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Increasingly severe cyanobacterial blooms and deep water hypoxia coincide with warming water temperatures in reservoirs

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Abstract

Cyanobacterial blooms are expected to intensify and become more widespread with climate change and sustained nutrient pollution, subsequently increasing threats to lentic ecosystems, water quality, and human health. However, little is known about their rates of change because long-term monitoring data are rare, except for some well-studied individual lakes, which typically are large and broadly dispersed geographically. Using monitoring data spanning 1987–2018 for 20 temperate reservoirs located in the USA, we found that cyanobacteria cell densities mostly posed low to moderate human health risks until 2003–2005, after which cell densities rapidly increased. Increases were greatest in reservoirs with extensive agriculture in their watersheds, but even those with mostly forested watersheds experienced increases. Since 2009, cell densities posing high human health risks have become frequent with 75% of yearly observations exceeding 100,000 cells mL⁻¹, including 53% of observations from reservoirs with mostly forested watersheds. These increases coincided with progressively earlier and longer summer warming of surface waters, evidence of earlier onset of stratification, lengthening durations of deep-water hypoxia, and warming deep waters in non-stratifying reservoirs. Among years, higher cell densities in stratifying reservoirs were associated with greater summer precipitation, warmer June surface water temperatures, and higher total Kjeldahl nitrogen concentrations. These trends are evidence that expected increases in cyanobacterial blooms already are occurring as changing climate conditions in some regions increasingly favor their proliferation. Consequently, their negative effects on ecosystems, human health, and socioeconomic wellbeing could increase and expand if warming trends and nutrient pollution continue.

Written Summary:

Cyanobacteria cell densities quickly increased in these 20 reservoirs since around 2005, increases were greatest in those with agriculturally dominated watersheds, and cell densities posing

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Supplementary information

Appendix 1. Tables and figures describing reservoirs, summarizing sample dates, and providing additional cyanobacteria details and analyses.

potentially high risk to human health have become common since 2009. Increases coincided with progressively earlier and longer summer warming of surface waters, evidence of earlier onset of stratification, lengthening durations of deep-water hypoxia, and warming deep waters in non-stratifying reservoirs (all since 1989). These results are evidence that increases in cyanobacterial blooms are occurring, could continue expanding geographically, and could remain recurrent problems in some regions if warming trends and changes in seasonality continue.

Keywords

harmful algae; climate change; human health; nutrients; lakes; oxygen; nitrogen; seasonality

Introduction

Cyanobacterial blooms are increasingly being observed around the world (Harke et al., 2012; Huisman et al., 2018; O'Neill et al., 2012), and recent evidence using remote sensing of phytoplankton biomass in large lakes (> 148 km²) indicates that this is not simply due to greater public awareness (Ho et al., 2019). Nationwide surveys of lakes in the United States also have found that the proportion of lakes with cyanobacteria cell densities posing high risk to human health (> 100,000 cells mL⁻¹) significantly increased by 8.3% from 2007 to 2012 (United States Environmental Protection Agency, 2016; 2020). Blooms can cause taste and odor problems for drinking water and often are dominated by cyanobacteria species capable of producing neurotoxins, hepatotoxins, and dermatotoxins, which can have acute and chronic human health effects (Carmichael & Boyer, 2016; Codd et al., 2005; Hilborn & Beasley, 2015). As a result, bloom events have socioeconomic consequences and can lead to beach closures, drinking water and recreational advisories, and pet, livestock, and wildlife deaths (Hilborn et al., 2015; Huisman et al., 2018). Lake sediment records show cyanobacterial biomass has increased with rising nitrogen and phosphorus concentrations associated with agricultural expansion, population growth, and industrialization since the 1940s (Taranu et al., 2015). Increased cyanobacterial biomass, in combination with other effects of eutrophication, reduces biodiversity, increases hypoxia, and alters food webs and biogeochemistry of lakes and reservoirs (Paerl & Huisman, 2009; Tranvik et al., 2009).

In addition to the stimulatory effects of nutrients, the rapid, albeit variable, warming of lake surface waters around the world (O'Reilly et al., 2015; Rose et al., 2016) has important consequences for cyanobacteria abundance and future conditions of lake ecosystems and drinking water sources. Experiments indicate that cyanobacteria have optimal growth rates at warmer temperatures than those of other groups of phytoplankton, such as diatoms and cryptomonads (Carey et al., 2012; Huisman et al., 2018; Paerl & Huisman, 2009), and their growth rates respond to warming waters more quickly than those of green algae (Visser et al., 2016), despite evidence of having similar optimal temperatures for growth (Lüring et al., 2013; Paerl et al., 2016). As a result, differences in the temperature dependence of phytoplankton growth rates can contribute to greater cyanobacteria abundances in warmer waters, even when nutrient concentrations are low (Freeman et al., 2020; Kosten et al., 2012; O'Neill et al., 2012). Warming trends, in combination with changes in water clarity, also increases the strength and duration of thermal stratification in lentic ecosystems (Kraemer et

al., 2015; Richardson et al., 2017; Rose et al., 2016). Longer durations of strong stratification likely favor cyanobacteria over other phytoplankton even more than direct effects of warmer temperatures on growth rates because many cyanobacteria species have the competitive advantage of regulating their buoyancy to acquire nutrients and optimal light conditions (Carey et al., 2012; Huisman et al., 2018; Lürling et al., 2013; Wagner & Adrian, 2009). Phytoplankton blooms and longer durations of stratification create additional problems by decreasing oxygen concentrations in deep waters and extending periods of hypoxia caused by microbial decomposition of plankton-derived organic matter (Hupfer & Lewandowski, 2008; Orihel et al., 2017).

Experiments and synoptic studies along latitudinal and temperature gradients indicate that blooms will become more severe, will have longer durations, and will affect more waterbodies with climate change due to warming surface waters, stronger stratification, and greater nutrient runoff (Chapra et al., 2017; Paerl & Huisman, 2008; Rigosi et al., 2014). However, little is known about how rapidly cyanobacteria abundance may increase in response to a changing climate and if these expected changes already are occurring. This is largely because long-term historical monitoring of cyanobacteria, especially in conjunction with nutrient and water temperature data, is uncommon (Burford et al., 2020; Wells et al., 2020) and mostly limited to a few well-studied individual lakes, which typically are large and broadly dispersed geographically (e.g., Ho et al., 2017; Posch et al., 2012; Qin et al., 2010). In addition, long-term analyses often focus on surface water temperatures during summer months (July–September; e.g., Kraemer et al., 2015; O’Reilly et al., 2015; Rose et al., 2016; Schneider & Hook, 2010), potentially missing other seasonal dynamics and deep water trends, but see Winslow et al. (2017) for an exception.

With the recent reports of a growing number of lakes being affected by cyanobacterial blooms, long-term monitoring data, though rare, can provide opportunities to improve our understanding of factors contributing to these observations by connecting decades of environmental changes to the rise in cyanobacterial blooms. Here, our objectives were to use monitoring data spanning 27–32 years from 20 temperate reservoirs (1) to determine if cyanobacteria cell densities changed over time, and if they have, to describe their magnitudes and rates of change, (2) to characterize relationships between cyanobacteria cell densities and environmental variables, and (3) to quantify long-term trends in environmental conditions important to cyanobacteria (e.g., nutrient concentrations, precipitation, and water temperature). We hypothesized that increases in cyanobacteria cell densities, if observed, would be associated with increases in one or more of the following: nutrient concentrations, precipitation, water temperatures, and durations of stratification. Synthesizing results among our three objectives contributes to characterizing the roles possible ecosystem changes have in affecting cyanobacterial blooms. Collectively, these findings can help inform expectations, decisions, and management practices that seek to improve and protect aquatic resources and ecosystems.

Methods

Descriptions of reservoirs and monitoring efforts

These 20 reservoirs were built by the United States Army Corps of Engineers (USACE) between 1953 and 1983, experience a temperate climate, and are located within the Temperate Plains and Southern Appalachian ecoregions of the United States of America (SI Appendix, Table S1) (Beaulieu et al., 2015). Having surface areas of 1–43 km², these reservoirs are among the most globally abundant lakes and reservoirs based on size and climate (Verpoorter et al., 2014), and reservoirs with 1–100 km² surface areas comprise an estimated 96.7% of reservoirs > 1 km² (Lehner et al., 2011). The USACE built these reservoirs for the primary purpose of flood control, but they also provide wildlife habitat and recreational opportunities with the USACE estimating ~24 million park visits year⁻¹. Eleven of the reservoirs also are drinking water sources.

Land cover in the watersheds of these reservoirs remained nearly unchanged from 2001–2011 (<https://www.mrlc.gov/data>; SI Appendix, Table S2)—years encompassing when cyanobacteria cell densities began increasing. Forested land cover in the 20 watersheds ranges from 1–84% and is strongly correlated with indicators of eutrophication, with increased forest cover being associated with greater water clarity and lower nutrient and chlorophyll *a* concentrations (SI Appendix, Tables S1, S3). For summarizing trends, we grouped five reservoirs as forested (> 65% watershed land cover) with strong yearly stratification, seven as agricultural (> 30% watershed land cover) with strong yearly stratification, and seven as agricultural reservoirs and one as an urban reservoir (74% developed) with weak or no yearly stratification as designated by the USACE (SI Appendix, Table S1).

The USACE has monitored these reservoirs intermittently since 1987 for phosphorus, nitrogen, and phytoplankton, which were collected from just below the surface and at 1.52, 3.05, and 6.10 m depths (including cyanobacteria cell densities), and since 1989 for depth profiles of temperature and dissolved oxygen concentrations. Water and phytoplankton samples were collected using Kemmerer samplers prior to 2012 and Van Dorn samplers thereafter. Cyanobacteria cell densities were determined using American Public Health Association standard methods (APHA, 1995). We only used samples collected from a consistent location where depth was deepest in each reservoir to analyze and interpret all cyanobacteria, temperature, dissolved oxygen, and nutrient data. Beginning in 2012, the USACE instituted additional monitoring in response to publicly reported harmful algal bloom events. These data, however, were excluded from analyses due to their targeted nature and differences in methods. We only analyzed data that were collected as part of the USACE's routine ambient monitoring program.

Data used for analyses

In our analyses, we included cyanobacteria samples collected from June to September because these months (1) had the greatest data coverage, (2) are between the annual raising and lowering of reservoir elevations by the USACE to summer and winter pool levels, respectively, (3) encompass periods of stratification for reservoirs in which this occurs, and

(4) spanned the times when cyanobacteria are expected to have their highest abundances and when recreational activities are greatest. The frequency and dates of phytoplankton sampling within and among years and reservoirs differed due to variability in resources, funding, and staffing, but no systematic bias or sudden change in the timing of sample collection was evident, though sampling intensity was greatest from 1992 to 2006 (SI Appendix, Tables S4–S5, Fig. S1). When a reservoir was sampled more than once within a year (which only occurred 11.4% of the time after 2006), we used the maximum cyanobacteria cell density observed in analyses. We also report trends in monthly maximum cell densities in the supplementary information. The trends we report are even more striking because the number of within year sampling events of reservoirs has been fewer since 2005 (SI Appendix, Table S4), which should reduce the likelihood of observing bloom events and increasing trends.

Depth profiles of temperature and dissolved oxygen at 1.524 m intervals began in 1989. A small number of sampling events with highly irregular depth profiles were excluded to reduce possible effects of extremely atypical conditions or data entry errors on interpretations of deep water temperatures and dissolved oxygen. Total Kjeldahl nitrogen, nitrate–nitrite (henceforth referred to as NO_x), ammonia, total phosphorus, chlorophyll a, and Secchi depth were sporadically sampled since 1987 and had variable numbers of samples among reservoirs and years. As a result, we used yearly means of nutrient concentrations collected during June–August (1) from surface, 1.52, 3.04, and 6.10 m depths to represent “surface water” concentrations and (2) from 1.524 m intervals at depths 7.62 m to represent “deep water” concentrations. Likewise, we used yearly means of nutrient concentrations intermittently measured from June to August in inflowing rivers for which monitoring data were available. Watershed percent forest, which was used to group types of reservoirs for analyzing trends in environmental variables, was a useful proxy of watershed disturbance in reservoirs because of its strong correlations with indicators of eutrophication (SI Appendix, Table S3). While nutrients, temperature, and dissolved oxygen have direct effects on biota, the effects of summer precipitation (June–August), which was consistently monitored by the USACE, may be variable due to watershed area and reservoir size and geomorphology. As a result, we used reservoir specific z-scores for interpreting precipitation trends and effects of on cyanobacteria. Yearly summer precipitation z-scores were calculated individually for each reservoir by subtracting the period mean (1987–2018) from each year’s value and then dividing by the standard deviation for the period.

In total among the 20 reservoirs, cyanobacteria were collected from 775 sampling events at the deepest location of reservoirs (SI Appendix, Fig. S1) and included 23,043 cyanobacteria cell density records of taxa from all surface, 1.52, 3.05, and 6.10 m depths. A total of 424 yearly maximum cyanobacteria cell densities were determined (SI Appendix, Fig. S1). Temperature and dissolved oxygen were monitored, often weekly, in May through October of most years, with a total of 20,215 water temperatures recorded at the surface and at 1.52 m depth, 101,853 deep water temperatures, and 98,688 deep water dissolved oxygen measurements. Data in other months were too sparse to provide a robust analysis of long-term trends. Means of surface and 1.52 m depths for surface temperatures and means of all depths 6.10 m with 1.52 m intervals for deep water temperatures and dissolved oxygen were used to produce one value per reservoir per sampling date for each variable. Roush

Lake and West Fork Lake were excluded from analyses of deep water dissolved oxygen and temperatures due to their shallow maximum depths of 6.6 and 3.6 m, respectively.

Statistical analysis

To show trends over time, we plotted the 424 observations of yearly maximum cyanobacteria cell densities in all reservoirs versus year with a locally weighted scatter plot smoothing trend line using a 0.5 sampling proportion. Cyanobacteria toxin concentrations were not monitored, so we used World Health Organization recommendations to identify densities that posed low (<20,000 cells ml⁻¹), moderate (20,000 \times 100,000 cells ml⁻¹), and high (>100,000 cells ml⁻¹) relative probabilities of human health risks (World Health Organization, 2003). We used linear regression to show descriptive trends in log-transformed yearly maximums of cyanobacteria cell densities for forested, agricultural, and urban reservoirs and for each reservoir, and we reported 20 fitted curves that were back-calculated from the linear regressions to better visualize their rates of change. Likewise, we used linear regressions to show trends in cell densities of cyanobacteria capable of producing toxins for each reservoir and to show monthly trends in total cyanobacteria cell densities for forested, agricultural, and urban reservoirs. Health risks posed by cyanobacteria over time were also plotted by year for each reservoir.

We used generalized additive models (GAMs), with reservoir designated as a random effect, to characterize relationships between cyanobacteria cell densities and environmental variables. GAMs do not rely on *a priori* model parameters or estimates of relationships between response and predictor variables. Instead, GAMs use iterative and nonparametric smoothing functions that search for the fit that best describes relationships between the response and predictors. Data from the 12 reservoirs that experience seasonal stratification and data from those that do not were analyzed separately. Prior to the final GAMs presented here, (1) Spearman correlations were used to identify environmental predictor variables related to cyanobacteria cell densities (SI Appendix, Table S6) and (2) the final GAMs included the minimal number of variables combining to explain the most deviance without having overfit smooths and without being strongly correlated with each other ($r < 0.5$). Due to the patchy nature of our dataset, Spearman correlations provided the fullest analysis of each univariate predictor, whereas GAMs provided the most complete multivariate analysis. We also examined GAMs that included the most strongly correlated variable within different groups of predictors: nutrients, precipitation, monthly surface temperatures, and monthly deep water dissolved oxygen. Deep water temperatures were examined for weakly or non-stratified reservoirs because they may represent cumulative warming of the water column, which also likely experiences greater mixing. Partial effect plots showed relationships between cyanobacteria cell densities and environmental variables.

Precipitation z-scores, surface water TKN concentrations, and June surface water temperatures were included in the final GAM for stratified reservoirs. Despite having similar correlation coefficients, we included surface water TKN instead of NH₃ concentrations in the GAM for stratified reservoirs because many NH₃ observations were below detection limits and TKN likely provides insights into the accumulation of biomass, nitrogen loads, and internal nutrient cycling within the water column over time (Cottingham et al., 2015).

June deep water dissolved oxygen was correlated with cyanobacteria cell densities and likely indicated effects of earlier stratification, but it was excluded from the final GAM because it had an overfitted smooth and did not add much explanatory power. June deep water dissolved oxygen and August deep water temperatures were the variables most strongly correlated with cyanobacteria cell densities in weakly or non-stratifying reservoirs and adding more variables did not improve the GAM.

Following the analysis of cyanobacteria-environment relationships, we examined trends in variables that often affect cyanobacterial blooms and are expected to contribute to future increases in their severities and durations, such as precipitation, nutrients, temperatures, and indicators of stratification duration (monthly deep water DO concentrations). To present a monthly mean of surface water temperatures, deep water temperatures, and deep water dissolved oxygen for each reservoir in each year, we first used linear regression with data from all years in each month to describe mean relationships (slope) of each response variable with day of month. For example, on average, May 1 will have colder temperatures and higher dissolved oxygen concentrations than measurements on May 31, and the reporting of monthly means needs to account for this effect. We used equations from each of the 360 regression models to adjust each temperature and dissolved oxygen concentration to a standard sampling day in the middle of each month ($[mx + b]$ in which m is the slope, x = day 15.5 minus actual sampling day that when multiplied by the slope adjusts values to a consistent mid-month day, and b = intercept). This led to 6 monthly regressions for each of the 20 reservoirs for each of the three variables. This adjustment improves interpretations of trends by accounting for the effect sampling day has on measurements. We then used the means of adjusted values to generate one temperature or dissolved oxygen concentration per month per reservoir for each year. The 360 regressions along with associated scatter plots also were used to screen for outliers, which we further examined by inspecting individual depth profiles and measurements collected before and after an outlier date was identified.

We used linear regression for characterizing descriptive trends in precipitation, nutrient concentrations, surface and deep water temperatures, and deep water dissolved oxygen concentrations over the years. Nutrient data were sparse, especially for 2000–2006, so we also used box plots to compare differences among reservoir types and between pre-2000 and post-2006 time periods. For examining trends among the three reservoir types, monthly means of water temperatures and dissolved oxygen were excluded for May–July from 2011–2015 and for August–October from 2011–2014 due to atypically low numbers of reservoirs being sampled. Surface water temperatures are presented as means of surface and 1.5 m depths. Deep water temperatures and dissolved oxygen concentrations are presented as means of measurements made 6.1 m (typically below expected thermoclines if they occurred). Figures show yearly means \pm standard errors for each category of reservoir. Slopes from linear regressions represent the yearly change in temperature or dissolved oxygen concentrations, and these slopes were nearly identical to those produced using the nonparametric Theil-Sen slope estimator (SI Appendix, Tables S7–S8, Fig. S2). Detection of significant linear regression trends were similar to nonparametric Mann-Kendall tests for significant monotonic trends, with the exception of one non-significant outcome (though with nearly identical slope) in the latter.

Data were organized in Microsoft Excel 2016 and with the exception of plotting GAM results, figures were made using SigmaPlot version 14.0 (Systat Software Inc., San Jose, California, USA). We used R v. 3.6.1 (R Development Core Team, 2014) and the ‘mgcv’ package for generalized additive models (Wood, 2019), the ‘zyp’ package for Theil-Sen slopes (Bronaugh & Werner, 2019), and the ‘kendall’ package for Mann-Kendall tests (McLeod, 2015).

Results

Trends in cyanobacteria cell densities

Prior to 2003, cyanobacteria mostly posed low-to-moderate risks to human health across all reservoirs, with 83% of observations ($n=132$) having cell densities $< 20,000$ cells mL^{-1} , 16% having 20,000–99,999 cells mL^{-1} ($n=26$), and one observation posing high risk to human health with $> 100,000$ cells mL^{-1} (Figs 1, [SI Appendix, Fig. S3]). The greater sampling coverage of all months through 2006 provided further evidence that blooms were uncommon in earlier years (SI Appendix Fig. S4, Table S4). Cyanobacteria cell densities began increasing in most reservoirs around 2003–2005 (Fig. 1c, [SI Appendix, Table S9]). Cell densities also increased in each month, which shows that trends were robust (1) despite less frequent sampling within years later in the dataset and (2) because each month was well represented in the earlier years of the monitoring program when blooms were rare (SI Appendix, Fig. S4, Table S4). From 2009–2018, 4% of observations indicated low risk ($n=6$), 21% of observations indicated moderate risk ($n=30$), and 75% of observations indicated high risk to human health ($n=110$; Fig. 1a). Increases in cyanobacteria densities were greatest in agricultural reservoirs and the urban reservoir, but densities also increased in forested reservoirs, with 53% of observations from forested reservoirs indicating high human health risk since 2009 (Figs 1b–1c, [SI Appendix, Fig. S3]). By the end of 2015, each reservoir had recorded at least one observation of cell densities posing high risk to human health, and in 2018 all 20 reservoirs had blooms with $> 100,000$ cells mL^{-1} (Figs 1a, [SI Appendix, Fig. S3]).

Cyanobacteria taxa known to produce toxins often dominated cell densities (SI Appendix, Fig. S5), with 9 of the 11 most abundant taxa among all reservoirs and sampling events being possible toxin producers, including (in decreasing order of abundance): *Chroococcus*, *Cylindrospermopsis* / *Raphidiopsis*, *Pseudanabaena*, *Aphanocapsa*, *Merismopedia*, *Aphanizomenon*, *Planktothrix*, *Anabaena* / *Dolichospermum*, and *Microcystis* (SI Appendix, Fig. S6). Cell densities of potential toxin producers have increased since 2001–2005 and had much greater increases in agricultural reservoirs and the urban reservoir than in those with forested watersheds (SI Appendix, Fig. S7).

Cyanobacteria–environment relationships

In reservoirs that seasonally stratify, cyanobacteria cell densities were positively correlated with phosphorus and nitrogen concentrations in surface and inflow waters, total organic carbon and alkalinity in surface waters, summer precipitation, and June surface water temperatures (SI Appendix, Table S6). Cyanobacteria cell densities were negatively correlated with deep water dissolved oxygen concentrations in May and June. Listed in

decreasing order of significance, summer precipitation z-scores, June surface water temperatures, and surface water total Kjeldahl nitrogen (TKN) explained 56.3% of the deviance in a generalized additive model for cyanobacteria cell densities. Lower cyanobacteria cell densities were associated with below average amounts of summer precipitation, while higher cell densities were associated with average to above average summer precipitation, warmer June surface water temperatures and higher TKN concentrations (up to approximately 1 mg L^{-1} ; Fig. 2).

In reservoirs with weak or no seasonal stratification, cyanobacteria cell densities were positively correlated with June surface water temperatures and June–August deep water temperatures and were negatively correlated with June deep water dissolved oxygen concentrations (SI Appendix, Table S6). Nutrient correlations were most likely non-significant due to these all being higher nutrient systems with agriculturally or urban dominated watersheds. August deep water temperatures and June dissolved oxygen were the most informative predictors of cell densities, but explained only 22% of the deviance in the generalized additive model. The highest cell densities were associated with warmer August deep water temperatures and lower June DO concentrations (SI Appendix, Fig. S8).

Environmental trends important to cyanobacteria

Nutrient data were sparse, especially between 2000–2006, but some descriptive patterns and trends emerged based on available data (SI Appendix, Fig. S9). In general, agricultural reservoirs had higher TN, TKN, and NO_x concentrations in surface waters, higher TN and NO_x in deep waters, higher TP, TN, and NO_x concentrations of inflows, and lower deep water DO concentrations than those in forested reservoirs (Fig. 3, [SI Appendix, Fig. S9]). Post-2000, surface water and deep water TP concentrations were greater in agricultural reservoirs than in forested ones, perhaps indicating an increasing contribution of legacy nutrients to internal loading.

Total nutrient concentrations were mostly unchanged over time. Concentrations of TN slightly increased in surface waters of forested reservoirs but remained mostly similar in stratifying and non-stratifying agricultural reservoirs (SI Appendix, Fig. S9). The concentrations of TKN have increased while those of NO_x have decreased in surface waters of all three reservoir types. These changes occurred despite inflow concentrations remaining mostly the same, except for a decrease in NO_x concentrations of inflows to forested reservoirs and an increase in TN and TKN concentrations of inflows to non-stratifying reservoirs. Deep water concentrations of TKN increased in stratifying and non-stratifying agricultural reservoirs and NO_x concentrations decreased in deep waters of forested and non-stratifying agricultural reservoirs. Total phosphorus slightly decreased in deep waters of forested reservoirs and increased in those of non-stratifying agricultural reservoirs. Dissolved phosphorus slightly increased in surface waters of forested reservoirs and increased in the surface and deep waters of non-stratifying agricultural reservoirs.

Despite the increases in cyanobacteria cell densities and changes in some nutrient concentrations, watershed land cover in all 20 reservoirs was nearly unchanged from 2001 to 2011—years encompassing when cell densities began increasing (SI Appendix, Table S2). The only exceptions were three highly forested watersheds that had 1.1–4.5% decreases in

forested land cover, which mostly resulted from 0.4–2.6% increases in barren land cover and 0.8–1.8% increases in herbaceous/grasslands between 2001 and 2011. Amounts of summer precipitation were variable among years with no clear trends from 1987–2018 for all three reservoir types (SI Appendix, Fig. S9), which suggests that the associated inflow volumes and nutrient loads were probably also variable among years with no increasing or decreasing trends.

The most obvious changes in reservoir characteristics over time were warming trends in surface and deep water temperatures and decreasing dissolved oxygen concentrations in deep waters (Table 1, Fig. 3). All three reservoir types saw the greatest rates of surface water warming in May, June, September, and October, with the exception of May for non-stratifying reservoirs. Deep water temperatures in May through October have increased in agricultural non-stratifying reservoirs, as have deep water temperatures in August–October in stratifying reservoirs. Decreasing DO in May and June indicate progressively earlier onset of stratification in forested and agricultural reservoirs that stratify, and deep water hypoxia now lasts two months longer in stratifying and non-stratifying agricultural reservoirs (Fig. 3, [SI Appendix, Table S7]). Seasonal hypoxia in stratifying agricultural reservoirs, on average, begins in June since 2002 and ends in October since 2009. Hypoxia in non-stratifying agricultural reservoirs, on average, begins in June and ends in September since 2004.

Discussion

Cyanobacteria cell densities posing high risk to human health are recent events in these 20 reservoirs and have rapidly increased, albeit at different rates and magnitudes, within the span of a decade. Genera capable of producing toxins also increased since 1987 and often dominated total cell densities. Furthermore, the rapidly increasing frequency of severe cyanobacterial blooms documented here is likely conservative because temporally sparse sampling (often once per year, especially since 2005) reduces the probability of capturing the true maximum cyanobacteria abundance. These increases in cell densities occurred despite no clear and consistent changes in watershed land cover, precipitation, and *total* nitrogen or phosphorus concentrations in surface waters or inflows among reservoirs. Additional studies also found no consistent changes in fertilizer use in this region from 2002–2011 (Glibert, 2020) or in nitrogen input to these 20 watersheds from 2002–2012 (Sabo et al., 2019). Collectively, the results indicate that the observed changes in seasonality, warming water temperatures, and their effects on reservoir conditions likely contributed to the broad-scale increases of cyanobacteria abundances in these reservoirs, which span approximately 110,000 km² and have different ages, geomorphology, and watershed land cover. The earlier and longer seasonal warming of surface and deep waters in these 20 reservoirs generally coincides with warming trends of air temperatures during April–June and August–September in this region since the 1980s (Winslow et al., 2017).

The warming of surface waters directly benefits cyanobacteria because their growth rates can peak between 25–35 °C (Huisman et al., 2018; Paerl & Huisman, 2009; Richardson et al., 2019), and evidence from marine systems indicates that cyanobacteria may adapt to warming temperatures at faster rates than do other groups of phytoplankton (Barton et al., 2020). Growth rates of other phytoplankton decline once they exceed optimal temperatures

of 15–25 °C (Huisman et al., 2018; Paerl & Huisman, 2008; 2009), though changes in growth rate responses can be quite variable among species and strains within all groups of phytoplankton (Huisman et al., 2018; Lüring et al., 2013; Rigosi et al., 2014) and other factors can be important and affect taxa differently (Freeman et al., 2020). In non-stratifying reservoirs, surface temperatures *on average* are 25.5 °C in June, after increasing by 2.4 °C since 1989. On average in stratifying reservoirs, surface water temperatures are ~26.7 °C in June after increasing by 2.2–2.7 °C since 1989 and are ~28.4 °C in August after increasing by ~1.5 °C (Table 1, [SI Appendix, Table S7]). September and October surface temperatures also have increased in these 20 reservoirs, with October experiencing the greatest rate of warming. Worsening blooms also could create positive feedbacks that further increase temperatures due to greater absorption of light energy (Kumagai et al., 2000; Moss et al., 2011). Warmer water temperatures also can affect ecosystems by increasing toxin production by cyanobacteria (Davis et al., 2009; Lüring et al., 2017; Mantzouki et al., 2018), by altering food webs through changes in the phenology and nutritional quality of phytoplankton (Winder & Schindler, 2004), and by impacting fish spawning and populations via changes in thermal and oxygen regimes (Adrian et al., 2009; Farmer et al., 2015).

The evidence of progressively earlier onset and longer durations of stratification gives further competitive advantages to cyanobacteria over other groups of phytoplankton because many species can vertically migrate in the water column to obtain nutrients and optimal light conditions for growth (Carey et al., 2012; Paerl & Huisman, 2009; Wagner & Adrian, 2009). As such, extended periods of warm temperatures and the associated increases in stratification strength and duration predicted in the future are expected to cause longer and more severe blooms (Chapra et al., 2017; Huisman et al., 2018; Ralston & Moore, 2020). However, we were unable to examine within year bloom dynamics due to data limitations. Earlier and longer durations of summer stratification also likely contributed to hypoxia beginning on average one month earlier and lasting one month longer in agricultural reservoirs. Longer durations of hypoxia in reservoirs increase the amount of time that anaerobic biogeochemical processes in sediments can contribute to internal loading of legacy nutrients (Hupfer & Lewandowski, 2008; Orihel et al., 2017) and could cause further concerns by enhancing methane production in lake sediments (Aben et al., 2017). In forested reservoirs, the lack of significant decreases in DO concentrations spanning July–October and consistent durations of hypoxia may have resulted from these being lower nutrient systems with less cyanobacterial biomass, and, therefore, likely having less accumulation of sinking organic matter in deep waters, which promotes microbial respiration (Hupfer & Lewandowski, 2008; Orihel et al., 2017).

These lengthening durations of beneficial conditions for cyanobacteria support greater nitrogen uptake and biomass production, thereby contributing to the observed decreases in NO_x and corresponding increases in TKN concentrations in the surface waters over time. The increases in TKN during this time span provide complementary evidence of worsening blooms and is indicative of greater seasonal buildup of phytoplankton biomass (organic nitrogen) and intensification of internal nutrient cycling (NH_4) within the water column, which is often associated with blooms (Cottingham et al., 2015; Yao et al., 2020). Associated with these observations, the GAM for stratifying reservoirs showed that warmer June surface water temperatures may set the stage for cyanobacteria growth, but dryer than

average summers might lessen bloom severities by possibly reducing the nutrient loads needed to fuel and sustain their growth.

The greater rates and magnitudes of increasing cyanobacteria cell densities in the agricultural reservoirs and one urban system, as compared to forested ones, indicate that changes in seasonality and warming have synergistic effects with nutrients. This synergy has been observed in field studies and experiments spanning nutrient and temperature gradients in freshwater and marine ecosystems (Beaulieu et al., 2013; Davis et al., 2009; Griffith & Gobler, 2020; Kosten et al., 2012; Rigosi et al., 2014; Wagner & Adrian, 2009), but might not always be consistent and may vary among lake types (Richardson et al., 2017; Richardson et al., 2018). Ultimately, earlier and longer seasonal warming can stimulate cyanobacteria growth rates and lengthen durations of stratification that further favor cyanobacteria, leading (1) to greater biomass production and bloom severities that increase at faster rates with higher nutrient concentrations and (2) to more severe and longer durations of deep water hypoxia. Recent results from synoptic national lake surveys further highlight the importance of warmer Spring temperatures and longer summers to greater cyanobacteria abundance (Ho & Michalak, 2020).

Lastly, warming of deep waters was another notable change with potential consequences for cyanobacteria and these reservoirs. Warming of deep waters in stratifying reservoirs during May likely reflects the earlier seasonal warming prior to stratification, and warming trends during August–October likely were associated with the greater buildup of heat as summers progressed. However, deep water temperatures in stratified lakes are typically expected to cool or remain stable when turbidity in the epilimnion increases, as would be expected with cyanobacterial blooms. This is because light energy absorbed as heat near the surface increases with higher turbidity, leading to stronger stratification and less transfer of heat to deeper waters (Richardson et al., 2017; Rose et al., 2016). This expected pattern was not evident in these reservoirs, but perhaps geomorphology, dam operations, and hydrologic dynamics unique to reservoirs could contribute to the warming of deeper waters. However, data were inadequate for examining these possibilities.

In non-stratifying reservoirs, the significant warming of deep waters during May–October likely was due to the more readily mixed water columns distributing heat to greater depths. Warming deep water temperatures, especially in non-stratifying reservoirs, could enhance the germination and mixing into the water column of cyanobacteria akinetes, or resting cells, possibly affecting bloom dynamics (Paerl, 1988; Wiedner et al., 2007). The significant warming of deep waters also likely increases rates of microbial activity that could lead to higher internal nutrient loads from sediment mineralization, which can be further exacerbated by longer durations of deep water hypoxia (Gibbons & Bridgeman, 2020; Jensen & Andersen, 1992; Orihel et al., 2017). Supporting this possibility, TKN (likely the NH_4 component), TP, and dissolved P concentrations of deep waters increased in non-stratifying reservoirs from 1987–2018, which could help explain why lower June deep water dissolved oxygen concentrations and warmer August deep water temperatures were associated with greater cyanobacteria cell densities in the GAM. Although water column mixing is unfavorable for cyanobacteria in these reservoirs, this effect may be overwhelmed by the stimulatory effects of warmer temperatures and increased internal nutrient loads.

The trends in the data, further informed by published literature, were used to conceptualize a general model that shows factors, pathways, and potential feedbacks that affect cyanobacteria cell densities and reservoir conditions (Fig. 4). Earlier, longer, and stronger stratification, warmer water temperatures, and greater amounts of nutrients directly favor cyanobacteria. Increased cyanobacterial biomass creates potential feedbacks to other processes, such as increasing nutrients via N-fixation (when applicable), intensifying nutrient uptake and recycling in the epilimnion during blooms, and increasing highly labile carbon that eventually sinks and stimulates microbial respiration that decreases deep water dissolved oxygen and increases sediment biogeochemical rates. Warming deep waters and longer durations of deep water hypoxia further stimulate microbial activity that can contribute greater internal loading of legacy nutrients from sediments, subsequently fueling cyanobacterial blooms depending on stratification strength and water column mixing. Precipitation, watershed features (e.g., topography, soils, and geology), and land use contribute nutrients via runoff, baseflow, and legacy loads over time. Although precipitation and runoff can increase nutrient loads and favor cyanobacteria to a point, too little of it could reduce nutrient loads and limit the transfer of deep water nutrients into the surface waters, thereby limiting seasonal cyanobacterial biomass. Excessive precipitation and severe storms can negatively affect cyanobacteria by increasing water column turbulence and flushing rates.

Collectively, results from our study are evidence that the predicted increases in cyanobacterial blooms associated with warming water temperatures are already occurring, could continue expanding geographically if warming trends and changes in seasonality continue, and given our experiences with the reservoirs in our data set, could remain recurrent problems once established. Globally, increases in cyanobacterial blooms are likely to complicate lake management efforts and reservoir operations given their multiple uses, cultural and economic importance, and ecosystem services, such as drinking water, flood control, and habitat important to biodiversity and food webs.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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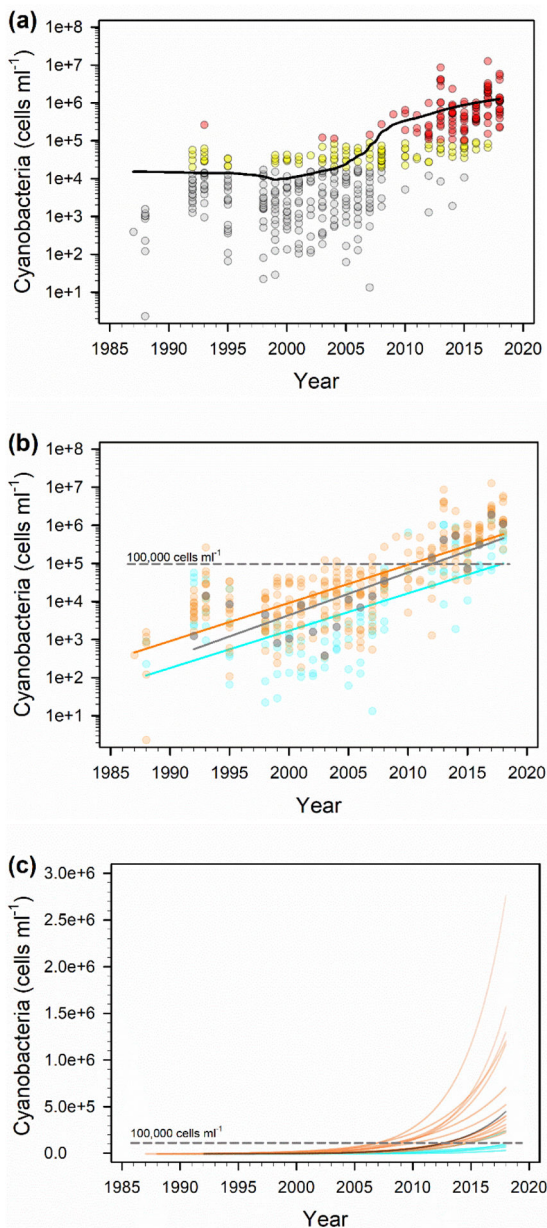


Figure 1.

Trends in maximum cyanobacteria cell densities. (a) Yearly maximum cell densities of cyanobacteria observed in each reservoir spanning 1987–2018 with a locally weighted scatter plot smoothing trend line (0.5 sampling proportion; $n = 424$). Gray, yellow, and red indicate densities posing low, moderate, and high probabilities of human health risk, respectively. (b) Yearly maximum cell densities of cyanobacteria observed in 14 reservoirs with agricultural watersheds (orange; $n = 299$), in five reservoirs with forested watersheds (cyan; $n = 104$), and in one reservoir with an urban watershed (gray; $n = 21$). Linear regressions used log-transformed cyanobacteria cell densities. (c) Fitted curves showing changes in maximum observed cyanobacteria cell densities for each reservoir over time (back calculated from linear regressions on log-transformed cyanobacteria cell densities).

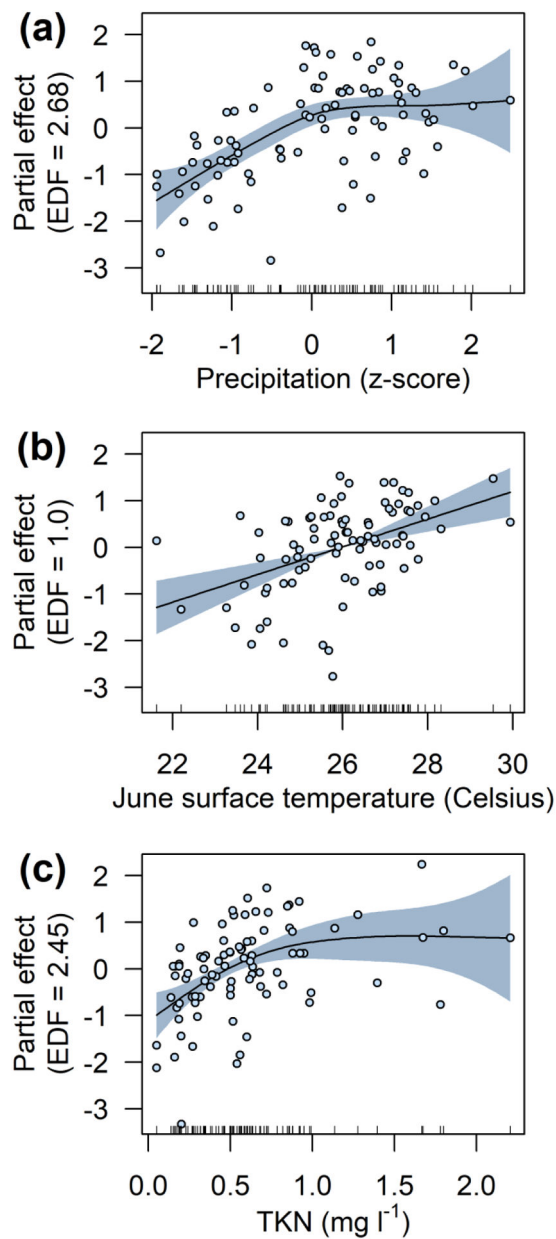


Figure 2. Generalized additive model with partial residuals (circles) showing relationships (with 95% confidence intervals) of log maximum cell densities of cyanobacteria with precipitation z-scores, June surface temperatures, and total Kjeldahl nitrogen (TKN) in reservoirs that experience seasonal stratification. Percent deviance explained = 56.3%; adjusted $R^2 = 0.534$. For the GAM, 88 observations with complete data were used for the analysis and included 23 spanning a period before blooms were common (1992–2003), 25 spanning the years in which blooms began increasing in severity (2006–2011), and 40 spanning years in which blooms have become common and severe (2012–2018); 37.5% of observations were from forested reservoirs and 62.5% were from agricultural reservoirs. EDF = expected degrees of freedom. Rug plots show distribution of the data.

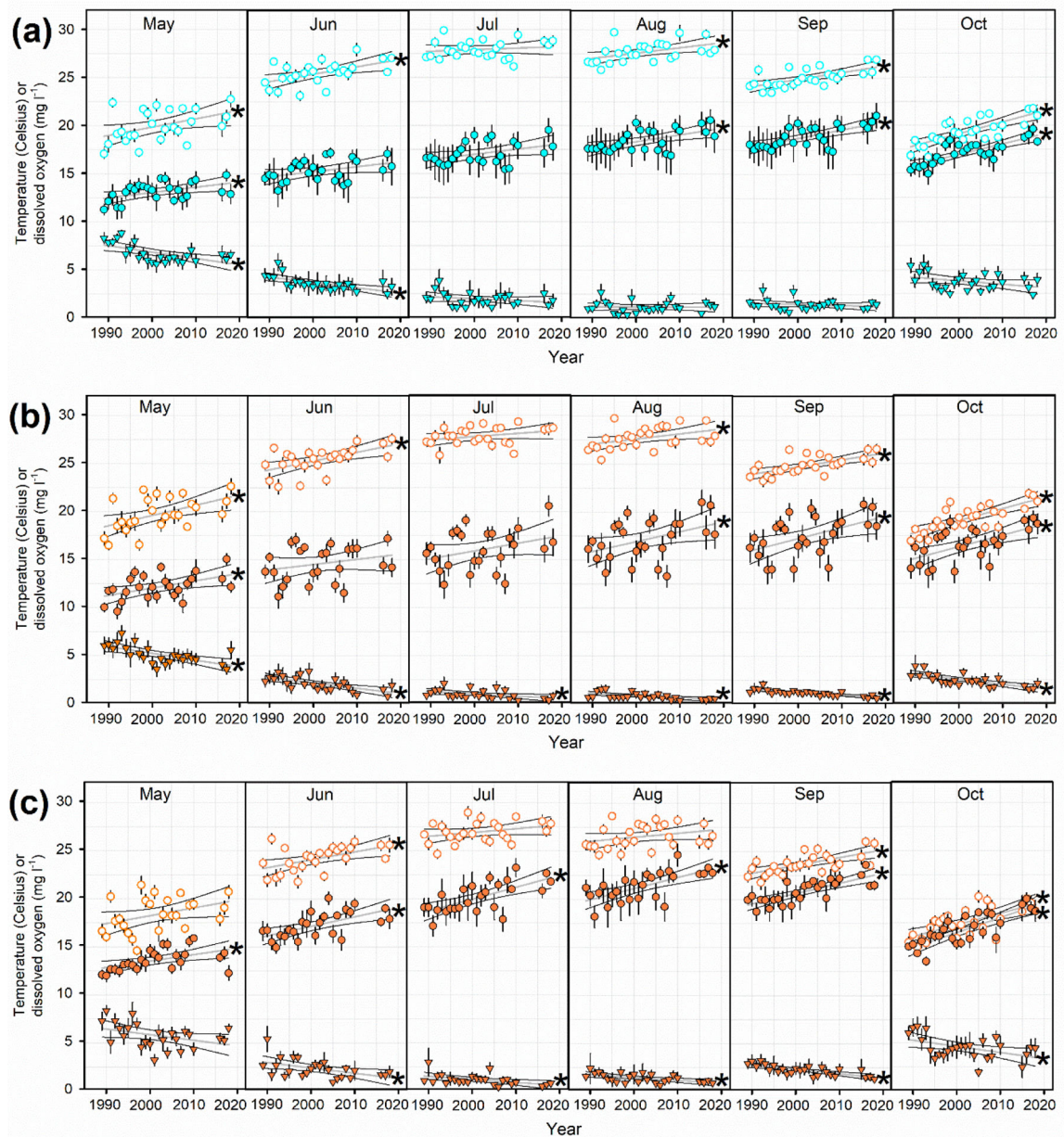


Figure 3.

Trends in temperatures and dissolved oxygen concentrations. Monthly means (with ± 1 standard error) of each year for surface (open circles) and deep water (filled circles) temperatures and deep water dissolved oxygen concentrations (triangles). (a) Reservoirs with yearly thermal stratification and forested watersheds. (b) Reservoirs with yearly thermal stratification and agricultural watersheds. (c) Reservoirs with weak or no thermal stratification and agricultural watersheds (one shallow agricultural reservoir and one shallow urban reservoir were excluded). Linear regressions with 95% confidence intervals of monthly means for each year ($n = 25$ for May–July, $n = 26$ for August–October) with asterisks denoting $P < 0.05$. See supplementary information for regression models and comparisons to Thiel-Sen slopes and Mann-Kendall tests for significant trends.

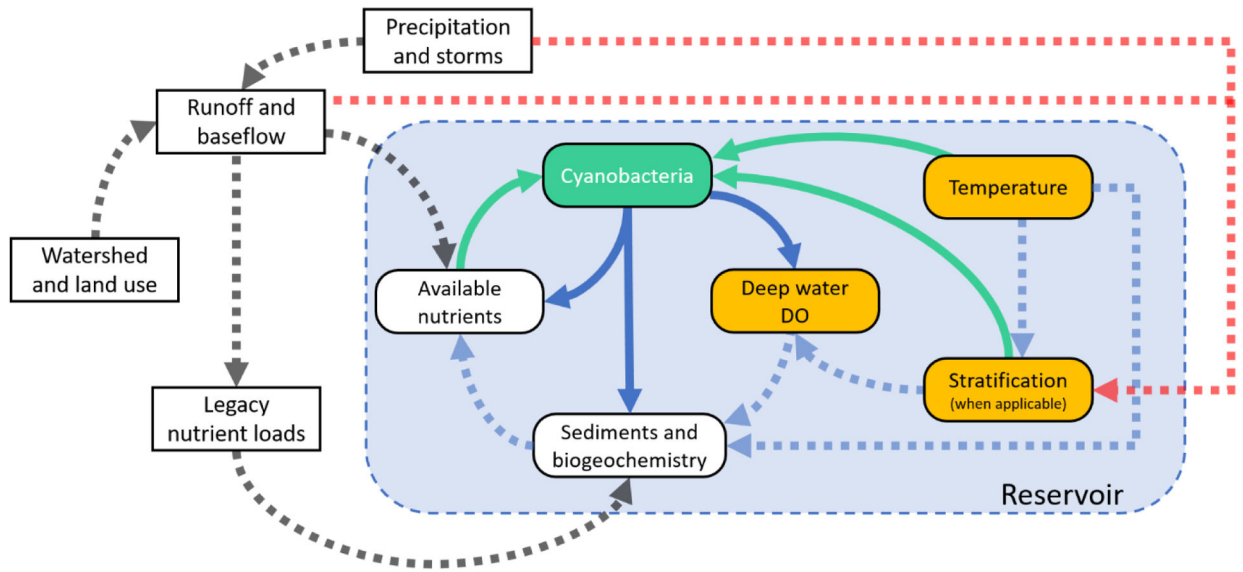


Figure 4. Conceptual model, based on results and informed by published literature, showing factors, pathways, and potential feedbacks that affect cyanobacteria and reservoir conditions. The blue box represents within reservoir dynamics affected by watershed features and climate. Orange boxes show factors with significant changes during our study’s timeframe. White boxes show factors that either did not change over time in our study or are unknown due to data limitations. Black dashed arrows are pathways by which watershed factors affect reservoir conditions. Red dashed arrows are pathways potentially leading to negative effects on cyanobacteria. Green solid arrows show direct effects favoring cyanobacteria. Blue solid arrows show potential feedbacks to other processes. Dashed blue lines are indirect pathways that could favor cyanobacteria due to warming deep waters and longer durations of deep water hypoxia.

Surface and deep water temperatures (Celsius) and deep water dissolved oxygen concentrations (mg/l) at the beginning and end of this study. Values were based on regression equations (see Table S7) for each group of reservoirs shown in Fig. 3. Bold and italic terms indicate significant and non-significant relationships, respectively. Change from 1989 to 2018 calculated before rounding.

Table 1.

	Stratifying forested reservoirs			Stratifying agricultural reservoirs			Non-stratifying agricultural reservoirs		
	1989	2018	Change	1989	2018	Change	1989	2018	Change
Surface temperature									
May	18.9	21.4	2.5	18.3	21.5	3.1	17.1	19.5	2.4
Jun	24.4	26.7	2.2	24.2	26.9	2.7	23.1	25.5	2.4
July	27.8	28.2	0.5	27.4	28.3	0.9	26.3	27.4	1.1
August	27.0	28.6	1.6	26.9	28.4	1.5	25.9	27.1	1.2
September	24.1	26.2	2.1	23.8	25.9	2.1	22.5	24.8	2.4
October	17.7	21.3	3.6	17.5	21.2	3.6	15.7	19.3	3.5
Deep temperature									
May	12.4	14.0	1.6	11.1	13.3	2.2	12.5	14.5	1.9
Jun	14.6	16.1	1.5	13.8	15.4	1.6	15.9	18.8	2.9
July	16.4	18.0	1.6	15.0	17.3	2.3	18.4	22.0	3.6
August	17.5	19.6	2.1	15.7	18.7	3.0	19.7	23.1	3.4
September	17.8	20.3	2.5	15.9	19.3	3.4	19.3	22.4	3.1
October	15.8	19.0	3.2	15.0	18.5	3.5	14.6	19.2	4.5
Deep dissolved oxygen									
May	7.5	5.6	-1.9	6.0	3.9	-2.1	6.3	4.6	-1.7
Jun	4.2	2.6	-1.6	2.7	1.1	-1.6	2.8	1.2	-1.6
July	2.2	1.6	-0.6	1.2	0.5	-0.7	1.3	0.4	-0.9
August	1.1	1.1	0.0	0.9	0.3	-0.7	1.6	0.7	-0.8
September	1.6	1.3	-0.3	1.4	0.5	-0.8	2.6	1.3	-1.3
October	4.2	3.2	-1.0	3.0	1.5	-1.5	5.0	3.2	-1.9