



Shorter blooms expected with longer warm periods under climate change: an example from a shallow meso-eutrophic Mediterranean lake

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Abstract Satellite data from the Climate Change Initiative (CCI) lakes project were used to examine the influence of climate on chlorophyll-a (Chl-a). Non-parametric multiplicative regression and machine learning were used to explain Chl-a concentration trend and dynamics. The main parameters of importance were seasonality, interannual variation, lake level, water temperature, the North Atlantic Oscillation, and antecedent rainfall. No evidence was found for an earlier onset of the summer phytoplankton

bloom related to the earlier onset of warmer temperatures. Instead, a curvilinear relationship between Chl-a and the temperature length of season above 20°C (LOS) was found with longer periods of warmer temperature leading to blooms of shorter duration. We suggest that a longer period of warmer temperatures in the summer may result in earlier uptake of nutrients or increased calcite precipitation resulting in a shortening of the duration of phytoplankton blooms. The current scenario of increasing LOS of temperature with climate change may lead to an alteration of phytoplankton phenological cycles resulting in blooms of shorter duration in lakes where nutrients become

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limiting. Satellite-derived information on lake temperature and Chl-a concentration proved essential in detecting trends at appropriate resolution over time.

Keywords Shallow lakes · Cyanobacteria · Chlorophyll-a · Climate change · Remote sensing

Introduction

Shallow lakes have been identified as providing up to 39 essential ecosystem services globally such as drinking water, biodiversity, and recreational use which can be linked to sustainable development goals (Janssen et al., 2021). Anthropogenic pressure can cause a shift in state from being dominated by macrophytes to phytoplankton with a resulting loss in ecological functioning and degraded ecosystem services (Scheffer, 1989; Scheffer & van Nes, 2007; Janssen et al., 2021). The abundance of phytoplankton is a key component used in assessments of trophic state and ecological quality of lakes (Council of the European Communities, 2000; Phillips et al., 2013). Some phytoplankton species, such as cyanobacteria, can form blooms or scum and can potentially produce toxins (cyanotoxins) that can have adverse effects on aquatic ecosystems and human health (Codd et al., 2005; Jöhnk et al., 2008; Ma et al., 2015). Physical and chemical parameters as well as seasonality affect phytoplankton distribution, abundance, and species diversity (Raymond, 1983; Ezra & Nwankwo, 2001). For example, cyanobacteria are typically more abundant in nutrient-rich freshwater and are regulated by seasonal drivers, such as warmer temperatures and calmer weather which influence water column thermal stratification (Reynolds, 2006). In large shallow lakes which are polymictic (lack stratification), calm warm weather and directional light wind can be associated with surface accumulations of phytoplankton as well as promoting nutrient increase through internal loading that can further fuel blooms following storms (Søndergaard et al., 2003; Shi et al., 2017; Bresciani et al., 2020; Free et al., 2021b).

Climate change has an important influence on global biodiversity in lakes and has been listed as the third most important driver after invasive species and land-use change (Sala et al., 2000). The global increase in surface temperature in lakes in summer

has been estimated as 0.34°C per decade but the influence of lake specific parameters like morphology frequently result in a lack of regional consistency to these trends (O'Reilly et al., 2015). Recent projections have indicated that lakes are predicted to get warmer for longer periods, with heatwaves potentially extending across multiple seasons (Woolway et al., 2021). Climate has been found to alter the seasonal pattern of phytoplankton in several ways, for example, through altering the physical environment with warmer winters reducing the incidence of stratification overturn and thereby altering nutrient cycling (Rogora et al., 2018; Free et al., 2021a). Whereas in high latitude lakes an increase in the length of growing season of phytoplankton has been attributed to an increasing proportion of rain relative to snow resulting in earlier delivery of nutrient loads to lakes (Maeda et al., 2019). For cyanobacteria, warmer temperatures have been found to result in the earlier occurrence of the growing season of *Microcystis* (Deng et al., 2014). Extreme increases in rainfall followed by warmer winter temperatures can combine to increase external and internal loading leading to earlier blooms of increased duration and extent (Qin et al., 2021). Warmer temperatures resulting from climate change have been predicted to lead to an increase in cyanobacteria through direct growth and also by promoting a stable water column under which buoyant cyanobacteria have a competitive advantage (Jöhnk et al., 2008). Future scenarios have predicted an increase in the intensity and frequency of cyanobacteria blooms resulting from warmer temperatures and eutrophication (Paerl & Huisman, 2009; O'Neil et al., 2012; Huisman et al., 2018).

Satellite remote sensing can enable the observation of a suite of indicators of water quality and ecosystem condition for the study of long-term environmental trends in lakes (Tyler et al., 2016; Free et al., 2020) and supports different studies on the consequences of climate change on algal blooms (Qin et al., 2019; Shi et al., 2019). Phytoplankton is one the most frequently studied parameters with chlorophyll-a (Chl-a) often used as a proxy of phytoplankton biomass. The spatial coverage and temporal sampling frequency achievable with satellite images allow novel insights into phytoplankton dynamic processes in lakes (Ho et al., 2019), especially when paired with high-frequency ground-based measurements (Bresciani et al., 2020) that cannot be easily captured through in situ sampling

(Palmer et al., 2015). Remote sensing has therefore been identified as a key component of future high-level lake water quality management strategies (Carvalho et al., 2019).

Here we examine a 16-year (2003–2018) time series for a shallow lake (Trasimeno) in central Italy in order to identify changes in Chl-a concentration trend and dynamics in the context of climate change. Satellite observations of Chl-a provide higher temporal resolution in addition to their capacity to integrate signals over a large spatial area of the lake. We expect that warmer summers should increase the intensity and duration of summer blooms in the lake in line with climate change predictions.

Materials and methods

Study area

This study focuses on Lake Trasimeno, a post-tectonic, shallow lake (maximum depth 6.3 m), situated at an altitude of 258 m in central Italy (43° 08' N; 12° 06' E; Fig. 1). It is the fourth largest lake in the country (surface area 120.5 km²) and has a circular shape (Ludovisi & Gaino, 2010). The catchment area (excluding the lake) is 264.5 km² and given the small catchment area relative to that of the lake, the annual input of water can be lower than that lost through evaporation with a residence time highly dependent on rainfall with estimates ranging from > 4 to > 20 years (Jørgensen et al., 2007; Frondini et al., 2019). Therefore, the water balance of the lake is strongly dependent on rainfall which is typically 700 mm—just sufficient to keep the lake level stable, and with no significant outflow the lake can be classified as endorheic (Dragoni, 2004; Frondini et al., 2019). Land cover as a percentage of total catchment area (i.e., lake plus its catchment) was estimated as water (39.1), agricultural—mostly dominated by arable (30.9), forest (22.3), baren land (4.9), and urban (2.9) (Giardino et al., 2010). Lake Trasimeno is of considerable conservation importance, being part of the largest Natural Regional Park in peninsular Italy, a Site of Community Interest, a Special Protection Zone and contains two Natura 2000 sites (IT5210018 and IT5210070). Lake Trasimeno is generally turbid (average Secchi disk depth 0.9 m) with an annual average total phosphorus concentration of 27 µg l⁻¹

for the years 2015–2017, while the annual average of Chl-a ranged from 5.37 to 14.73 mg m⁻³ for this period (Cingolani & Charavgis, 2018). This can be compared with the background reference concentrations of Chl-a assigned in legislation of 3.3 mg m⁻³ (DM, 2010). The values for Chl-a and TP would place the lake at the mesotrophic–eutrophic boundary according to the OECD trophic classification system, with TP not significantly changing since the 1970s (OECD, 1982; Ludovisi & Gaino, 2010). Average alkalinity for the years 2015–2017 was 191 mg l⁻¹ CaCO₃. The water column is unstratified, with recurrent sediment resuspension due to wind action. According to the Water Framework Directive (WFD) system of classification, the lake is currently classified at moderate ecological status (Council of the European Communities, 2000, 2013; Cingolani & Charavgis, 2017, 2018). Lake Trasimeno has a phytoplankton assemblage dominated by chlorophytes and dinoflagellates. Cryptophytes can also comprise a relatively large portion of the biomass, whereas euglenophytes and diatoms are relatively scarce (Havens et al., 2009). In summer, the high nutrient availability favors the occurrence of phytoplankton blooms, including cyanobacteria species (e.g., *Cylindrospermopsis raciborskii*, *Planktothrix agardhii*) (Havens et al., 2009; Charavgis et al., 2020).

WISPstation in situ data

The WISPstation (Peters et al., 2018) is a fixed position, above water autonomous spectroradiometer. It was installed on April 24th, 2018, 400 m north of Polvese island in Lake Trasimeno (Fig. 1) and collects remote sensing reflectance (Rrs) data every 15 min. It measures the radiance and irradiance in the spectral range of 350–900 nm with a spectral resolution of 4.6 nm (full width at half maximum). The system is calibrated relative to a reference instrument (calibrated in a certified laboratory using a lamp and integrating sphere with National Institute of Standards and Technology traceable calibrations). The WISPstation is watertight and built into a highly climate-resistant case. Temperature of the sensor and humidity in the case are registered with every measurement. Data are automatically sent using 3G connectivity to the database (WISPcloud). The instrument can be remotely accessed and, e.g., updated or configured to a specific time interval or measurement frequency. It is



Fig. 1 True color composition of Lake Trasimeno from satellite (Sentinel-2 acquired on 5 June 2019) together with the WISPstation position (red dot)

autonomously powered by a solar panel and internal large battery. Its hyperspectral features allow a simulation of the band setting of satellite data and hence provides valuable reference data. For water quality monitoring purposes, the remote sensing reflectance observations are run through standard water quality algorithms to make a first estimate of Chl-a (Gons, 1999). The WISPstation-derived data of Chl-a concentrations were validated against values measured in water samples analyzed by ARPA Umbria (Bresciani et al., 2020). The WISPstation also enables estimates of the concentration of phycocyanin using specific algorithms (Simis, 2006). A subset of the data from July 1st until September 30th, 2019, was used for analysis.

Long-term EO dataset

The European Space Agency's Climate Change Initiative (CCI) aims to exploit the long-term global Earth Observation record to produce Essential Climate Variables (ECVs) supporting the United Nations Framework Convention on Climate Change (UNFCCC). The objective of the CCI dataset for the ECV Lakes is to use satellite Earth Observation data to create the largest and longest possible consistent, open global record of five lake thematic variables: lake water level, lake area extent, temperature, water-leaving reflectance, and ice cover. The main characteristics of this dataset (Crétau et al., 2020) are as follows:

- Spatial coverage: 250 globally distributed lakes, set to expand to around 2000 in the second phase
- Spatial resolution: 1/120° global grid
- Temporal resolution: daily netCDF files containing all thematic variables including uncertainty
- Temporal coverage: from 1992 up to 2019.

For Lake Trasimeno, lake surface water temperature (LSWT) and Chl-a (derived from water-leaving reflectance data from MERIS and OLCI sensors) were extracted from the CCI Lakes database version 1.0. Quality level 4 and 5 were used to filter temperature values; these represent the level of confidence that the LSWT is valid and are classified as suitable for climate applications, similarly only a Chl-a uncertainty below 60% was used for analysis (Simis et al., 2020). The dataset for LSWT dates from 1993 while that for Chl-a starts in 2002. A total of 24 satellites were used to compile data in the CCI Lakes project and are listed in the product user guide (Simis et al., 2020). The CCI dataset presents an opportunity to examine what parameters are important in controlling the size of phytoplankton blooms and their interannual variation and phenology. There is a significant data gap in Chl-a from 2012 to 2015 when optical satellite data with the same characteristics (i.e., MERIS and OLCI) were not available, while other approaches, e.g., Huang et al. (2019) who used MODIS for long-term mapping of phytoplankton in Lake Taihu, were not yet considered suitable for Lake Trasimeno. In addition, gaps are also present due to satellite overpass limitations, where images were contaminated by cloud cover or where marked invalid for analysis (Simis et al., 2020). One of the objectives of the work was to test the ECV Lakes dataset, exploring potential for scientific research and also the current limitations of the dataset.

Few in situ environmental datasets are available to match this temporal resolution so daily climatic data were obtained from ERA5, the fifth generation of the European Centre for Medium-Range Weather Forecasts (ECMWF) reanalysis for the global climate and weather (<https://cds.climate.copernicus.eu/cdsapp#!/home>). Data used for analysis included the following: wind vectors to represent speed and direction, 2 m air temperature (temperature of air at 2 m above the surface), total precipitation, and the sum of rainfall for the preceding seven days. Lake level at S. Savino station (Magione village) was obtained from the regional authority (Umbrian Regional Hydrographic

Service. Available online: <https://annali.regione.umbria.it/#> (accessed on 15 March 2021). Several studies have detected changes in Italian lakes linked to long-term climate change and fluctuations in large scale regional climate drivers such as the North Atlantic Oscillation index (NAO) and the East Atlantic pattern (EA) during winter (Rogora et al., 2018; Salmaso et al., 2018). Daily values of the North Atlantic Oscillation (NAO) were obtained from NOAA-CPC (<https://www.cpc.ncep.noaa.gov/products/precip/CWlink/pna/nao.shtml>).

Analysis

For the analysis, two approaches were trialed—Google AI (Artificial Intelligence) and Nonparametric Multiplicative Regression (NPMR). NPMR (McCune, 2006) was used to estimate the response of average daily Chl-a concentration to climate and environmental parameters listed above. NPMR can define response surfaces using predictors in a multiplicative rather than in an additive way. This method is progressive in better defining unimodal responses than other methods such as multiple regression (McCune, 2006). It has previously been applied to model tree species distribution (Yost, 2008), the response of lichens to climate change (Ellis et al., 2007), and in time-series analysis (Nicolaou & Constantinou, 2016). NPMR was applied using the software HyperNiche version 2.3 (McCune & Melford, 2009). The response of Chl-a was estimated using a local mean multiplicative smoothing function with Gaussian weighting. NPMR models were produced by adding predictors stepwise with fit expressed as a cross-validated R^2 (χR^2) which can be interpreted in a similar way as a measure of fit as a traditional R^2 . The sensitivity, a measure of influence of each parameter included in the NPMR model, was estimated by altering the range of predictors by ± 0.05 (i.e., 5%) with resulting deviations scaled as a proportion of the observed range of the response variable. Sensitivity can be used to evaluate the relative importance of variables included in models because NPMR models are unlike linear regression and have no fixed coefficients or slopes. Google AI AutoML was also used to develop a model for Chl-a as a designated feature. The supervised learning model followed a regression approach with chronological assignment using the first 80% of the time series for

model training with each subsequent 10% used for validation (a tuning of the models hyper parameters) and testing (independent data used to derive the model's performance statistics) (<https://cloud.google.com/automl-tables>). For AI and NPMR analysis, the Chl-a concentration and lake surface water temperature were linear-interpolated to daily values using the temporal smoothing and gap filling (tsgf) linear function in the R package greenbrown (Forkel & Wutzler, 2015; R Core Team, 2019). Theil-Sen estimates for slope of air temperature were carried out in the openair package in R (Carslaw & Ropkins, 2012). Spearman rank (rS) correlation was calculated using DataDesk (Velleman, 1989).

For phenological analysis, calculation of the start of season (SOS), end of season (EOS), and length of season (LOS), a spline interpolation was used as this smoothed the seasonal patterns. Interpolation and smoothing is a standard and essential step in phenological analysis in order to identify the timing of seasonal change and this technique has been used to determine the changes in land cover phenology (Forkel et al., 2013, 2015; García et al., 2019). For phenological analysis, we used 15 mg m^{-3} of Chl-a as a level that could be considered as a starting point for the summer bloom for Lake Trasimeno, and this concentration has been used as a trigger value for instigating enhanced bloom monitoring (Touchette et al., 2007). We calculated the SOS as the day of year when the Chl-a concentration first reached 15 mg m^{-3} and the EOS when it subsequently declined below 15 mg m^{-3} . The LOS was the difference between the two values. For comparison with LSWT, we followed the same approach using 20°C to define SOS, EOS, and LOS. This temperature was selected as the optima for many cyanobacteria have been considered above 20°C (Konopka & Brock, 1978; Jöhnk et al., 2008).

Results

The Chl-a concentration in lake Trasimeno ranged from < 1 to 130 mg m^{-3} with an annual pattern dominated by a summer bloom (Fig. 2). Focusing on a summer period from July to September in 2019, we can see that the increase in Chl-a starts in July and peaks in August and September (Fig. 3). Comparing the CCI estimates of Chl-a with that of the high-frequency WISPstation revealed a close

correspondence between the two estimates, for example, both detecting a steep increase around the 12th of August. The WISPstation estimate of the concentration of phycocyanin rapidly increased around this period indicating that cyanobacteria were likely causing the increase in Chl-a concentration. Counts of cyanobacteria taxa are carried out under government regulations (Ministry of Health, 1998) and were reported by the regional authority (ARPA, Umbria; Charavgis et al., 2020) at approximately weekly intervals during bathing season. These show the underlying changes in composition and abundance of cyanobacteria during this period (Fig. 3). The cyanobacteria community was dominated by *Cylindrospermopsis raciborskii* during the bloom period of mid-to-late August with its increase and decline being broadly matched by estimates of Chl-a and phycocyanin.

In order to understand the factors influencing the dynamics of Chl-a in Lake Trasimeno, we first carried out a NPMR including the variables day of year (DOY), year, lake level, lake surface water temperature, wind vectors, the NAO, and the sum of the antecedent rain for 7 days (Table 1). The best model had an xR^2 of 0.62 and included DOY, year, lake level, and the NAO; however, the NAO was interchangeable with lake surface water temperature. The sensitivity value provides an indication of the importance of the variables in the models. The DOY had the highest sensitivity value (0.338) followed by year (0.065), lake level (0.014), and the NAO (0.004), while interchanging the latter with LSWT in a second model yielded a sensitivity of 0.006 (Table 1). Contour plots were produced to visualize estimates for Chl-a for DOY with lake level, NAO, and LSWT (Fig. 4). The contour lines and color intensity represent Chl-a in 4 mg m^{-3} increments. Common to all the plots are the higher concentrations centered around day 250 (7th September). Chl-a concentration was estimated to be higher at more positive values of the NAO, at lower lake levels and at warmer temperatures. The similar responses and tight intertwining of seasonal parameters obviously present a difficulty in either deciding on key factors or partitioning influence. We also applied Google AI AutoML to develop a model for Chl-a as a designated feature. Overall the model also had an R^2 of 0.62 and the parameters with the highest estimated percentage feature importance were date (83.3), the seven-day antecedent sum of rainfall (6.5), LSWT

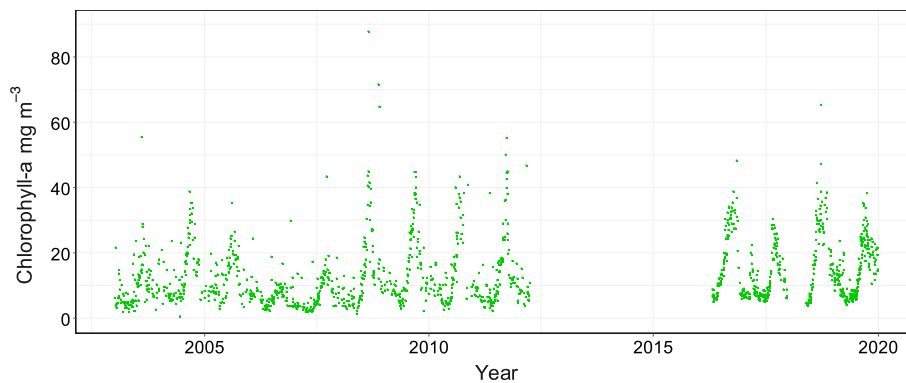


Fig. 2 Satellite-derived Chl-a in Trasimeno from 2003 to 2019. Significant data gap from 2012 to 2015 is due to the unavailability of optical satellite data with the same

characteristics of MERIS and OLCI sensors. One high value of 130 mg m^{-3} on the 16/09/2008 was removed for clarity

(5.8), and NAO (3). While parameters estimated to have less importance included the v wind component (0.8), u wind component (0.6), and the lake level (0).

In order to examine the increase in temperature, we needed a long time series and used the ERA5 data to examine the increase in air temperature for Lake Trasimeno. The Theil-Sen estimate for slope for annual average temperature between 1980 and 2019 was 0.05 ($P \leq 0.001$) estimating an increase from 12.7 to 14.5°C. Similarly the increase in temperature for the summer period (June, July, August) had a slope of 0.06 ($P \leq 0.001$) increasing from 22 to 24°C. For shallow Lake Trasimeno, the LSWT was highly correlated with air temperature ($R^2 = 0.94$) as previously found (Ludovisi & Gaino, 2010). As the temperature is increasing and its importance in influencing blooms is evident either directly or indirectly through the significance of the seasonal component or via the NAO index, it deserves further analysis to determine if there is an influence on the phenology of phytoplankton blooms. It had been postulated that perhaps blooms might occur earlier with warmer temperatures or be of longer duration. Using 15 mg m^{-3} to define the SOS for Chl-a, we found that the timing was variable and ranged from DOY 196 (July 15, 2016) to 242 (August 30, 2007) (Fig. 5). Comparing with LSWT, the timing of the SOS (when LSWT exceeded 20°C) ranged from DOY 117 (April 27, 2005) to 155 (June 4., 2004) (Fig. 5). The SOS for temperature was not significantly correlated with the SOS for Chl-a ($r_s, -0.023, P = 0.95$).

However, the LOS of Chl-a appeared related to the LOS of temperature which could be described by a

quadratic equation ($R^2 = 0.92, P \leq 0.001$, Fig. 6). It appears that if the LOS for temperature is either too short or too long, it may constrain the LOS of Chl-a with an optimum of around 130 days (Fig. 6). The Chl-a LOS was also related to the SOS for temperature ($r_s = 0.72, P = 0.012$) with years where 20°C was reached earlier like in 2005 and 2007 having a shorter Chl-a LOS (Fig. 5). A similar negative correlation ($r_s = -0.811, P \leq 0.001$) was found between LSWT LOS and average Chl-a concentration (calculated for a 14-day window around DOY 250 when values are typically at a maximum).

In order to understand the implications of this, we examined a longer time series, available for air temperature, to see if there were any trends in the summer temperature phenology that could have implications for lake phytoplankton (Fig. 7).

We found evidence for an increase in the LOS ($R^2 = 0.28, P \leq 0.001$), a decrease in SOS ($R^2 = 0.27, P \leq 0.001$) but not the EOS ($R^2 = 0.06, P \leq 0.12$) with an estimated increase in 16 days LOS over the period. To answer the question as to why earlier and longer occurrence of higher temperatures might lower the Chl-a LOS, we looked at the nutrient data from the local authority (<https://apps.arpa.umbria.it/acqua/qualita-acque-superficiali>). Phosphate concentrations were occasionally below the level of detection in summer months; the concentrations for July for the last three years were 16, 18, and $< 10 \mu\text{g l}^{-1} \text{ PO}_4\text{-P}$ for 2019, 2018, and 2017, respectively. However, both the temporal resolution (bimonthly) and the spatial coverage (two stations) prevented more detailed analysis. Another potential mechanism could be that

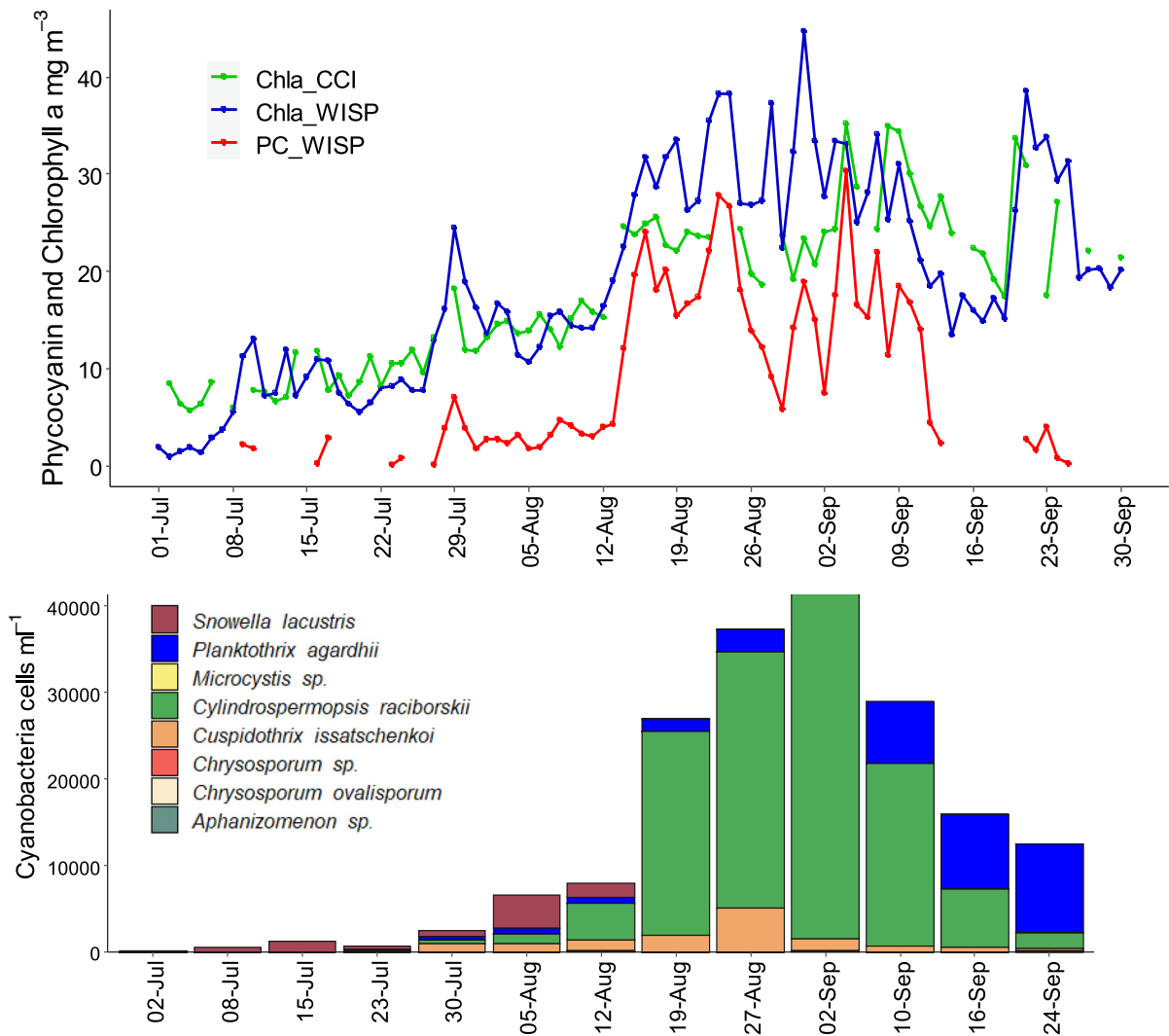


Fig. 3 (Top) estimates of Chl-a from the CCI project (Chla_CCI) and WispStation estimated Chl-a (Chla_WISP) and phycocyanin (PC_WISP) in 2019. (Bottom) counts of cyanobacteria cells per ml in 2019 reported by Charavgis et al.

(2020). Note continuous and discontinuous x-axis on top and bottom figures, respectively. Counts of *Microcystis* sp., *Chrysochloris* spp. and *Aphanizomenon* sp. were below 120 and are not visible on the graph

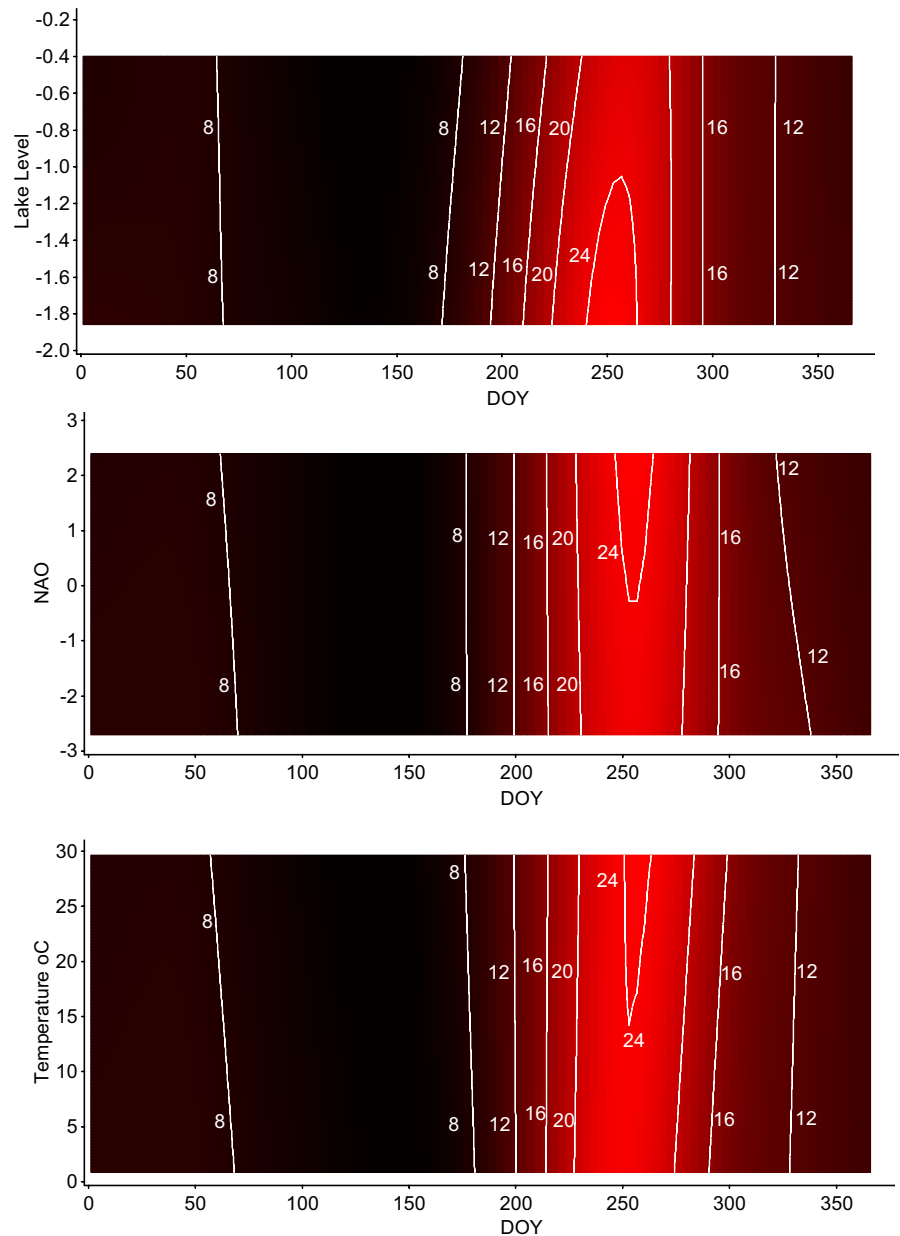
Table 1 Results of NPMR (nonparametric multiplicative regression) models for chlorophyll-a

xR ²	Ave size	Variable 1	Tol.	Sen.	Variable 2	Tol.	Sen.	Variable 3	Tol.	Sen.	Variable 4	Tol.	Sen.	P
0.62	99.1	DOY	18.3	0.338	Year	1.2	0.065	Level	0.7	0.014	NAO	3.3	0.004	0.045
0.62	98.7	DOY	18.3	0.331	Year	1.2	0.064	Level	0.6	0.017	LSWT	13.0	0.006	0.045

First model (row 1) included NAO and second model (row 2) LSWT. The second model shows that NAO was interchangeable with LSWT

xR² cross-validated R²; Ave. size Average neighborhood size; Tol. tolerance; Sen. sensitivity; NAO North Atlantic Oscillation; Level lake level; LSWT lake surface water temperature

Fig. 4 Nonparametric multiplicative regression estimates for Chlorophyll-a (mg m^{-3} ; contour lines) against DOY (day of year) for lake level (m), NAO (North Atlantic Oscillation) and lake surface water temperature ($^{\circ}\text{C}$)



the longer period of warmer temperature could be increasing the amount of calcium carbonate precipitation which could reduce resources through the coprecipitation of phosphorus (Otsuki & Wetzel, 1972). Using chemistry data on major ions (Ludovisi & Gaino, 2010), we followed the recommendations of (Tang et al., 2021) in using the PHREEQC software to calculate the calcium carbonate precipitation potential (CCPP) for an open system for various temperature increments (Fig. 8). Values of CCPP increased with

increasing temperature, for example, from 0.68 to 0.76 mmol kg^{-1} from 15 to 25 $^{\circ}\text{C}$, an increase of 12%.

Discussion

Examination of the satellite time series of Chl-a concentration showed that the annual pattern was dominated by a summer bloom that regularly occurred over the years examined. There was good

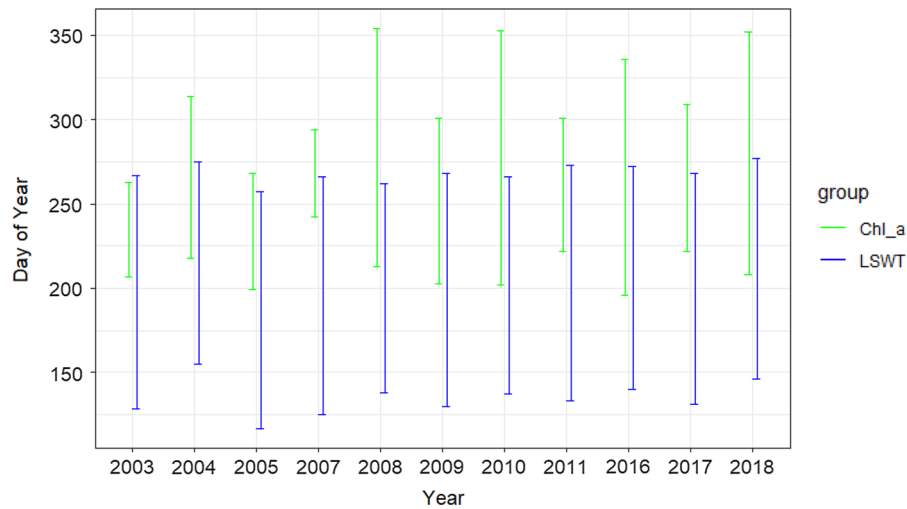


Fig. 5 Start, end, and length of season for Chl-a ($\geq 15 \text{ mg m}^{-3}$) and lake surface water temperature (LSWT) ($\geq 20^\circ\text{C}$)

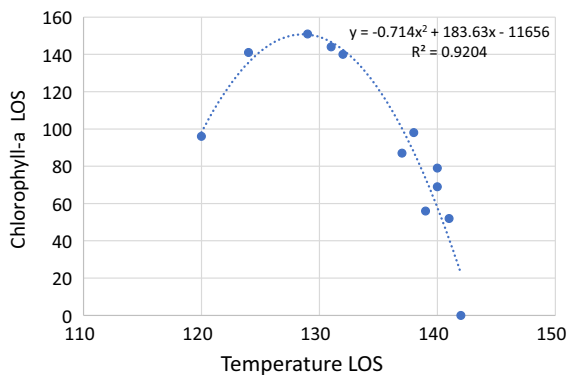


Fig. 6 Chlorophyll-a length of season (LOS) ($> 15 \text{ mg m}^{-3}$) and temperature LOS ($> 20^\circ\text{C}$) with quadratic equation line fit

correspondence between the Chl-a estimated by the WISPstation high-frequency monitoring and that of the lakes CCI project derived from Sentinel 3 OLCI images. The increase, duration, and decline of the seasonal bloom were adequately delineated and were also substantiated by the changes in abundance and composition in cyanobacteria determined at weekly interval by the local authority (Charavgis et al., 2020). Such rapid shifts in Chl-a concentration over a period of weeks have been found before (Bresciani et al., 2018) and underline the value of high-frequency monitoring but also indicate that the data gathered by the three optical sensors, including data obtained from the lakes CCI project (Crétaux et al., 2020), perform well in detecting dynamic changes underlain by a rapidly changing phytoplankton community.

Google AI AutoML, and NPMR were used to examine the environmental parameters influencing Chl-a concentration dynamics between 2003 and 2011. Both modeling approaches found the time component to be the most important accounting for 83.3% as feature importance in Google AI while in NPMR, a sensitivity value was recorded of 0.338 and 0.065 for DOY and year, respectively. The seven-day antecedent rainfall was the next most important for the Google AI (6.5%) while this parameter was not included in the NPMR. In NPMR, the lake water level was the next most sensitive (0.014) followed by either the NAO (0.004) or temperature (0.006). These variables were also included in the Google AI AutoML ($> 3\%$) with the exception of lake level. One of the drawbacks in the Google AI approach is the lack of interpretable diagnostic output to examine the behavior of individual parameters. For the NPMR, the contour plots indicated higher concentrations centered around day 250 (7th September). Chl-a concentration was estimated to be higher at more positive values of the NAO, at lower lake levels and at warmer temperatures. It may be difficult to isolate the relative importance of these parameters. The models already incorporate the seasonal and temporal components and while the inclusion of other variables indicates that they explain additional variation, a lot of the variation may also be already explained by the seasonal component (also for other variables). However, the estimated response of Chl-a to higher summer temperatures and a more positive NAO is

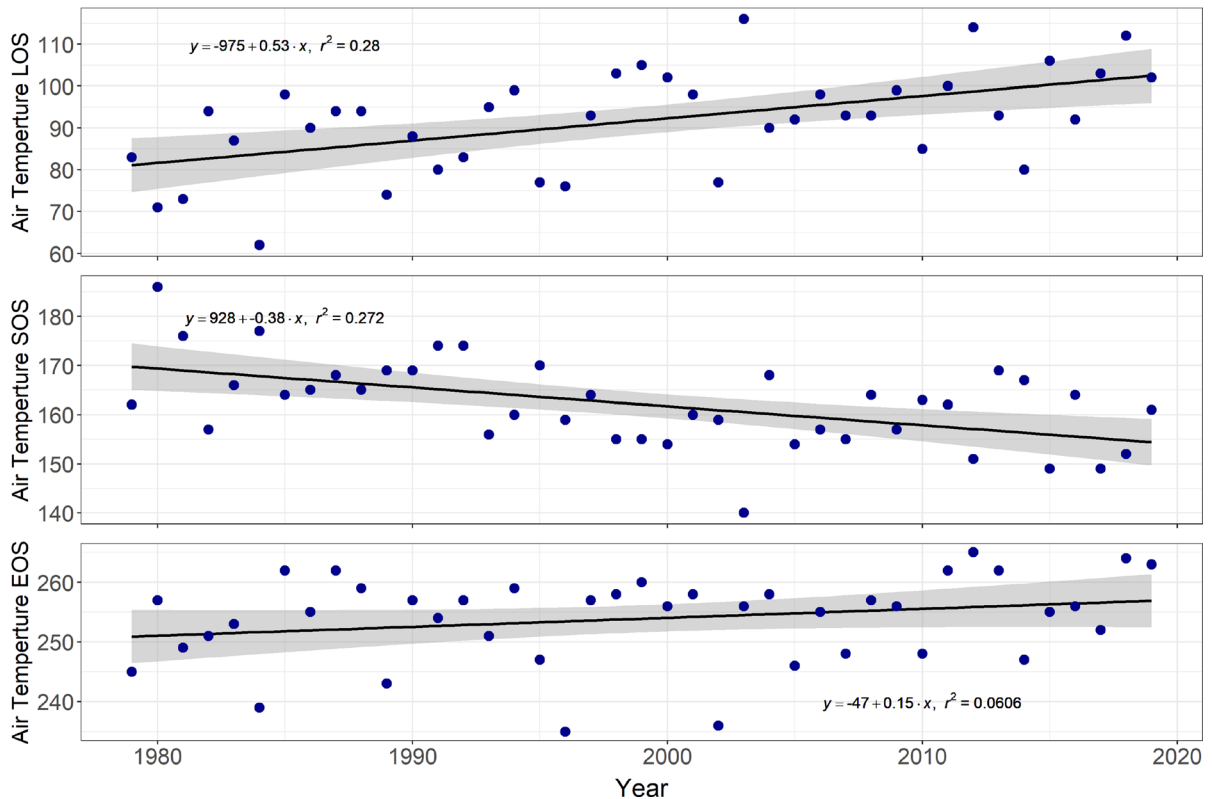


Fig. 7 Start, end, and length of season where average daily air temperature was $\geq 20^{\circ}\text{C}$ in lake Trasimeno from 1979 to 2019 (SOS, EOS, and LOS, respectively)

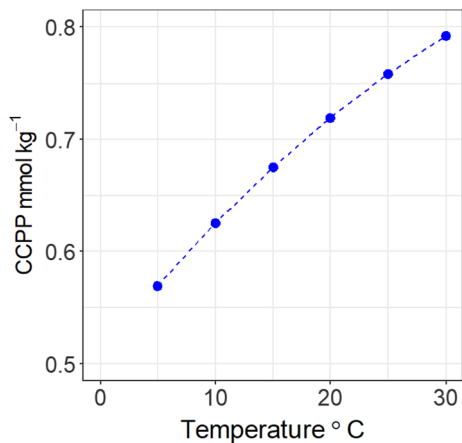


Fig. 8 Increase in the calcium carbonate precipitation potential (CCPP) with increasing temperature estimated for Lake Trasimeno

not surprising. Cyanobacteria are well known to respond to higher temperatures and a more positive NAO around this time period reflects high pressure with warm sunny weather (Konopka & Brock, 1978;

Criado-Aldeanueva & Soto-Navarro, 2020). The incorporation of indices such as the NAO likely reflects the importance of other parameters associated with summer heatwaves such as low cloud cover, reduced wind speed, as well as higher temperatures that promote cyanobacteria growth directly or indirectly through water column stability (Jöhnk et al., 2008). The positive influence of lower lake levels may reflect increased suspension of sediments by wave action potentially increasing nutrient levels and promoting bloom development (Søndergaard et al., 2003; Ludovisi & Gaino, 2010). In addition, lower lake levels can be associated with higher phytoplankton biomass in shallow lakes through increasing light availability alone (Nöges et al., 2003). While the seven-day antecedent sum of rainfall was not included in NPMR, its inclusion in Google AI may reflect the importance of inflow events transporting nutrients to the lake from the catchment. Some visual evidence of the importance of this in bloom development has been seen in satellite images in 2018 for Lake Trasimeno

(Bresciani et al., 2020). However, significant storm events and flushing can suppress blooms in shallow lakes (Havens et al., 2019).

The examination of the phytoplankton phenology found that there was no evidence for an earlier increase in summer blooms that was related to the earlier onset of higher temperatures. It was also anticipated that a longer warmer period with temperatures above 20°C would lead to a longer bloom period but the relationship was more complex. Contrary to expectations, an earlier onset and longer duration of warmer temperatures appeared to be related to a shorter phytoplankton bloom. The relationship could be described by a quadratic equation where initially Chl-a increased with a longer LOS for temperature but started to decline after 130 days. The relationship likely reflects aspects of resource availability. The decline after 130 days could be the result of a longer LOS, typically with an earlier SOS, leading to more or earlier uptake of nutrients resulting in lower amounts to support later bloom development or duration. A significant proportion of the phytoplankton biomass was found to be comprised of chlorophytes in early summer (Havens et al., 2009) and these could play a role in reducing resources for other succession species. While the frequency of chemical monitoring did not allow incorporation into analysis, phosphate concentrations were occasionally below the limit of detection ($< 10 \mu\text{g l}^{-1} \text{PO}_4\text{-P}$) and monitoring was not carried out for the month of August which may be the critical period for bloom development. However, for at least some years, phosphate is likely to limit bloom development and overall, there is a close relationship between total phosphorus and summer Chl-a ($R^2 = 0.65$) (Bresciani et al., 2021, in press). During the 2003 heatwave in Europe, examples were recorded of very large cyanobacteria blooms but this was under hypertrophic conditions (Jöhnk et al., 2008). Similarly, in shallow lake Taihu in China, high total phosphorus concentrations ($> 130 \mu\text{g l}^{-1}$) have led to extensive blooms, despite restoration attempts (Qin et al., 2019, 2021). In addition, earlier onset of *Microcystis* blooms has been found to be dependent on sufficient nutrient concentrations (Deng et al., 2014). Furthermore, the fact that SOS can vary spatially within a lake underlines the importance of other local factors such as nutrients in addition to climate warming (Shi et al., 2019). An interplay during summer between nutrient availability and the

increasingly more optimal climatic conditions (temperature, water column stability, cloud cover) for cyanobacteria is to be expected in lakes that are not nutrient rich. This may cover the majority of monitored lakes in Europe as only 16% had phosphorus conditions classified as less than good (although 36% were not classified) (Kristensen et al., 2018).

The potential for warmer temperatures to increase the rate of calcite precipitation was also examined, and an increase from 15 to 25°C estimated an increase of 12% in the calcium carbonate precipitation potential (CCPP). This may lead to more coprecipitation of phosphorus leading to smaller blooms, especially considering the longer period of warmer weather, and also the fact that pH may be higher with increased photosynthesis (Otsuki & Wetzel, 1972; Homa & Chapra, 2011). It may be possible to examine the presence and extent of this process in future as methods have recently been developed to use remote sensing to detect calcite spatially in lakes (Heine et al., 2017).

A more systematic examination of the response of Chl-a concentrations to climate change in summer is needed. While the increasingly more optimal conditions for cyanobacteria has been predicted to lead to an increase in frequency and abundance of blooms, it may also be plausible that higher temperatures for longer periods may alter the phenology of many limnetic organisms and catchment processes, altering nutrient and other geochemical cycles and resulting in unanticipated responses in summer phytoplankton, including blooms of shorter duration. There may be a tendency for publications to confirm the former anticipated response (Simundic, 2013). Given the increase in LOS observed using the ERA air temperature data since 1980, climate change may continue to alter the phenology of the phytoplankton, even if larger or more prolonged blooms are not expected, this can lead to asynchronization with other groups such as zooplankton thereby altering energy transfer between trophic levels (Winder & Sommer, 2012). The lakes CCI database may be suited to exploring the incidence of such patterns as it contains information on lake level, temperature, Chl-a, turbidity, lake area, and ice cover and is due to expand to about 2000 lakes in 2021 (<https://climate.esa.int/en/projects/lakes/>). One of the limitations of the current dataset used here is the presence of gaps—especially between 2012 and 2015. One potential solution would be to use data from the

MODIS satellite which has been used successfully to define bloom phenology previously in Lake Taihu in China (Shi et al., 2017, 2019). This solution is currently being evaluated for incorporation into later versions of the lakes CCI database, but would have to be evaluated for lake Trasimeno. Lake Trasimeno may have provided us with a ‘tidy’ example in that there is essentially one well-timed and well-defined Chl-a peak per year and innovative ways may be needed for more widespread application of this approach to lakes with more complex phytoplankton dynamics.

Conclusions

Lake Trasimeno has a well-defined summer bloom of phytoplankton and its seasonal timing could be described using satellite data dating back to 2003. Larger summer blooms were associated with warmer temperatures, a lower lake level and a more positive NAO, indicative of high pressure and warm sunny calm weather. The relative role of these parameters and other factors in influencing Chl-a is difficult to apportion because they are correlated seasonally. Interestingly, blooms were not occurring earlier but the length of season where water temperatures were above 20°C appeared to play a role in controlling the duration of blooms. A longer warmer season, typically commencing earlier in the year, was found to lead to a shorter duration of blooms likely owing to seasonal nutrient limitation and perhaps increased calcite precipitation. As the duration of warmer temperatures is increasing, this is likely to be more important in future with implications for species phenology and lake ecosystem functioning.

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Data availability All CCI and ERA data are available online as cited.

Code availability Not applicable.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval Not applicable.

Consent to participate All authors have agreed to participate.

Consent for publication All authors have read and agreed to this version of the manuscript.

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