the near future there will be continued warming driven by an increase in anthropogenic greenhouse gas emissions (Brown and Caldeira, 2017). Parallel to a future projected increase in global air temperature, climate models also predict an increase in the frequency, intensity, and duration of extreme heat events (i.e., heatwaves) (Frolicher et al., 2018; Perkins-Kirkpatrick and Lewis, 2020; Woolway et al., 2021b). Heatwaves are defined as persistent extreme climatic events with temperatures exceeding a predefined threshold or the 90th percentile threshold relative to the average of a 30 yr climatological baseline (Frolicher et al., 2018; You et al., 2017). Notably, recent evidence has suggested that heatwaves have become increasingly prevalent, more intense and of longer duration in some regions in recent decades (Frolicher et al., 2018; Oliver et al., 2018; Perkins-Kirkpatrick and Lewis, 2020; Woolway et al., 2021b). Notable examples of extreme heatwaves include, among others, the European heatwave of 2003 (Jankowski and Livingstone, 2006; Johnk et al., 2008), the Siberian heatwave of 2010 (Barriopedro et al., 2011; McMichael and Lindgren, 2011; Shaposhnikov et al., 2014), and the summer heatwave of 2013 in Australia (Roberts et al., 2019). More recently, during the summer of 2022, many parts of the Northern Hemisphere were gripped by a series of extreme and dangerous heatwaves, which damaged vital infrastructure, affected agricultural production, and had adverse impacts on human health, causing more than 1,700 deaths in Spain and Portugal alone (Lancet, 2022). The unprecedented 2022 extreme summer heatwaves that occurred in the Yangtze River basin surpassed any recorded since meteorological records for the region first started being kept in 1960 (Wang et al., 2023).

Heatwaves have a dramatic negative influence on terrestrial and aquatic ecosystems (Bartosiewicz et al., 2016; IPCC, 2021; Smale et al., 2019; Smith et al., 2021). For lakes, the most direct and recognized impact of heatwaves includes an increase in lake surface water temperature (Woolway et al., 2020). This can also have a knock-on influence on the entire physical lake environment (Jankowski and Livingstone, 2006) and likewise can influence other key processes, such as oxygen dynamics, greenhouse gas emissions, and the presence of toxic substances (Audet et al., 2017; Bartosiewicz et al., 2016; Jankowski and Livingstone, 2006). Previous studies have also shown that heatwaves can lead to an increase in the occurrence of harmful cyanobacteria blooms (Huang et al., 2021; Johnk et al., 2008; Paerl et al., 2011; Woolway et al., 2021c), which are already increasing in size, frequency and duration in many parts of the world due to ongoing climate change and anthropogenic nutrient enrichment (Ho et al., 2019; Hou et al., 2022; Huisman et al., 2018; Paerl and Huisman, 2008). Critically, global warming and abnormally high precipitation (and thus often high external nutrient loading) have already been shown to promote harmful cyanobacteria blooms in the early spring, more intense blooms in summer (Deng et al., 2014; Free et al., 2022; Qin et al., 2021; Shi et al., 2019), and more frequent events in autumn (Winter et al., 2011). Ultimately, climate change is considered a potential catalyst for the extension and intensification of harmful cyanobacteria blooms in eutrophic lakes (Jeppesen et al., 2021; Paerl and Huisman, 2008), and more severe and longer lasting heatwaves can considerably amplify these effects. Although it has been widely reported that warmer lake temperatures promote harmful algal blooms, the relationship between heatwaves and cyanobacteria bloom responses in lakes remains sparsely elucidated (Guo et al., 2018; Huang et al., 2021; Huber et al., 2012; Johnk et al., 2008). For example, a record-low cyanobacteria biomass in 2003 and harmful cyanobacteria blooms in 2006 were observed in eutrophic Lake Müggelsee, Germany, during heatwaves (Huber et al., 2012). In contrast, a serious cyanobacteria bloom induced by the record-setting heatwave in 2003 was observed in a field experiment conducted in Lake Nieuwe Meer, the Netherlands (Johnk et al., 2008). Notably, cyanobacteria blooms caused by warm temperatures are typically weaker in nutrient-poor waters and stronger in nutrient-rich waters (Woolway et al., 2021c). Although some studies have increased our awareness of heatwave effects on both physical and biological processes in lakes, research into the impact and potential mechanisms of heatwaves on lake ecosystems remains comparatively limited. Due to the increased frequency and intensity of heatwaves in recent years, there is an urgent need to understand their crucial influence on harmful cyanobacteria blooms in eutrophic lakes in order to predict the risk of harmful cyanobacteria blooms and mitigate the negative impact on water quality.

In the summer of 2022, Lake Taihu, a shallow eutrophic lake, suffered from record-setting extreme heatwaves since meteorological records began in 1960. This lake has suffered from severe and frequent harmful summer cyanobacteria blooms since the 1980s (Qin et al., 2015; Qin et al., 2019; Shi et al., 2015). Despite restoration measures taken to alleviate eutrophication and cyanobacteria blooms after 2007, a higher frequency and earlier onset of harmful blooms were observed from 2003 to 2018 due to climate change (Qin et al., 2021; Qin et al., 2019). We hypothesized that heatwaves can promote harmful cyanobacteria blooms via meteorological, physical, and chemical conditions favorable for cyanobacteria growth and aggregation. Therefore, based on a real-time ground-based proximal sensing system (GBPSs) monitoring of Chl*a* at 20-second intervals combined with meteorological data, we investigated the effects and potential mechanisms of heatwaves on harmful cyanobacteria blooms in northern Lake Taihu, which is dominated by cyanobacteria. Specifically, this study aimed to (1) quantify the intensity and duration of the 2022 heatwave and resulting harmful cyanobacteria blooms, (2) discuss the responses of harmful cyanobacteria blooms to heatwaves, and (3) elucidate the potential driving mechanisms of heatwaves on harmful cyanobacteria blooms in eutrophic lakes.

2 Methods and materials

2.1 Study area

As the third largest freshwater lake (area: 2338 km^2, average depth: 1.9 m) in China and located in the heavily urbanized and densely populated Yangtze River Delta region, Lake Taihu not only provides drinking water to more than 20 million people but also plays a key role in tourism, fisheries, and shipping (Qin et al., 2021; Shi et al., 2020) (Figure 1a). Unfortunately, due to a dramatic increase in nutrient loading from industry and agriculture coupled with climate change, Lake Taihu has been seriously plagued by eutrophication and frequent harmful cyanobacteria blooms (Guo et al., 2019). This has also resulted in its transformation from a macrophyte-dominated to an algae-dominated ecosystem (Zhang et al., 2022; Zhang et al., 2016). Notably, with the implementation of a series of restoration measures after 2007, a reduction in annual average total nitrogen concentrations from 4.62 to 2.46 mg/L occurred from 2007-2018, and the annual average total phosphorus at first exhibited a descending and then an ascending tendency from 0.16 mg/L in 2007 to 0.12 mg/L in 2010 and then reached a peak of 0.19 mg/L in 2017 (Qin et al., 2021). However, the occurrence of harmful cyanobacteria blooms has not been markedly alleviated due in part to climate change (Qin et al., 2019) but rather has been amplified by a massive stocking of carp in an attempt to restore the lake (Mao et al., 2020).

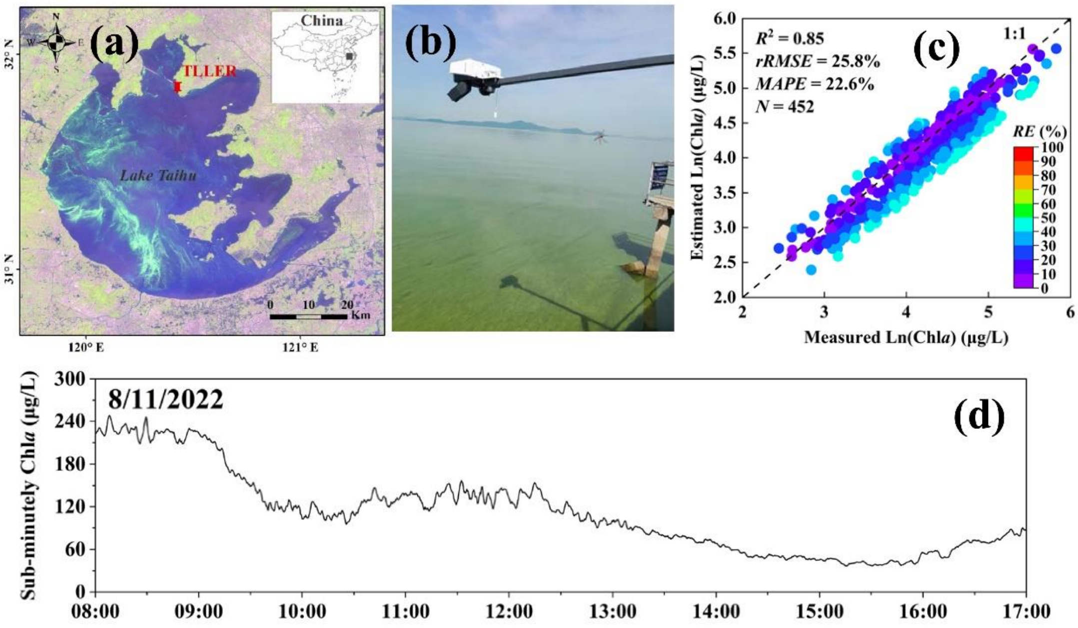


Figure 1. Showing (a) the location of Lake Taihu, (b) the ground-based proximal sensing system (GBPSs) for monitoring Chl*a*, and (c) an independent validation of a high accuracy pro-developed model for GBPSs, as well as (d) subminute time series of Chl*a* on August 11, 2022.

2.2 Meteorological and hydrological data and heatwave definition

Meteorological observations of air temperature, wind speed, photosynthetically active radiation (PAR), and rainfall were provided at hourly intervals from the nearby Lake Taihu Laboratory Ecosystem Research (TLLER) meteorological station (120°12′56″ E, 31°25′9″ N) from January 2021 to August 2022. In addition, daily data, including maximum air temperature, average wind speed, PAR and rainfall, from the Wuxi meteorological station (120°12′36″ E, 31°22′12″ N) from 1960 to 2020 were downloaded from the China meteorological data sharing service system (http://cdc.cma.gov.cn/home.do) to represent the long-term characteristics of Lake Taihu. In this study, we have cited the Chinese Meteorological Administration definition of a heatwave, which is defined as lasting at least three consecutive days with a maximum air temperature (MAT) exceeding 35 ℃ (Huang et al., 2021; Huang et al., 2010). To characterize the heatwave event, the MAT, number of heatwave days and its intensity were counted. Heatwave intensity was defined as the temperature, which was subtracted by 35 ℃ from the daily MAT. Furthermore, the daily average water level from January 1992 to August 2022 and the daily average water temperature at 50 cm below the water surface from April 1993 to December 2021 were obtained from TLLER to explore the effects of heatwaves on the Lake Taihu ecosystem.

2.3 *In situ* water quality measurement

A total of 452 water samples were measured at TLLER from July 12 to August 25, 2022 (Figure 1a). All water samples were taken by a 2.5 L collector within a range of 0 m to 0.5 m below the water surface and immediately filtered using GF/F fiberglass filters with a pore size of 0.7 μm. First, GF/F fiberglass filters were stored at -20 ℃ for at least 24 hours to allow the cyanobacterial cells to fully rupture. Then, after the GF/F filters were heated in 90% alcohol at boiling point temperature for 5 minutes, the Chl*a* was extracted for at least 4 hours in a dark environment at room temperature. Finally, Chl*a* was determined by the difference in optical density of the final extract before and after the acidification step between 665 nm and 750 nm measured by a Shimadzu UV-2550PC UV–Vis spectrophotometer (https://www.iso.org/obp/ui/#iso:std:iso:10260:ed-1:v1:en). In addition, pH at 0.1 m above the sediment–water interface was measured at 30 min intervals using a YSI-6600 sonde deployed at TLLER.

2.4 Real-time Chl*a* data acquisition

GBPSs, innovative proximal sensing instruments, were proposed to monitor high-frequency water quality dynamics in real time by Zhang et al. in 2018 (Zhang et al., 2021). The GBPSs single-point high-resolution spectrometer has a maximum sampling frequency of 20 s with a spectral resolution of 1 nm from 400 nm to 900 nm (Li et al., 2022; Sun et al., 2022). The GBPSs spectra were acquired by a fixed spectrometer, which was usually placed 2-5 m away from the shore and a height of 4-5 m above the water surface, between 8:00 and 17:00 to avoid low sunlight and sensor response deviation (Li et al., 2023). Although the GBPSs spectrum is the ratio of upwelling and downwelling irradiance collected by two independent spectrometers in the upward and downward directions, it is consistent with the synchronous remote-sensing reflectance measured by the FieldSpec spectroradiometer (Analytical Spectral Devices, Inc., Boulder, CO, USA) under different weather conditions after correction, with a slope value of 0.98 and a coefficient of determination (R^2) value of 0.997 ($p < 0.001$) (Li et al., 2023). In previous studies, GBPSs have successfully estimated Chl*a*, total nitrogen, total phosphorus, and total suspended matter based on the complex relationship between the water quality and characteristic bands, which are jointly determined by the absorption and scattering of material components and concentrations (Li et al., 2022; Sun et al., 2022; Wang et al., 2022).

Given the short-term continuity of heatwaves and the rapid hourly and daily phytoplankton changes (Qi et al., 2018; Ye et al., 2014), a real-time GBPSs was introduced to acquire data on subminute Chl*a* dynamics to represent cyanobacterial biomass, given that *Microcystis* contributed 80%-90% of the total algal biomass during summer in northern Lake Taihu (Guo et al., 2019; Xu et al., 2015) (Figure 1b). In this study, GBPSs were deployed in an open area 240 m away from the shore with a mean depth of 1. 5 m (TLLER) to acquire data on real-time water spectra from July to August 31 in 2022 (Li et al., 2022; Sun et al., 2022). The GBPSs displayed the Chl*a* of the surface waters calculated from the predeveloped Chl*a* machine learning model and the real-time spectrum under complex weather conditions. In addition, an independent dataset including 452 *in* *situ* Chl*a* measurements was used to further validate the applicability and accuracy of the GBPSs preset Chl*a* model for Lake Taihu.

2.5 Statistical analyses

Statistical analyses, including maximum, minimum, mean, standard deviation (S.D.), *t* test, Pearson correlation analysis and linear fitting were carried out using Statistical Program for Social Science (SPSS) 23.0. A result was regarded as statistically significant if $p \leq 0.05$. One-way analysis of variance (ANOVA) and the Mann–Whitney U test were used to compare the differences in parameters. The R^2, mean absolute percentage error (*MAPE*), relative root mean square error (*rRMSE*), and relative error (*RE*) were calculated using the following formulas to evaluate the performance and accuracy of the predeveloped Chl*a* model:

$$MAPE = \frac{1}{n} \times \sum_{i=1}^{n} \frac{|Meas_i - Esti_i|}{Meas_i} \times 100\% \qquad (1)$$

$$rRMSE = \sqrt{\frac{\sum_{i=1}^{n}\left(\frac{Meas_i - Esti_i}{Meas_i}\right)^2}{n}} \times 100\% \qquad (2)$$

$$RE = \frac{|Meas_i - Esti_i|}{Meas_i} \times 100\% \qquad (3)$$

where n denotes the number of samples, $Meas_i$ represents the measured value, and $Esti_i$ represents the estimated values.

3 Results

3.1 Independent validation of Chl*a* from GBPSs

Chl*a* concentrations from *in situ* measurements ranged from 11.5 µg/L to 339.4 µg/L with a median value of 77.92 µg/L and quantile of 25% and 75% values of 48.91 µg/L and 109.47 µg/L, respectively. Figure 1c demonstrates that the *rRMSE* and *MAPE* for the validation dataset were

25.8% and 22.6%, respectively, with the *RE* ranging from 0.05% to 44.9%. Moreover, the measured and estimated Chl*a* from the GBPSs after the logarithmic transformation were in good agreement ($R^2 = 0.85$, $p < 0.05$, $N = 452$) and were distributed evenly along the 1:1 line (Figure 1c). The high R^2 and low errors suggest that the Chl*a* monitoring from the GBPSs had satisfactory performance and good applicability for Lake Taihu. For example, subminute time series data depicting the variation in Chl*a* in detail from 30.2 to 246.8 µg/L on August 11, 2022, demonstrated high-frequency cyanobacteria bloom dynamics (Figure 1d).

3.2 Extreme summer heatwaves in 2022

Daily MAT from July to August 2022 was generally higher than the climatological average (1960 to 2021), ranging from 26.3 ℃ on August 31 to 43.3 ℃ on August 23, with an average MAT as high as 37.1 ± 3.4 ℃ (mean ± S.D., the same below) (Figure 2a). In general, 3 heatwave and 4 non-heatwave events occurred alternately from July to August 2022. Three unique heatwave events lasting a total of 44 days were recorded with an average MAT of 38.8 ± 2.0 ℃, which is 6.6 ℃ above the climatological average from 1960 to 2021 (Figure 2a and 3a), while four non-heatwave periods lasted 18 days with an average MAT value of 33.0 ± 2.7 ℃, which was significantly lower than the MAT value for heatwaves (*Mann–Whitney U test*, $p < 0.05$) (Figure 3a). Specifically, three heatwave events occurred on July 4-15, July 22-August 16, and August 18-23, with average MAT values of 38.1 ± 1.8 ℃, 38.7 ± 1.9 ℃, and 40.2 ± 2.1 ℃, respectively (Figure 3b). Furthermore, we calculated an average daily heatwave intensity of 3.8 ℃, which increased by 49.9% from the value of 2.5 ℃ in 2013, making this one of the hottest summers ever recorded in the Lake Taihu region (Sun et al., 2014). From a long-term perspective, the annual average MAT, annual MAT, number of heatwave days and average daily intensity of summer heatwaves in 2022 were the highest (Figure S1). Compared with the data from 1960, the increase in these parameters exceeded the sum of the annual average increase for the past 62 years (Figure S1). Hence, unprecedented heatwaves occurring for Lake Taihu in the summer of 2022 were rare, as evidenced by the highest annual average MAT, the maximum intensity, and the longest number of heatwave days.

Given that heatwaves are extreme climate events, we assessed meteorological factors to explore the characteristics of the 2022 summer. A total rainfall of 110.8 mm was observed from July to August for Lake Taihu, with the largest rainfall of 30.4 mm on July 15 and the second largest rainfall of 27.8 mm on August 27 (Figure 2b). Moreover, we calculated that negligible rainfall was experienced on 74.2% of days and that rainfall of less than 10 mm was experienced on 21.0% of days (Figure 2b). The wind speed ranged from 0.6 m/s on July 22 to 3.1 m/s on August 28, with an average of 1.7 ± 0.5 m/s. In general, wind speeds in summer 2022 were lower than the 3.0 m/s threshold of cyanobacteria bloom formation on Lake Taihu except for on August 28 (Cao et al., 2006; Qin et al., 2018; Webster and Hutchinson, 1994) (Figure 2b), suggesting a stable water column favoring cyanobacteria floating to the water surface. Marked PAR variation was observed during the 2022 summer from 7.2 w/s^2 on August 30 to 52.1 w/s^2 on August 8, with an average PAR of 37.5 ± 10.7 w/s^2 (Figure 2b). Furthermore, variance analysis demonstrated that the daily PAR, MAT, and sunshine hours during the heatwaves were significantly higher than those during non-heatwave days, while the daily wind speed demonstrated the opposite pattern (*Mann–Whitney U test,* $p < 0.01$) (Table S1). Hence, high temperature, strong PAR, low wind speed and low rainfall are the characteristics of heatwaves for Lake Taihu.

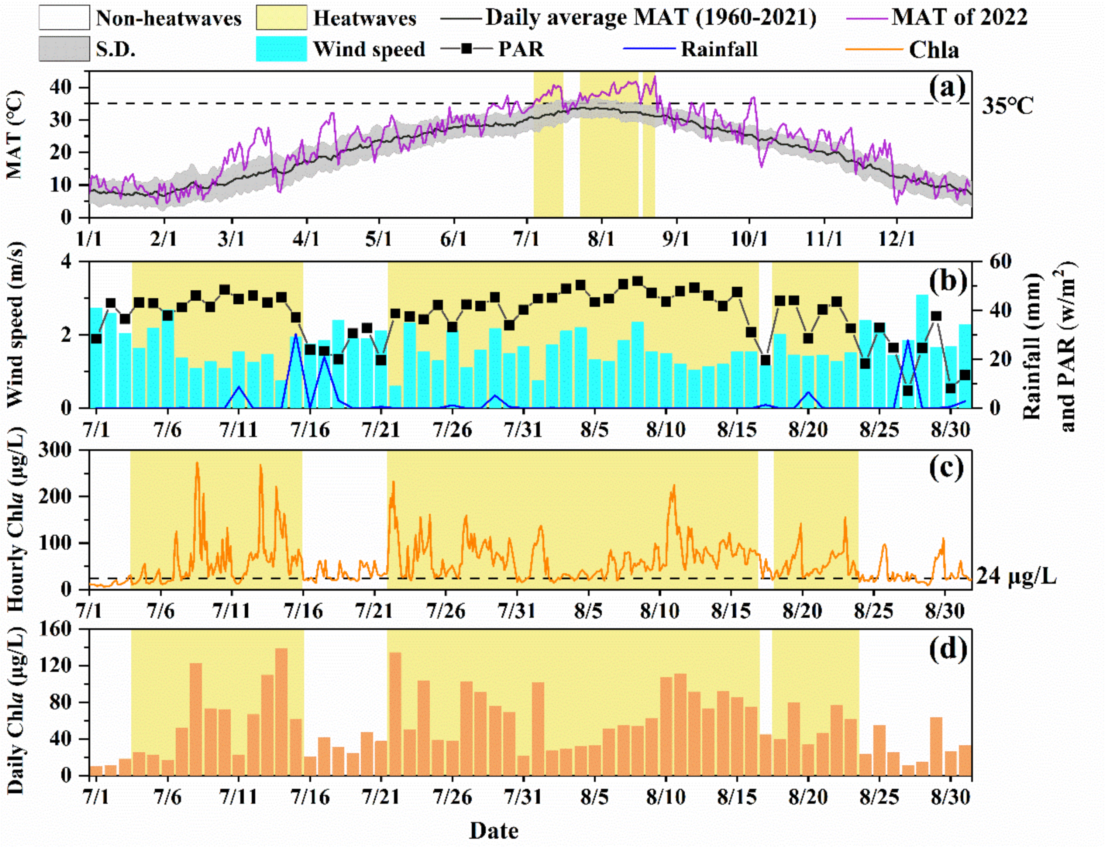


Figure 2. Long- and short-term variations in MAT, wind speed, rainfall, PAR and Chl*a* for Lake Taihu. Comparison of MAT in 2022 with climatological averages during 1960-2021 (a); daily variations in meteorological conditions during July and August 2022 (b); daily and hourly Chl*a* derived from GBPSs (c and d).

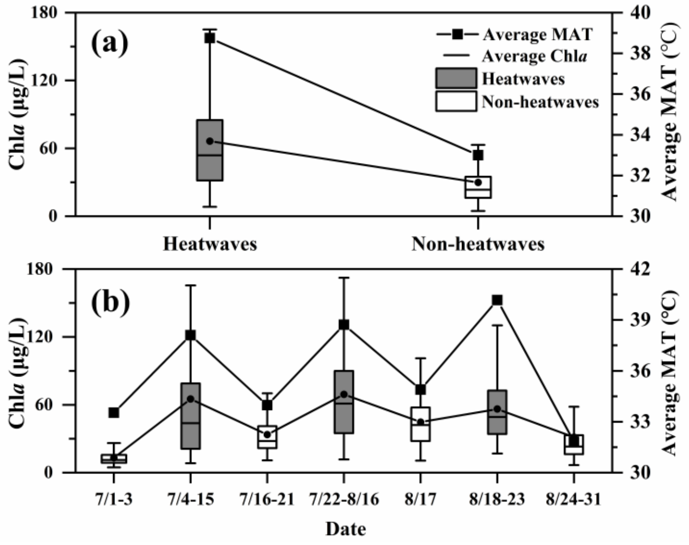


Figure 3 Comparison of average daily Chla and MAT during heatwaves and non-heatwaves periods (a) and during 3 individual heatwave events and 4 individual non-heatwaves (b).

3.3 Cyanobacteria bloom during the 2022 summer heatwave

The time series of hourly and daily averaged Chl*a* were generated from GBPSs using the developed Chl*a* model. Hourly Chl*a* exhibited variations from July to August from 6.2 to 272.9 μg/L, with an average value of 56.0 ± 42.9 μg/L (Figure 2c). High Chl*a* (above 24.0 μg/L) indicated that Lake Taihu experienced frequent high cyanobacteria concentrations (Figure 2c). Overall, there was no significant continuous trend of Chl*a* during the observation period, with the highest daily Chl*a* value of 138.2 μg/L on July 14 during heatwaves and the lowest daily Chl*a* value of 10.1 μg/L on July 1 during non-heatwaves (Figure 2d). However, a clear increasing tendency in daily Chl*a* was observed from the first non-heatwave to the first heatwaves (July 1 to July 15) (Figure 2d). In addition, the average daily Chl*a* showed a 123% increase during heatwaves from the Chl*a* concentrations during non-heatwave days, with average values of 66.4 ± 49.4 μg/L and 29.8 ± 21.2 μg/L, respectively (Figure 3a). Specifically, the daily Chl*a* of three heatwaves was significantly higher than that of four non-heatwaves (Mann–Whitney U test, $p < 0.05$). The three Chl*a* peak values were 65.1 ± 64.6 μg/L from July 4-15, 69.3 ± 44.5 μg/L from July 22-August 16, and 56.3 ± 28.9 μg/L from August 18-23 during heatwaves, while the four daily Chl*a* values were 13.0 ± 6.5 μg/L from July 1-3, 33.7 ± 16.2 μg/L from July 16-21, 44.8 ± 21.5 μg/L from August 17, and 31.3 ± 24.5 μg/L from August 24-31 during non-heatwaves (Figure 3b). Moreover, the field results showed a maximum daily wind speed of 3.08 m/s with a low Chl*a* of 14.6 μg/L on August 28 during non-heatwaves and a minimum daily wind speed of 0.6 m/s with a high Chl*a* of 134 μg/L on July 22 during heatwaves (Figure 2b and 2d). These results indicated the positive response of cyanobacterial blooms to heatwaves.

3.4 Effect of heatwaves on cyanobacteria bloom

To quantitatively explore the effects of heatwaves on cyanobacterial blooms, significant correlation coefficients of 0.83 and -0.78 were counted between average daily Chl*a* and MAT and wind speed during 3 heatwaves and 4 non-heatwaves ($p < 0.01$) (Figures 4a and 4b). In addition, there was a strong and significant correlation between average daily Chl*a* and average daily PAR ($r = 0.91$, $p < 0.05$), except for the first non-heatwave with maximum wind speed, but the overall correlation was not significant ($r = 0.54$, $p > 0.05$) (Figure 4c). Additionally, the product of PAR and MAT divided by wind speed was used to further assess the comprehensive compound effect of heatwaves and was significantly correlated with average daily Chl*a* ($R^2 = 0.79$, $p < 0.01$) (Figure 4d). The results suggested that the 2022 extreme summer heatwaves with high air temperatures and strong PAR but low wind speed would have increased harmful cyanobacterial blooms for Lake Taihu.

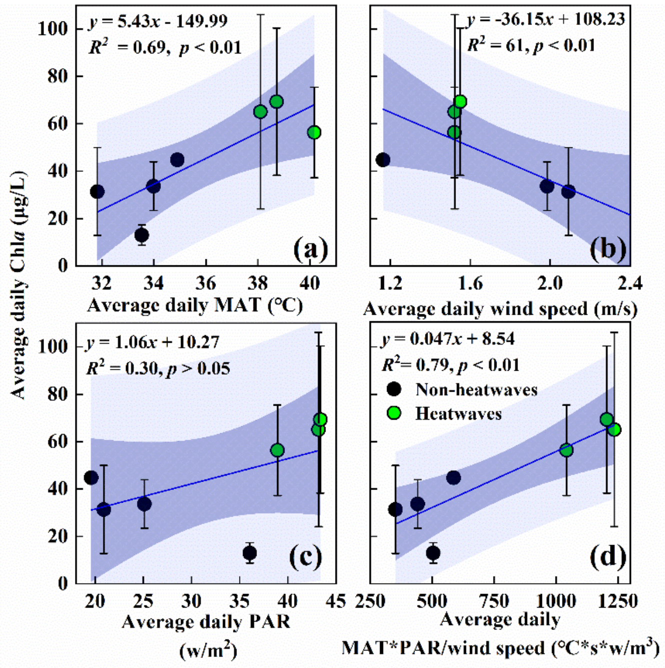


Figure 4 The linear relationship between average daily Chl*a* and MAT (a), wind speed (b), PAR (c) and the compound index calculated with MAT, PAR and wind speed (d) during three heatwave and four non-heatwave periods. The solid lines indicate the linear fit to the data, and the dark and light blue colors illustrate the 95% confidence interval and the prediction interval of the linear fit, respectively.

To further explore the potential mechanism of heatwaves promoting cyanobacteria blooms, we analyzed the daily Chl*a* and daily MAT, wind speed and PAR from July 1 to August 31 (Figure 5). Significant positive correlations were observed between daily Chl*a* and daily MAT ($R^2 = 0.30$, $p < 0.01$) and daily PAR ($R^2 = 0.20$, $p < 0.01$) (Figure 5a and 5b), while a significant negative correlation between daily Chl*a* and daily wind speed ($R^2 = 0.47$, $p < 0.01$) was found (Figure 5c), indicating that Chl*a* increased with increasing MAT and PAR, as well as with decreasing wind speed in the summer of 2022. Due to the simultaneous occurrence of high temperature, strong PAR, and low wind speed during heatwaves, the compound effect of heatwaves on cyanobacteria blooms was explored. The significant linear correlation between the daily compound index of MAT, PAR and wind speed and daily Chl*a* with the highest R^2 value of 0.58 suggested that the variation in Chl*a* could mainly be attributed to the compound effect of MAT, PAR and wind speed (Figure 5d). This explained the low daily Chl*a* during heatwaves, similar to that of non-heatwaves in Figure 2c-2d.

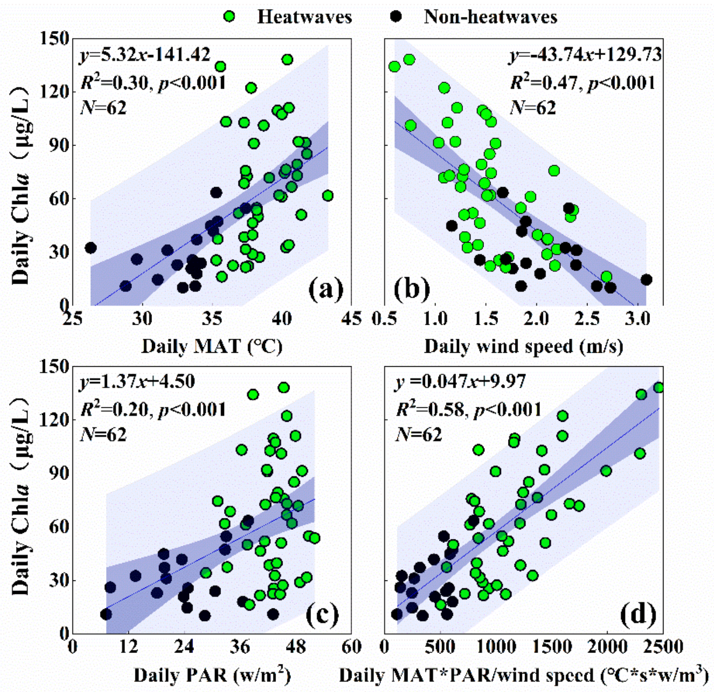


Figure 5 The linear relationships between daily Chla and daily MAT (a), wind speed (b), PAR (c) and the compound index calculated by daily MAT, PAR and wind speed (d).

4 Discussion

4.1 Increasing heatwaves for Lake Taihu

In the summer of 2022, unprecedented heatwaves lasting 44 days were observed in the eutrophic shallow Lake Taihu, with a daily average MAT 6.6 °C higher than the climatological averages from 1960 to 2021. This was markedly higher than the history record during the hottest summer of 2013 in Eastern China (Sun et al., 2014). In the past 63 years, there were significant increases in the average MAT, MAT, number of heatwave days and the average daily heatwave intensity from July to August, with increase rates of 0.30 °C, 0.48 °C, 2.6 d and 0.18 °C per decade, respectively ($p < 0.01$) (Figure S1). The annual average MAT for Taihu Lake has increased significantly ($R^2 = 0.58$, $p < 0.05$), especially since the 1980s, with an average temperature increase of 0.7 °C per decade (Figure S2a).

Increases in the frequency, duration, and intensity of marine and lake heatwaves have been recorded as well as projected (Frolicher et al., 2018; Oliver et al., 2018; Woolway et al., 2021a). For example, studies of China's marginal seas have revealed that the duration, frequency, and intensity of heatwaves increased significantly from 1982 to 2018, especially in the Bohai Sea, where values were twice the global average (Yao et al., 2020). A prediction based on global lake data showed that the intensity and duration of lake heatwaves would increase by 46% and 11-fold at the end of the 21st century under a high-greenhouse gas emission scenario (Representative Concentration Pathway 8.5) (Woolway et al., 2021b). Hence, Lake Taihu is projected to be exposed to increasingly frequent and intense lake heatwaves due to the high consistency between air temperature and water temperature (Figure S2b and S2c).

4.2 Potential driving mechanisms of summer heatwaves on cyanobacterial blooms

Although it has been accepted that climate warming can intensify and magnify cyanobacterial blooms in eutrophic freshwater (Huisman et al., 2018; Shi et al., 2019), direct evidence of the effects of heatwaves on harmful cyanobacterial blooms is sparse, and the driving mechanisms are unclear. Studies on temperature and cyanobacteria have revealed that their relationships are complex and are not always simply linear, which may be attributed to nutrients (Bonilla S, 2023; Reinl et al., 2023). Previous studies have shown that the impact of heatwaves on cyanobacteria blooms is subject to background nutrient levels, with a weak impact in oligotrophic water but significantly aggravating cyanobacteria blooms in eutrophic water (Hayashida et al., 2020; Woolway et al., 2021c). High levels of total nitrogen (2.0 mg/L) and total phosphorus (0.10 mg/L) for Lake Taihu are conducive to the growth of cyanobacteria blooms (Qin et al., 2010; Xu et al., 2015). Therefore, extreme heatwaves may directly and indirectly favor harmful cyanobacterial blooms by the particularity of meteorological conditions to further amplify cyanobacteria blooms in eutrophic water, such as that of Lake Taihu.

High temperatures during heatwaves can directly and selectively favor the growth of cyanobacterial blooms, as supported by significant correlations between daily MAT and daily Chl*a* (Figure 4a and 5a). Temperature is an important factor affecting the growth and dynamics of phytoplankton in eutrophic lakes (Huisman et al., 2018; Paerl and Huisman, 2008; Qin et al., 2015). Compared with other phytoplankton species, such as diatoms and dinoflagellates, with maximum growth rates of approximately 20 ℃, cyanobacterial growth is easily promoted by high temperatures due to their maximum growth rate being at temperatures above 28-30 ℃ (Johnk et al., 2008; Paerl et al., 2011). High temperature enhances the stability of the water column and reduces vertical mixing, which is beneficial for buoyant cyanobacteria floating and forming dense surface cyanobacteria blooms (Johnk et al., 2008; Paerl and Huisman, 2008). In turn, the intense light absorbed by dense surface cyanobacteria blooms has also been found to slightly increase the water temperature, further favoring cyanobacteria growth (Hense, 2007; Johnk et al., 2008). Hence, in the present study, high temperature partly explains the high synchronization between heatwaves and high Chl*a*, with a doubling of the Chl*a* concentrations compared to non-heatwave days (Figure 2c-2d and 3a-3b).

Apart from high temperatures, low wind speed and strong PAR accompanied by heatwaves are also conducive to the growth and accumulation of harmful cyanobacteria blooms, as reflected in the fact that daily Chl*a* significantly increased with increasing PAR and decreasing wind speed in the summer of 2022 (Figure 4b-4c and 5b-5c). In large shallow lakes, wind speed is an important driving factor for inducing water mixing, which affects the vertical distribution of cyanobacteria by mixing the water column (Blottière et al., 2013; Cao et al., 2006; Moreno-Ostos et al., 2008; Qi et al., 2018). At low wind speeds and quiescent conditions with less disturbance and mixing, buoyant cyanobacteria float upward more easily in the water column via gas vesicles and gather on the surface, where they occupy the dominant niche for light and CO_2 competition (Huisman et al., 2004; Sandrini et al., 2016; Yu et al., 2019). Notably, during the extreme heatwaves of Lake Taihu in 2022, the maximum daily wind speed of 2.7 m/s was below the threshold of bloom aggregation (3.0 m/s) (Cao et al., 2006; Qin et al., 2018; Webster and Hutchinson, 1994) (Figure 2b), which provided ideal growth and accumulation conditions for harmful cyanobacteria blooms. Hence, compared with non-heatwaves, during heatwaves a more stable water column caused by low wind during heatwaves promoted the aggregation of cyanobacteria on the surface (Table S1). At the same time, the higher temperature, higher PAR and longer sunshine hours during heatwaves (Table S1) provided sufficient light energy and growth times, stimulating photosynthesis and biomass accumulation of cyanobacteria and consequently further amplifying the intensity of cyanobacteria blooms compared to the non-heatwave period (Zhang et al., 2012) (Figure 5c).

Moreover, heatwaves also indirectly affect harmful cyanobacteria blooms by changing the physical and chemical characteristics of the water body (Zhan et al., 2021). Low wind speed and high water temperature during heatwaves not only promote a more stable stratification of the water column with less vertical mixing but also reduce the dissolved oxygen (DO) (Huisman et al., 2018). Although periodically stable thermal stratification has seldom been observed in large shallow lakes, temporary stratification and water column stability were found to be markedly enhanced due to the synergistic effects of increasing water temperatures and low wind speeds for

Lake Taihu (Deng et al., 2018). Observations and experiments for Lake Taihu have revealed that the low DO at the lake bottom caused by a long stable water column with low wind speed enhances the release of phosphorus from the sediment, especially in summer (Deng et al., 2018). In turn, high phosphorus from the sediment supported cyanobacteria bloom growth (Shi et al., 2020). Finally, the positive feedback triggered by heatwave conditions promoted cyanobacteria bloom expansion by enhancing internal nutrient cycling (Chen et al., 2018; Deng et al., 2018; Huber et al., 2012; Shi et al., 2020) (Figure 6). Hence, heatwaves indirectly promote harmful cyanobacteria blooms by enhancing the stability of the water column and by promoting phosphorus release from sediments due to reducing DO.

In the present study, heatwaves promoted cyanobacterial blooms, as directly evidenced by the significant linear correlation between daily Chla and the product of MAT and PAR divided by wind speed ($R^2 = 0.58$, $p < 0.01$) (Figure 5d). Specifically, taken together, the abnormally high temperatures, higher PAR and low wind speed during the 2022 heatwaves provided ideal growth and surface aggregation conditions for cyanobacteria by boosting the optimal growth and light availability and enhancing the stability of the water column and nutrient release from the sediment (Figure 6). Field videos and photographs of GBPSs provided evidence that summer heatwaves promoted harmful cyanobacteria blooms under warm and quiescent conditions (Figure S3). Several other studies have shown that heatwaves promote harmful cyanobacteria blooms in eutrophic waters through direct and indirect temperature effects in combination with decreased wind speed and rainfall, increased sunshine hours and enhanced nutrient release from the sediment (Blagrave et al., 2022; Hayashida et al., 2020; Huber et al., 2012; Zhan et al., 2021). For example, the summer heatwaves of 2003, which made for one of the hottest summers ever recorded in

Europe, promoted blooms of the harmful cyanobacterium *Microcystis* in Lake Nieuwe Meer, a eutrophic lake in the Netherlands (TN: 2.40 mg/L, TP: 0.26 mg/L in 2006) (Johnk et al., 2008).

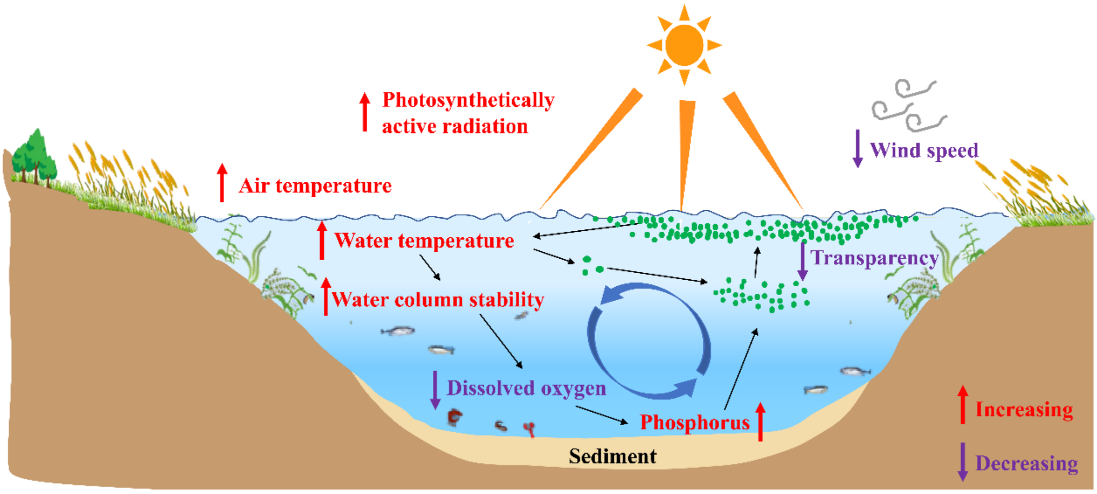


Figure 6 An illustration of the mechanism by which summer heatwaves boost cyanobacterial blooms by coupling suitable growth temperatures, enhancing the stability of the water column and nutrient release from the sediment.

4.3 Other effects and future work

Given the projected increase in the frequency, intensity, and duration of heatwaves under future climate change (Woolway et al., 2021a), heatwaves will have other profound negative effects on the structure, function, and ecosystem services of aquatic systems (Smale et al., 2019; Smith et al., 2021; Till et al., 2019; Tye et al., 2022). At the same time, eutrophication has become a primary ecological problem for more than 60% of the global inland waters covering an area of more than 25 km^2 (Ho et al., 2019; Wang et al., 2018), and even remote northern oligotrophic lakes have been reported to have cyanobacterial blooms (Favot et al., 2019; Pick, 2016). As an ecologically sensitive and vulnerable eutrophic lake, Lake Taihu will be exposed to heatwaves of higher duration, extent, and frequency with the future increase in temperatures and decrease in wind speed (Figure S1, S2 and S4), thus creating more challenges and risks. Hence, in the future, our priority should be to further reduce external nutrient inputs to diminish the basis of cyanobacterial bloom outbreaks. Second, systematic monitoring, prediction and early warning concerning heatwaves and harmful cyanobacteria blooms should be implemented to mitigate the impact of heatwaves on lake ecosystems and to reduce the risk of harmful cyanobacteria blooms under climate change. Finally, it is necessary to explore the impact of past and present heatwaves on harmful cyanobacteria blooms and the ecosystem evolution of lakes with different nutrient levels based on extensive and long-term data to formulate strategies to address and adapt to climate change.

5 Conclusions

In this study, the unprecedented heatwaves of 2022 characterized by abnormally high temperature, strong PAR, low wind speed and little rainfall were recorded for Lake Taihu, with the longest duration of 44 days and an average daily MAT of 6.6 ℃ above the historical average (1960 to 2021). A novel high-frequency GBPSs system with a predeveloped Chl*a* model was validated with satisfactory validation accuracy for cyanobacteria bloom monitoring. Subsequently, the high synchronization between Chl*a* and high MAT, strong PAR and low wind speed as well as a significant increase of 123% for Chl*a* against non-heatwaves (*t* test, $p < 0.05$) directly revealed the facilitation of cyanobacteria blooms by heatwaves. Abnormally high air temperatures, strong PAR, and low wind speed during heatwaves provided ideal growth and surface aggregation conditions for cyanobacteria blooms by boosting the growth rate, enhancing the stability of the water column and increasing nutrient release from sediment. With heatwaves projected to increase with further climate warming, it is essential to continue to reduce the nutrient input of eutrophic lakes and improve prediction and early warning to reduce the risk of cyanobacteria blooms and ensure ecological and water security.

Declaration of conflicts competing interest

The authors declare that there are no competing financial interests or personal relationships that may influence the work reported in this paper.

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Appendix A. Supplementary material

Data availability statement

The data that support the finding of this study are available from the corresponding author upon reasonable request.

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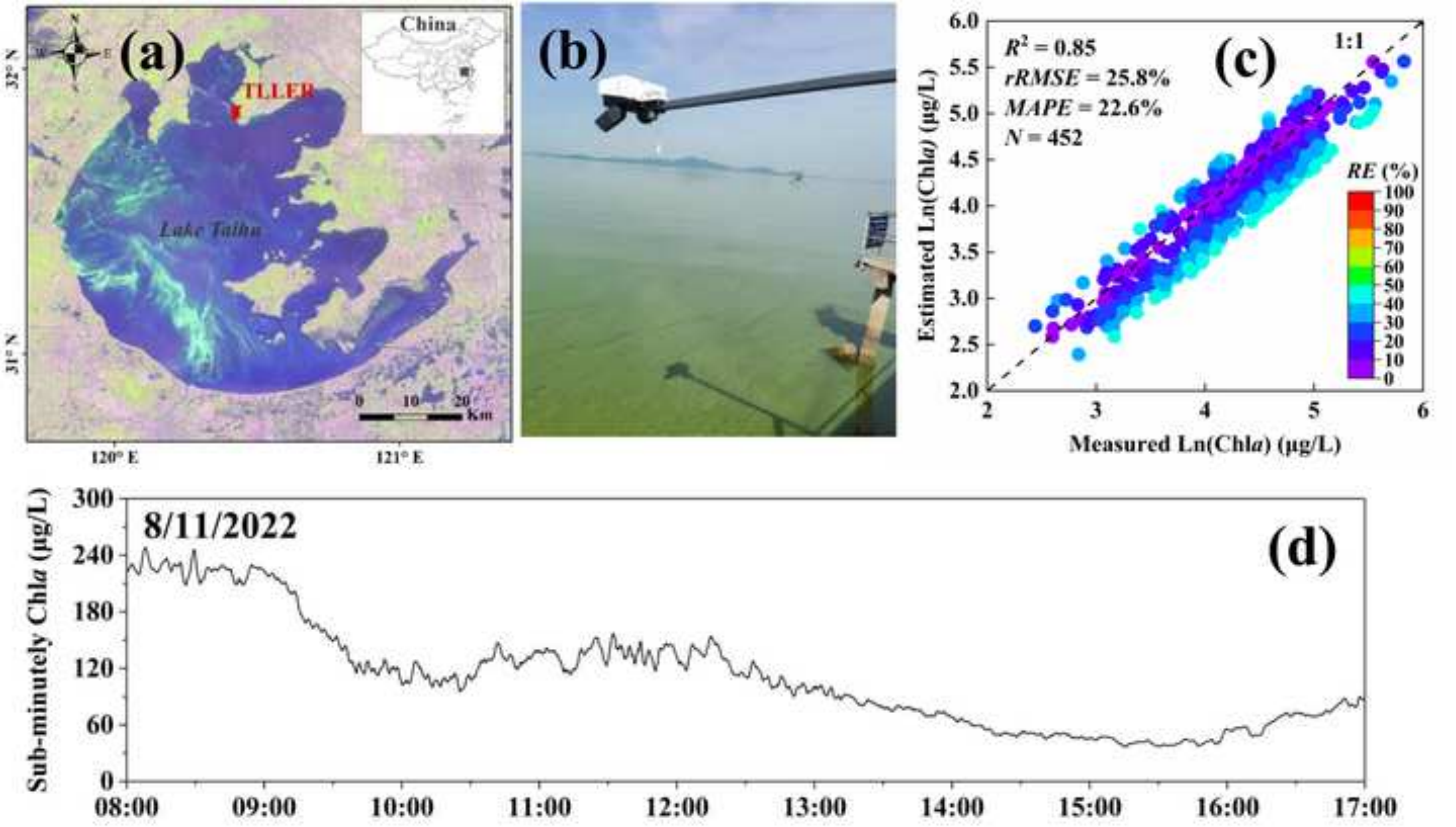
Table S1 Daily average values of meteorological factors during non-heatwave and heatwave in Lake Taihu region from 1960 to 2022.

	Meteorological factors	Non-heatwave	Heatwave
2022	Daily MAT* (℃)	33.0 ± 2.7	38.8 ± 2.0
	Wind speed* (m/s)	2.1 ± 0.5	1.5 ± 0.5
	Rainfall (mm)	3.2	1.2
	PAR* (w/s^2)	24.8 ± 9.9	42.7 ± 5.3
1960-2021	Daily MAT* (℃)	31.4 ± 2.9	36.6 ± 1.2
	Rainfall* (mm)	6.6 ± 15.8	1.0 ± 4.3
	Wind speed* (m/s)	2.9 ± 1.4	2.5 ± 0.9
	Sunshine hours* (h)	6.2 ± 4.3	10.0 ± 2.4

* represents a significant difference in meteorological factor between heatwaves and non-heatwaves under t-test and $p < 0.05$.


(a)
N
W
E
S
TLLER
China
Lake Taihu
0 10 20 Km
32° N
31° N
120° E
121° E
(b)
(c)
R^2 = 0.85
rRMSE = 25.8%
MAPE = 22.6%
N = 452
1:1
RE (%)
100
90
80
70
60
50
40
30
20
10
0
Estimated Ln(Chla) (μg/L)
Measured Ln(Chla) (μg/L)
6.0
5.5
5.0
4.5
4.0
3.5
3.0
2.5
2.0
2
3
4
5
6
8/11/2022
(d)
Sub-minutely Chla (μg/L)
300
240
180
120
60
0
08:00
09:00
10:00
11:00
12:00
13:00
14:00
15:00
16:00
17:00

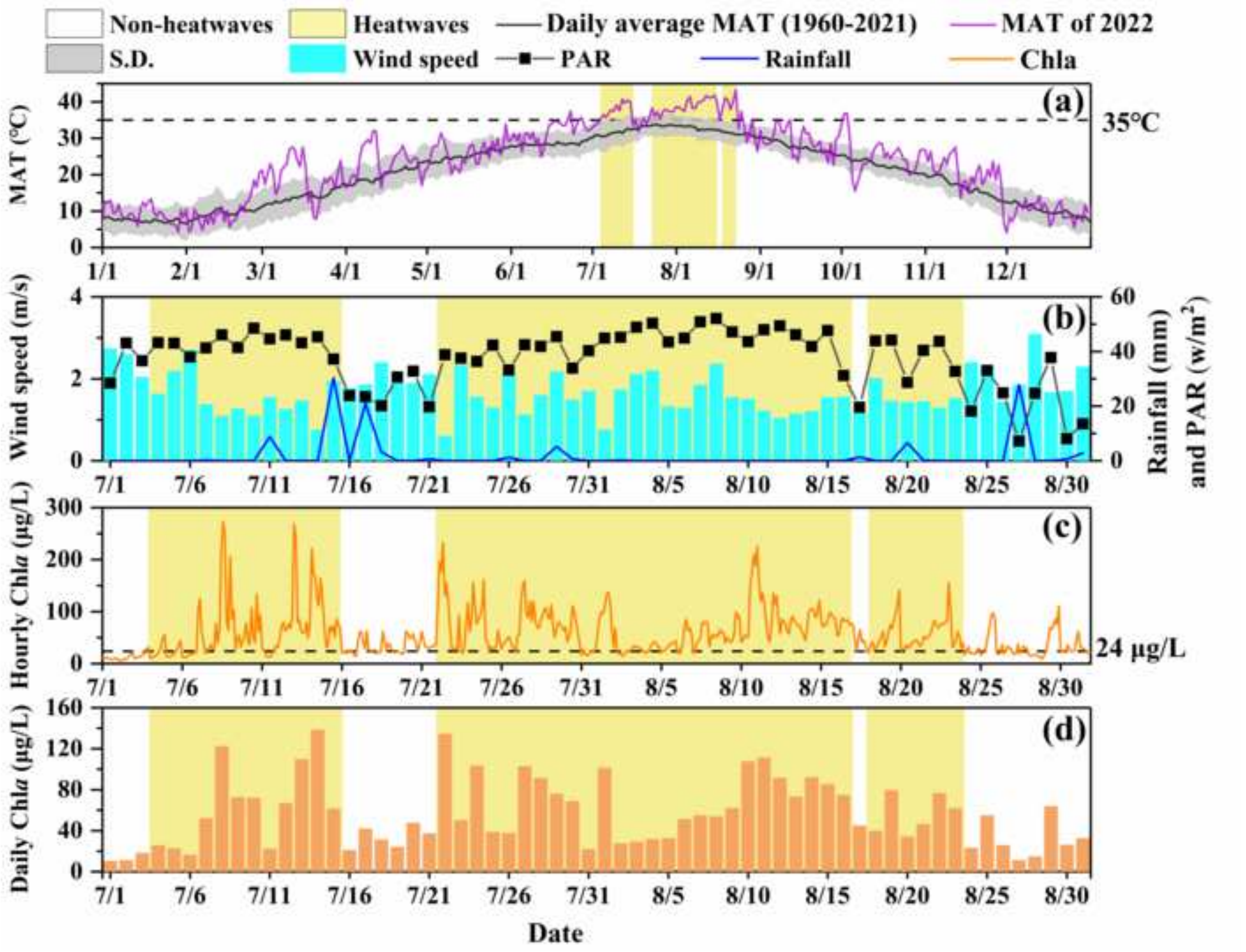
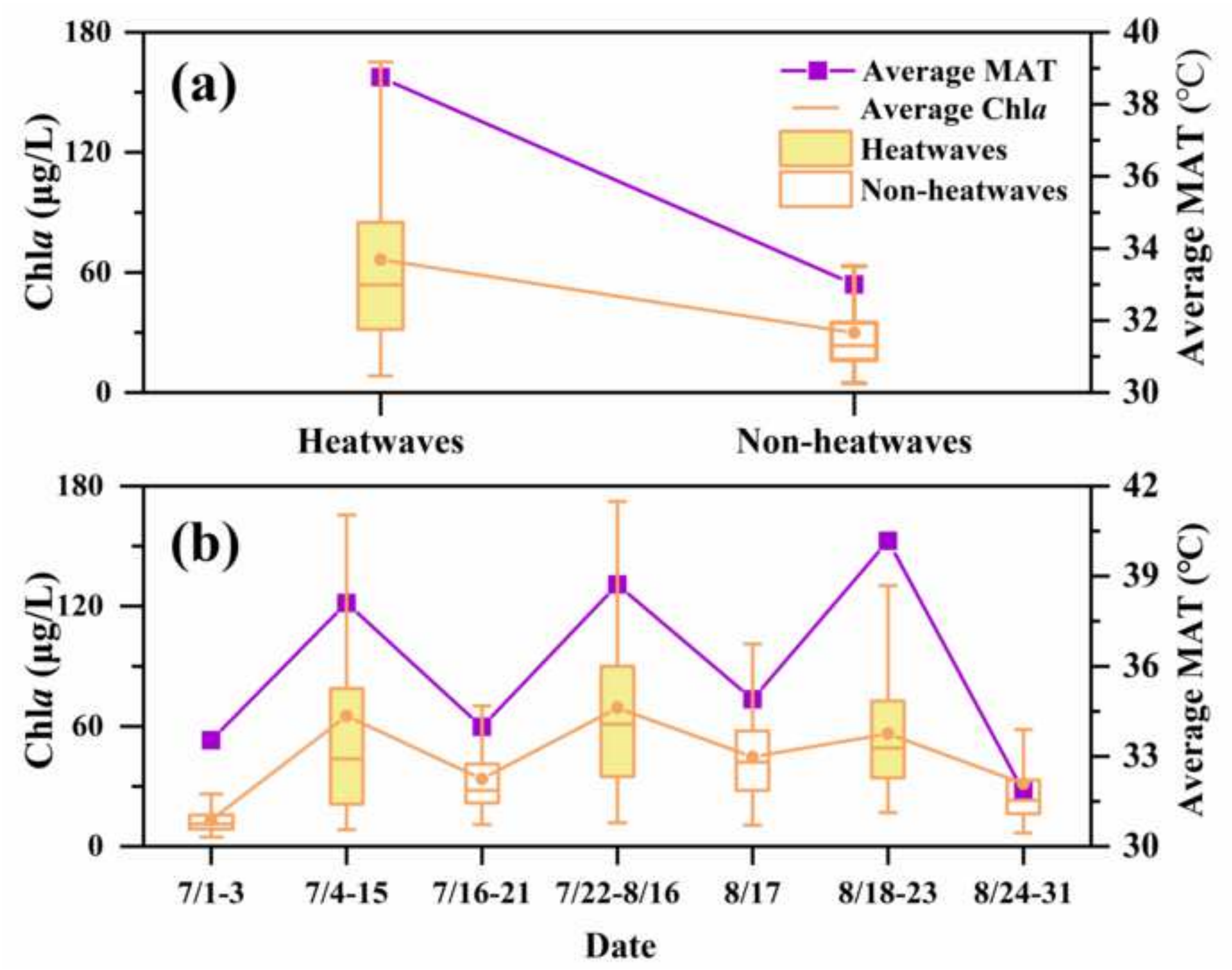

Non-heatwaves
Heatwaves
Daily average MAT (1960-2021)
MAT of 2022
S.D.
Wind speed
PAR
Rainfall
Chla
(a)
MAT (°C)
35°C
0
10
20
30
40
1/1
2/1
3/1
4/1
5/1
6/1
7/1
8/1
9/1
10/1
11/1
12/1
(b)
Wind speed (m/s)
Rainfall (mm) and PAR (w/m²)
0
2
4
0
20
40
60
(c)
Hourly Chl*a* (μg/L)
24 μg/L
0
100
200
300
(d)
Daily Chl*a* (μg/L)
0
40
80
120
160
7/1
7/6
7/11
7/16
7/21
7/26
7/31
8/5
8/10
8/15
8/20
8/25
8/30
Date

Figure 3


(a)
Chl*a* (μg/L)
180
120
60
0
40
38
36
34
32
30
Average MAT (°C)
Average MAT
Average Chl*a*
Heatwaves
Non-heatwaves
Heatwaves
Non-heatwaves
(b)
Chl*a* (μg/L)
180
120
60
0
42
39
36
33
30
Average MAT (°C)
7/1-3
7/4-15
7/16-21
7/22-8/16
8/17
8/18-23
8/24-31
Date

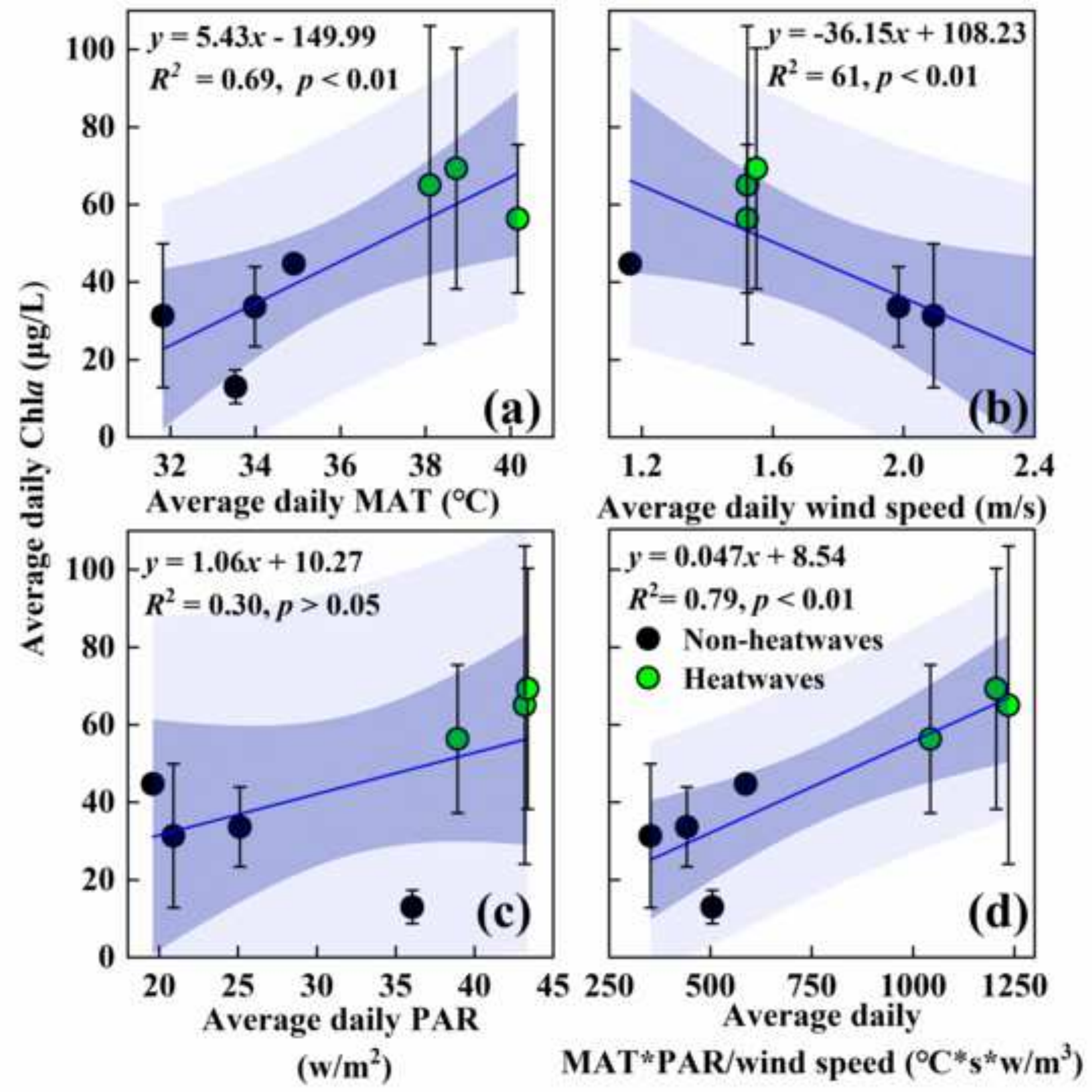
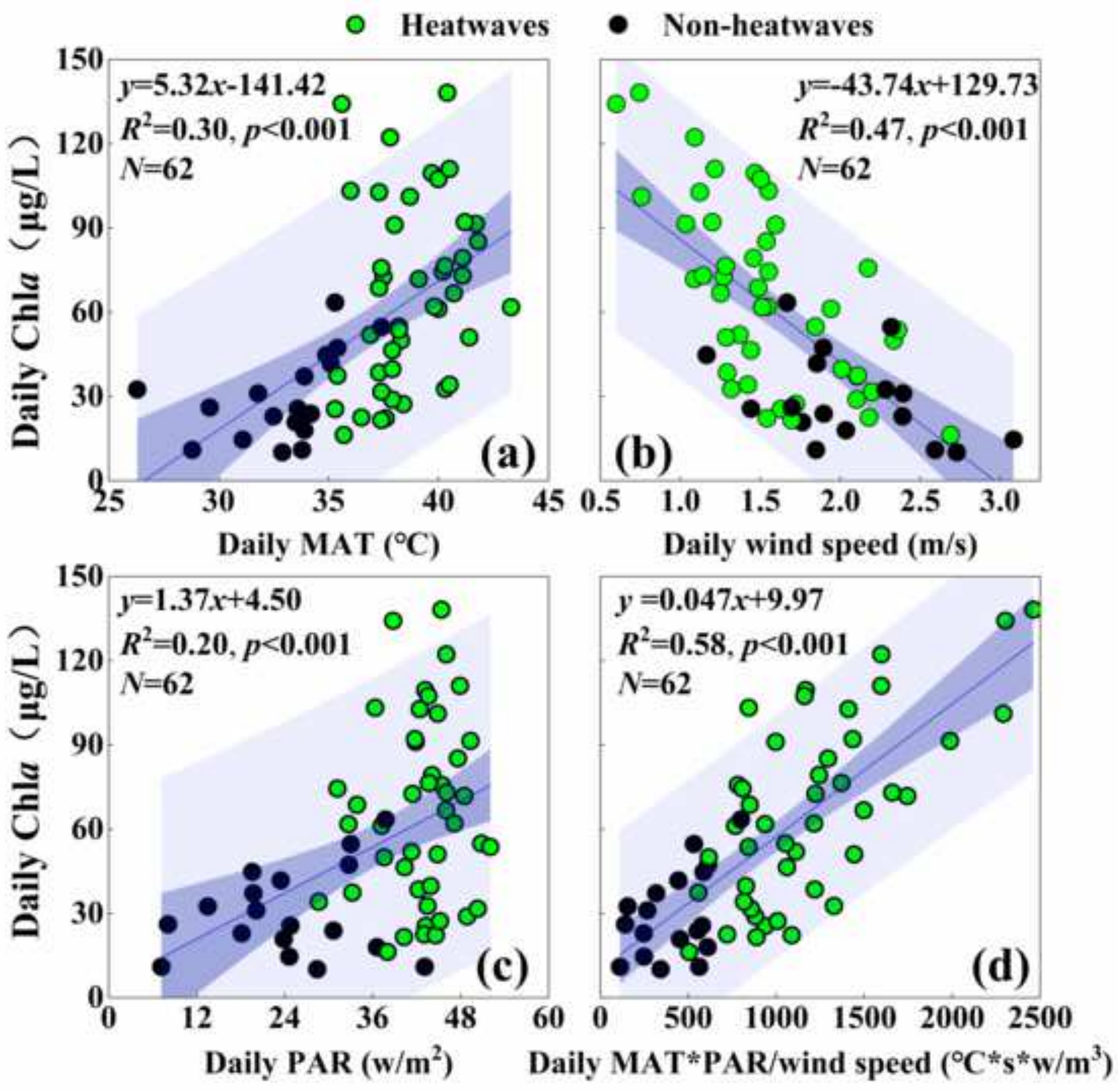
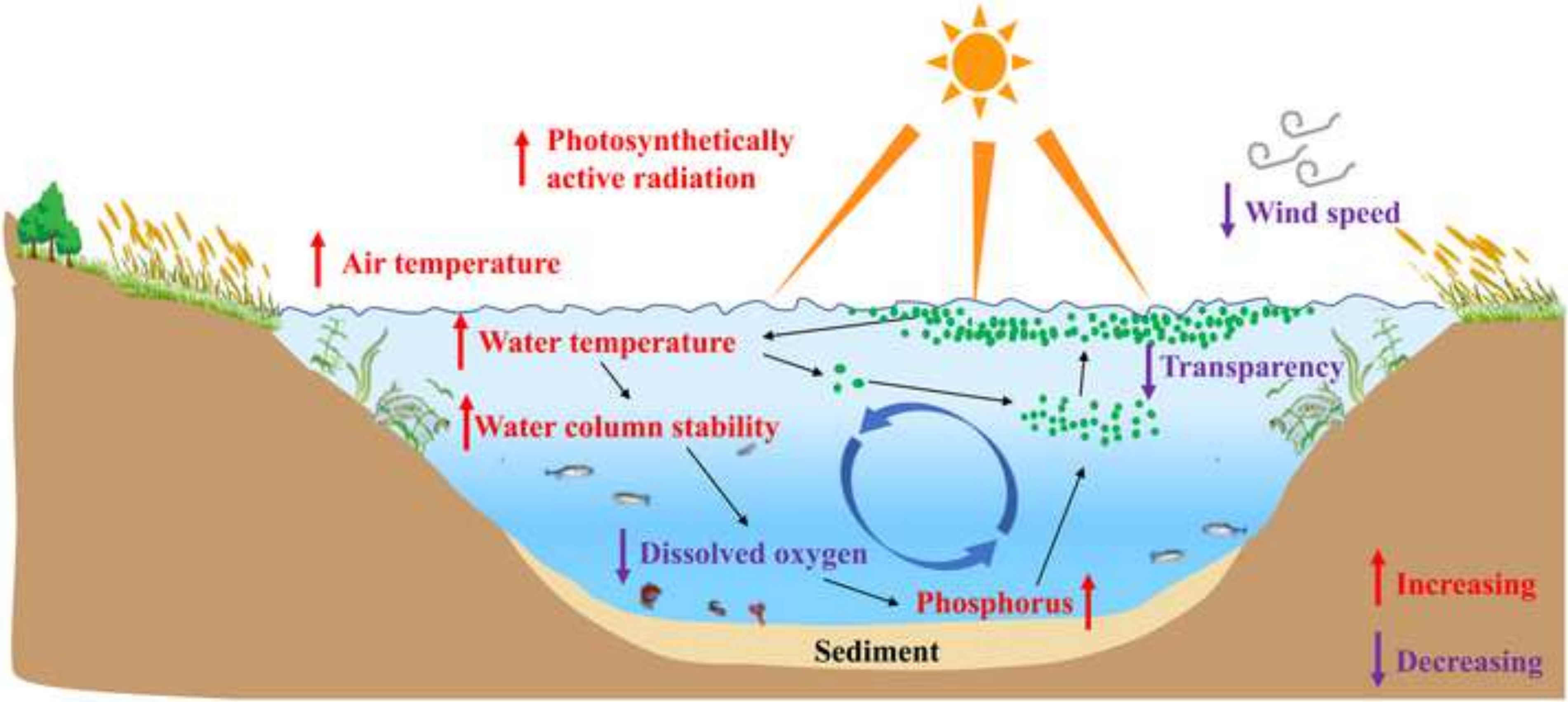
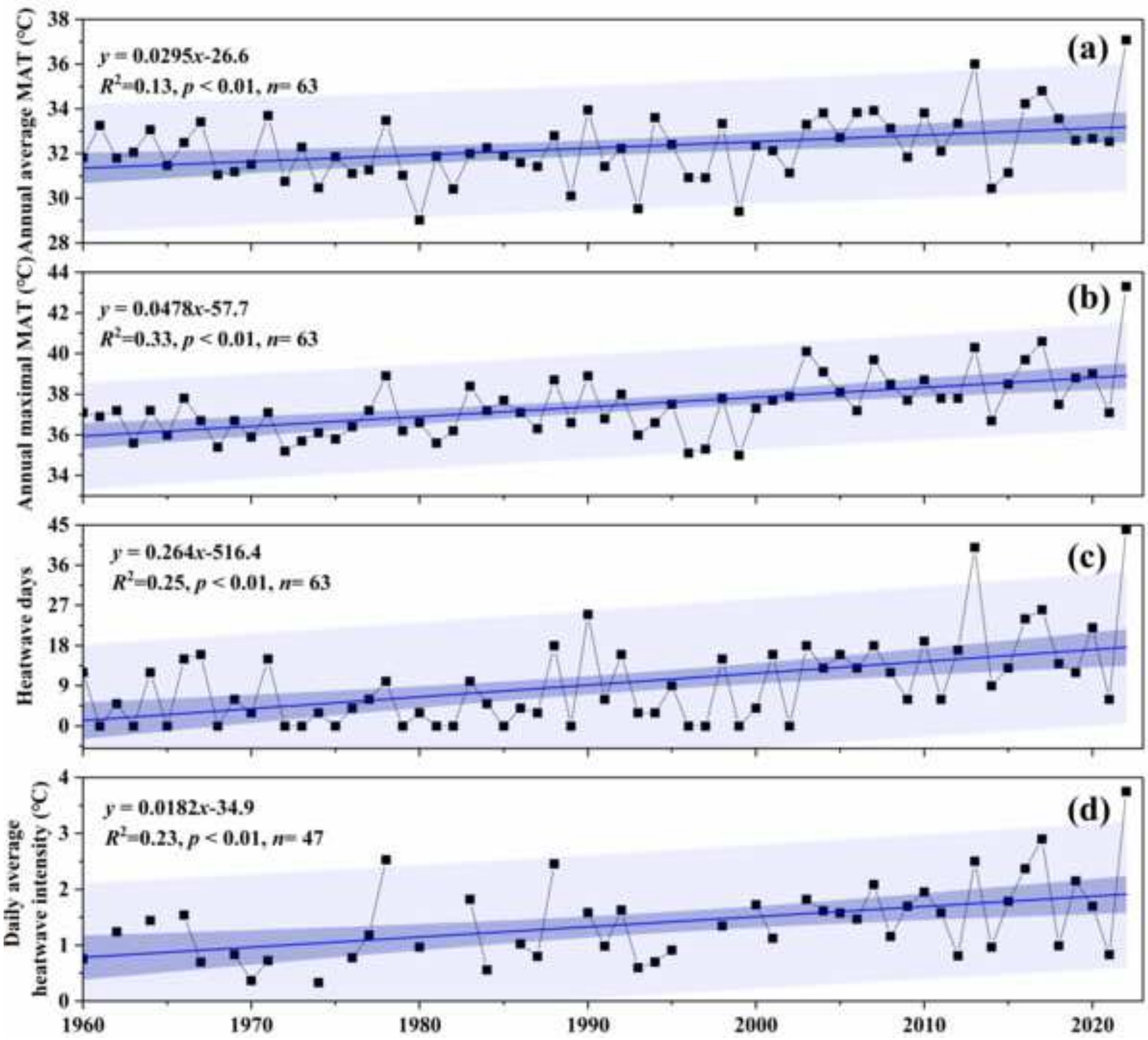
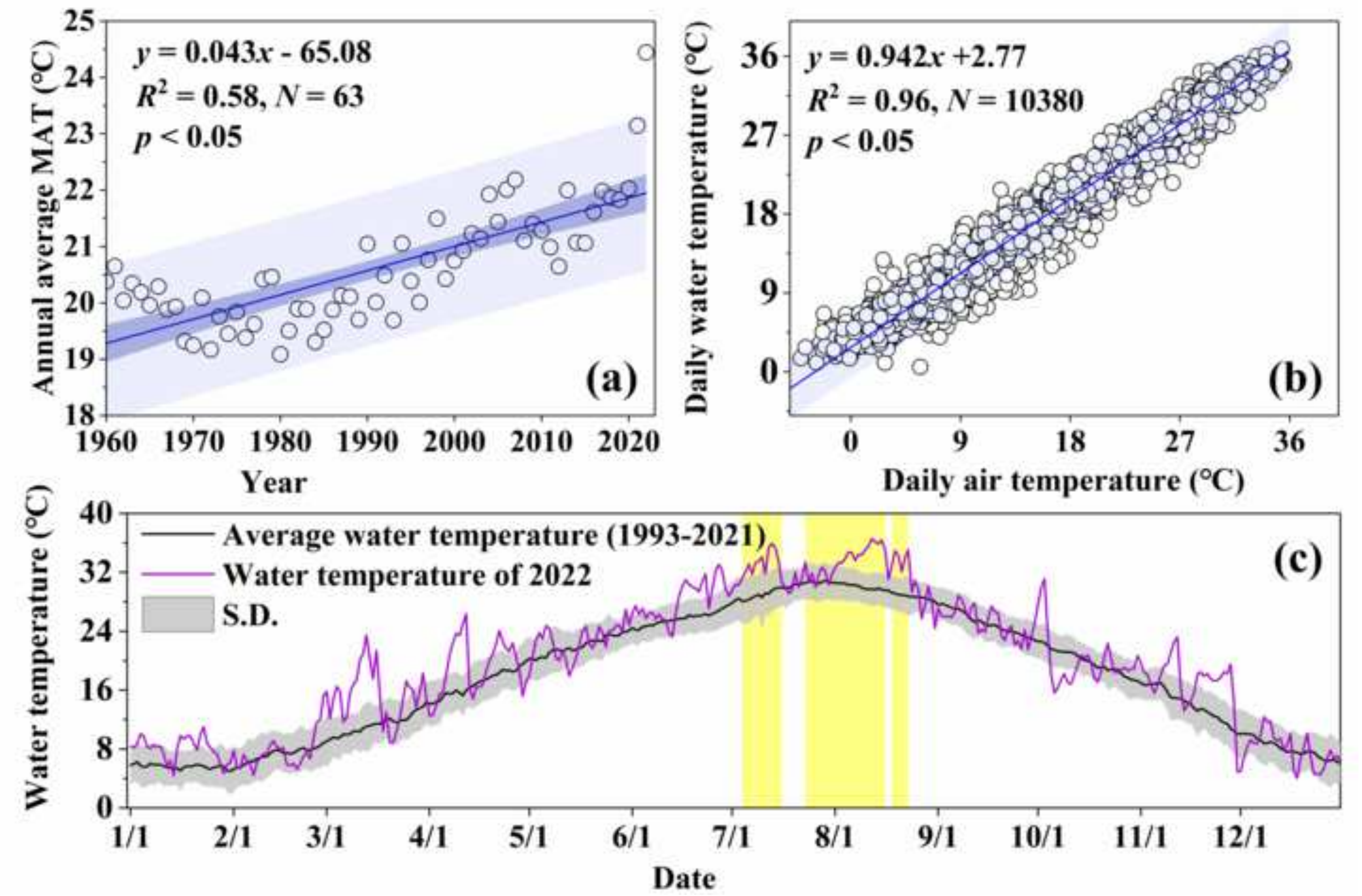

Average daily Chla (μg/L)
y = 5.43x - 149.99
R² = 0.69, p < 0.01
(a)
Average daily MAT (°C)
y = -36.15x + 108.23
R² = 61, p < 0.01
(b)
Average daily wind speed (m/s)
y = 1.06x + 10.27
R² = 0.30, p > 0.05
(c)
Average daily PAR (w/m²)
y = 0.047x + 8.54
R²= 0.79, p < 0.01
Non-heatwaves
Heatwaves
(d)
Average daily MAT*PAR/wind speed (°C*s*w/m³)
0
20
40
60
80
100
32
34
36
38
40
1.2
1.6
2.0
2.4
20
25
30
35
40
45
250
500
750
1000
1250

Figure 5


● Heatwaves
● Non-heatwaves
y=5.32x-141.42
R^2=0.30, p<0.001
N=62
(a)
Daily Chl$a$ （μg/L）
Daily MAT (°C)
0
30
60
90
120
150
25
30
35
40
45
y=-43.74x+129.73
R^2=0.47, p<0.001
N=62
(b)
Daily wind speed (m/s)
0.5
1.0
1.5
2.0
2.5
3.0
y=1.37x+4.50
R^2=0.20, p<0.001
N=62
(c)
Daily Chl$a$ （μg/L）
Daily PAR (w/m^2)
0
12
24
36
48
60
y =0.047x+9.97
R^2=0.58, p<0.001
N=62
(d)
Daily MAT*PAR/wind speed (°C*s*w/m^3)
0
500
1000
1500
2000
2500


Photosynthetically active radiation
Wind speed
Air temperature
Water temperature
Transparency
Water column stability
Dissolved oxygen
Phosphorus
Sediment
Increasing
Decreasing


Annual average MAT (°C)
38
36
34
32
30
28
(a)
y = 0.0295x-26.6
R²=0.13, p < 0.01, n= 63
Annual maximal MAT (°C)
44
42
40
38
36
34
(b)
y = 0.0478x-57.7
R²=0.33, p < 0.01, n= 63
Heatwave days
45
36
27
18
9
0
(c)
y = 0.264x-516.4
R²=0.25, p < 0.01, n= 63
Daily average heatwave intensity (°C)
4
3
2
1
0
(d)
y = 0.0182x-34.9
R²=0.23, p < 0.01, n= 47
1960
1970
1980
1990
2000
2010
2020


y = 0.043x - 65.08
R² = 0.58, N = 63
p < 0.05
(a)
Annual average MAT (°C)
25
24
23
22
21
20
19
18
1960
1970
1980
1990
2000
2010
2020
Year
y = 0.942x +2.77
R² = 0.96, N = 10380
p < 0.05
(b)
Daily water temperature (°C)
36
27
18
9
0
Daily air temperature (°C)
Average water temperature (1993-2021)
Water temperature of 2022
S.D.
(c)
Water temperature (°C)
40
32
24
16
8
0
1/1
2/1
3/1
4/1
5/1
6/1
7/1
8/1
9/1
10/1
11/1
12/1
Date

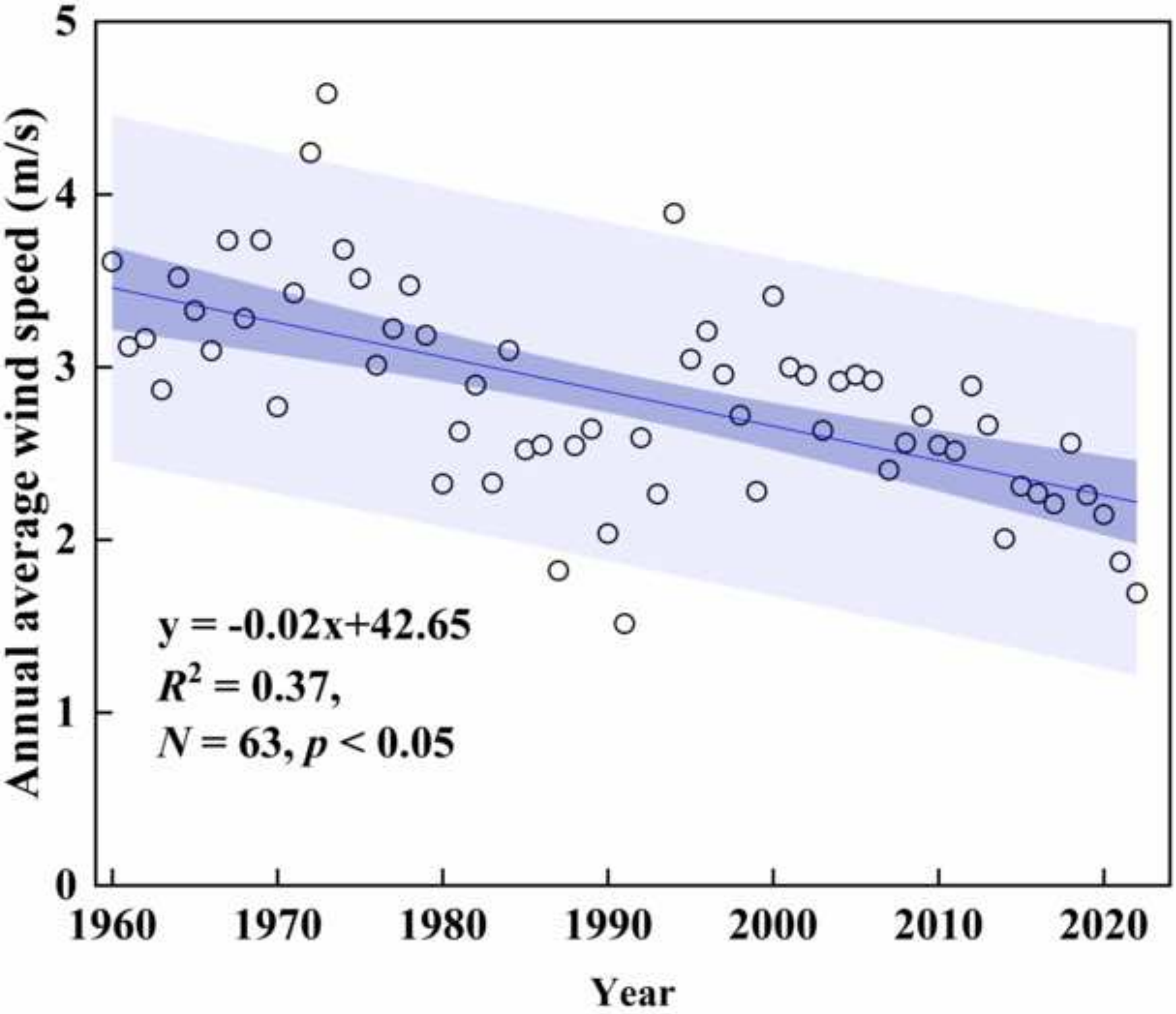

Annual average wind speed (m/s)
5
4
3
2
1
0
1960
1970
1980
1990
2000
2010
2020
Year
y = -0.02x+42.65
$R^2 = 0.37$,
$N = 63, p < 0.05$

Figure s3


7/17/2022
Non-heatwave
7/18/2022
Non-heatwave
7/19/2022
Non-heatwave
7/22/2022
Heatwave
7/24/2022
Heatwave
7/25/2022
Heatwave

Declaration of interests

☒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.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Authors Contributions Statement

Na Li: Investigation, data curation, software, visualization, methodology, writing - original draft， formal analusis

Yunlin Zhang: Conceptualization, supervision, Writing - review & editing, funding acquisition

Yibo Zhang: Software, writing - review & editing, supervision, funding acquisition

Kun Shi: Resources, funding acquisition, supervision

Haiming Qian: Investigation, data curation

Huayin Yang: Investigation, data curation

Yongkang Niu: Investigation, data curation

Boqiang Qin: Resources

Guangwei Zhu: Resources

R. Iestyn Woolway: Writing - review & editing

Erik Jeppesen: Writing - review & editing, funding acquisition

All authors have read and approved the submitted manuscript.