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# Cyanobacterial Contribution to Annual Cycles of Phytoplankton in Lake Murray, SC

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**Abstract.** Freshwater lakes provide valuable recreational and tourism resources and are a major source of municipal drinking water for local communities. A primary management goal for lake systems is the maintenance of good water quality and a healthy aquatic ecosystem. Blooms of harmful or noxious species of cyanobacteria can result in severe water quality degradation. The purpose of this project was to provide baseline data on phytoplankton community composition, with special emphasis on cyanobacteria, and water quality parameters for Lake Murray, SC. The objective of this study was to determine the annual cyanobacterial contribution to total phytoplankton biomass in the lower reaches of Lake Murray. Measurements for this study were obtained at weekly to biweekly intervals from May 2021 to August 2022 on the northeast side of Lake Murray Dam, SC. Phytoplankton community composition was determined using a combination of high-performance liquid chromatography (HPLC) and ChemTax methods to measure the relative abundances of different algal groups. The phytoplankton community in Lake Murray is composed of a diverse assemblage of primarily green algae, diatoms, cyanobacteria, cryptophytes, and dinoflagellates. Community structure varied seasonally and annually. Total phytoplankton biomass remained below 7 µg of chl *a* $l^{-1}$ and never reached "bloom" proportions (e.g., > 40 µg of chl *a* $l^{-1}$). Planktonic cyanobacteria were present year-round in the lower reaches of Lake Murray and comprised 5–40% of the total phytoplankton biomass. Peaks in cyanobacteria abundance occurred during the late summer months. Even at the peak in August 2021, concentrations of cyanobacteria were low (1.79 µg chl *a* $l^{-1}$). Over annual cycles, cyanobacteria had a median chl a concentration of 0.63 µg $l^{-1}$ and a median contribution of 14.9%. Although we were unable to identify any specific causal mechanisms for the fluctuations in cyanobacterial biomass, we demonstrated that cyanobacteria are a consistent component of the phytoplankton community in lower Lake Murray. Baseline measures of phytoplankton during "good" water quality conditions provide invaluable data essential for managers to establish criteria for early prediction of bloom events and evaluate the effectiveness of mitigation strategies. Departures from the norm, especially during the summer and early fall, may signal the beginning of a cyanobacterial (or other algal group) bloom and provide an early warning for recreational users and municipal water intakes.

## INTRODUCTION

Freshwater lakes and rivers are a major source of municipal drinking water and provide valuable recreational and tourism resources to local communities. Maintenance of good water quality and healthy aquatic ecosystems is a primary management goal for these systems. Dense phytoplankton blooms, especially those composed of harmful or noxious species of cyanobacteria, can result in severe water quality degradation (Anderson et al. 2002; Rastogi et al. 2015; Chorus and Welker 2021). Blooms of cyanobacteria are an emerging and growing problem for many lake systems in the southeastern US (Coffer et al. 2020). Contamination of municipal water intakes can impact large populations and incur very expensive water polishing procedures (Jetoo et al. 2015; Coffer et al. 2021; Mustapha et al. 2021). Unfortunately, more frequent and larger magnitude cyanobacterial blooms are forecast due to increasing eutrophication and a warming climate (Paerl and Huisman 2008, O'Neil et al. 2012; Huisman et al. 2018). A mechanistic understanding of biotic and abiotic conditions that promote large nuisance and toxic phytoplankton blooms is essential for developing effective mitigation and management strategies (O'Neil et al. 2012; Mantzouki et al. 2016; Wurtsbaugh et al. 2019). Furthermore, measurements of baseline non-bloom conditions are invaluable for identifying causal mechanisms, establishing mitigation targets, and assessing the effectiveness of management actions (Buelo et al. 2022). In addition to standard water quality parameters, monitoring efforts should include measurements of phytoplankton community composition to provide insights into the ecological context within which blooms are initiated and sustained (Srivastava et al. 2013; Mantzouki et al. 2016). Unusual changes in phytoplankton community composition may provide an early warning for impending nuisance or toxic algal blooms (Lee et al. 2015).

Cyanobacterial blooms pose serious issues for water quality, fisheries resources, aquaculture, and toxicity to animals and humans (Huisman et al. 2018). Foul odors, undesirable tastes (off-flavors), hypoxia and anoxia of underlying waters, and fish kills are all common products of cyanobacterial blooms (O'Neil et al. 2012; Wurtsbaugh et al. 2019; Chorus and Welker 2021). Recreational use and aesthetic values of affected waters are often seriously impaired by high toxin concentrations, hypoxia/anoxia, and fish kills. In addition, nutrient fluxes and biogeochemical cycling can be altered by the substantial (and sometimes dominant) contribution of cyanobacteria to phytoplankton biomass (Paerl and Pinckney 1996). Management-wise, there is a compelling need to be proactive in identifying causative agents and effective steps to mitigate the most harmful effects of freshwater cyanobacterial blooms (Paerl and Huisman 2008; O'Neil et al. 2012; Huisman et al. 2018).

Lake Murray, SC is a 182 km$^2$ man-made hydroelectric reservoir with municipal water intakes and is a center of recreational activities for the region. The cities of Columbia and West Columbia have an average combined intake of 155 m$^3$ (41 million gallons) per day. The primary water source for the lake is the Saluda River and the local watershed contains residential developments, marinas, and managed forests. From 2018–2020, the lake experienced high levels of unfavorable natural chemicals (geosmin and methylisoborneol produced by cyanobacteria) that tainted municipal drinking water (Mustapha et al. 2021). Between 2021–22, concentrations of cyanobacterial toxins (microcystins) in Lake Murray ranged from 0 – 0.50 µg l$^{-1}$ with a median of 0.14 µg l$^{-1}$ and were below the EPA-recommended contact recreational value for water closures (8 µg l$^{-1}$) (Emily Bores, SC DHEC, pers. comm.; EPA 2019). Although the sampling location for the current study has not experienced large blooms of cyanobacteria, blooms commonly occur in the upper areas of Lake Murray.

The purpose of this project was to provide baseline data on phytoplankton community composition, with special emphasis on cyanobacteria, and water quality parameters for Lake Murray, SC. The goal was to provide data on "normal" conditions and assess the contribution of cyanobacteria to the total phytoplankton community over weekly to yearly time intervals. Although a large cyanobacterial bloom did not occur during our study period, our results provide a valuable reference for baseline conditions in the downstream region of Lake Murray.

## MATERIALS AND METHOD

### STUDY SITE

Measurements for this study were obtained from a floating dock at the recreational boat ramp on the northeast side of Lake Murray dam (34.0664°N, 81.2234°W) (Fig. 1). Water depth at the sampling site ranged from 5–6 m. Samples were collected around noon at weekly to biweekly intervals from May 2021 to August 2022. This sampling frequency was selected to balance logistical constraints and the ability to detect bloom events.

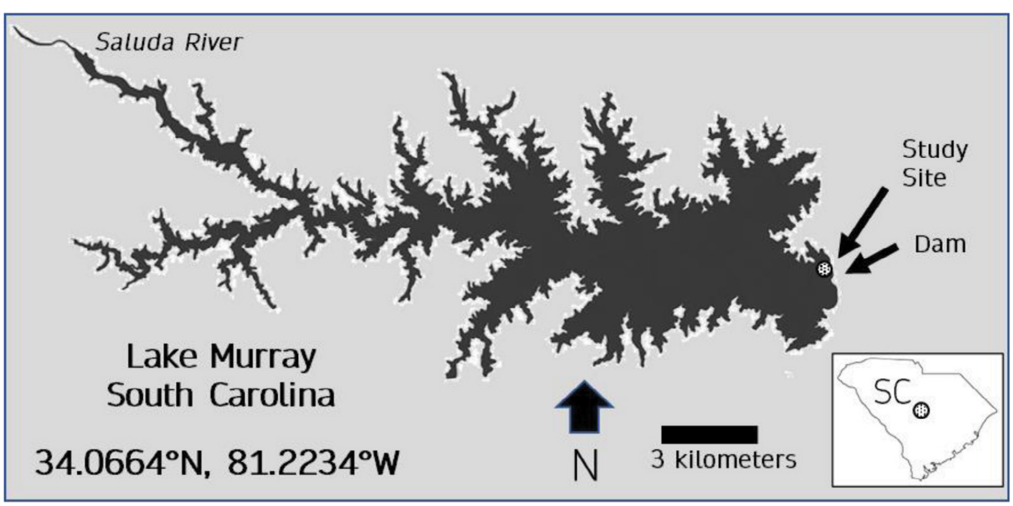


**Figure 1.** Location map for the study site at Lake Murray, SC.

### FIELD SAMPLING

Water quality measurements were obtained using a YSI 6820 multiparameter sonde to record depth, temperature, conductivity, dissolved oxygen, and pH profiles. *In situ* irradiance profiles for photosynthetically active radiation (PAR) were measured at 0.5 m intervals using a Li-Cor 193SA spherical quantum sensor. Replicate (3) water samples were collected from the upper 1 m of the water column using an integrated sampler and at 4 m depth using a Niskin bottle and transported on ice to the lab. For phytoplankton analyses, 250 ml of water was vacuum (-50 kPa) filtered onto 2.5 cm GF/F glass microfiber filters and stored at -80˚C.

### PHOTOPIGMENT ANALYSIS

High-performance liquid chromatography (HPLC) was used to determine chemosystematic photosynthetic pigment concentrations. Samples were lyophilized for 24 h at -50° C, placed in 90% acetone (1 ml) and extracted at -20° C for 18–20 h. Filtered extracts (0.45 µm, 250 µl) were injected into a Shimadzu 2050 HPLC equipped with a monomeric (Rainin Microsorb-MV, 0.46 x 10 cm, 3 µm) and a polymeric (Vydac 201TP54, 0.46 x 25 cm, 5 µm) reverse-phase C18 column in series. A nonlinear binary gradient of 80% methanol:20% 0.50 M ammonium acetate and 80% methanol:20% acetone was the mobile phase (Pinckney et al. 1996, 2001). Absorption spectra and chromatograms (440 ± 4 nm) were acquired using a Shimadzu SPD-M10av photodiode array detector. Pigment peaks were identified by comparison of retention times and absorption spectra with pure carotenal and chlorophyll standards (DHI, Denmark). The synthetic carotenoid β-apo-8'-carotenal (Sigma) was used as an internal standard.

ChemTax (v. 1.95) was used to estimate the relative concentrations of major algal groups based on measured photopigment concentrations (Pinckney et al. 2001; Higgins et al. 2011). Total chlorophyll *a* (chl *a*) was partitioned into algal group (e.g., diatoms, cyanobacteria, cryptophytes, etc.) abundances. Samples were examined by qualitative microscopy to confirm algal groups included in the ChemTax analysis. The initial ratio matrix randomization procedure with 60 simulations was used to minimize errors in algal group biomass resulting from inaccurate pigment ratio seed values (Higgins et al. 2011).

### NUTRIENT ANALYSIS

Nutrient concentrations (orthophosphate, $PO_4^{3-}$; nitrite, $NO_2^-$; nitrate, $NO_3^-$; and ammonium, $NH_4^+$) were measured for filtered (0.2 µm) samples in summer 2022 only using a Seal Analytical AQ300 nutrient analyzer. Aliquots were frozen (-80˚C) and analyzed within 1 month of collection. Analytical methods used for the determination of inorganic N were Standard Methods 4500-NH3 G, 4500-NH3 F, 4500-NO3- E, 4500-NO3- F (Eaton et al. 2005). Standard Methods 4500-P E and 4500-P F methods were used for measures of inorganic P (Eaton et al. 2005).

## RESULTS

The phytoplankton community in Lake Murray was composed of a diverse assemblage of algal groups including green algae (euglenophytes and chlorophytes), diatoms, cryptophytes, cyanobacteria, and dinoflagellates. A comparison of surface and bottom measurements of the concentrations of the different algal groups was performed using a paired t-test. There was no significant difference in the surface and bottom concentrations (in µg of chl *a* $l^{-1}$) of cyanobacteria ($t = 0.531$, $p = 0.599$) or euglenophytes ($t = -1.597$, $p = 0.119$). However, surface and bottom concentrations of total chl *a* ($t = -3.351$, $p = 0.002$), chlorophytes ($t = -3.015$, $p = 0.005$), dinoflagellates ($t = -2.097$, $p = 0.043$), cryptophytes ($t = -2.954$, $p = 0.006$), and diatoms ($t = -2.668$, $p = 0.011$) were significantly different with higher concentrations in the bottom water (4 m) samples. Although there were significant statistical differences between surface and bottom concentrations, the differences are very small (< 1 µg chl *a* $l^{-1}$) and are most likely not ecologically relevant.

Surface and bottom phytoplankton concentrations were pooled (6 replicates for each date) to analyze community composition differences over the study period (Fig. 2). Total phytoplankton biomass (µg chl *a* $l^{-1}$) ranged from 1.94—6.56 µg chl *a* $l^{-1}$ over the study period and peaked during the summer months. The mean phytoplankton concentration was 4.29 (SD = 1.13, median = 4.37) µg chl *a* $l^{-1}$. The highest concentrations occurred in August (ca. 6 µg chl *a* $l^{-1}$). However, the major contributors differed in 2021 and 2022. Green algae and cyanobacteria were the major components in 2021 while diatoms and cryptophytes were dominant in 2022.

The contribution of cyanobacteria to total phytoplankton biomass was calculated for each of the sampling dates (Fig. 3). Concentrations of cyanobacteria ranged from 0.04 to 1.79 µg of chl *a* $l^{-1}$ (mean = 0.71, median = 0.63, SD = 0.42). In terms of the percent contribution of cyanobacteria to total phytoplankton biomass, values ranged from 2.0 to 40.6% (mean = 16.1, median = 14.9, SD = 8.5). Cyanobacteria concentrations and contributions were usually highest during mid and late summer, with a notable peak in October 2021. In May and June 2022, cyanobacteria concentrations were much lower than the previous year, which corresponded with an increase in the relative concentrations of diatoms and cryptophytes.

The relationship between cyanobacterial concentrations and water temperature was examined using linear regression analysis (Fig. 4). Cyanobacterial abundance was weakly related to temperature (adj $r^2 = 0.18$, $n = 33$, $p = 0.008$). Highest concentrations occurred at temperatures above 25°C, with a maximum at 28°C.

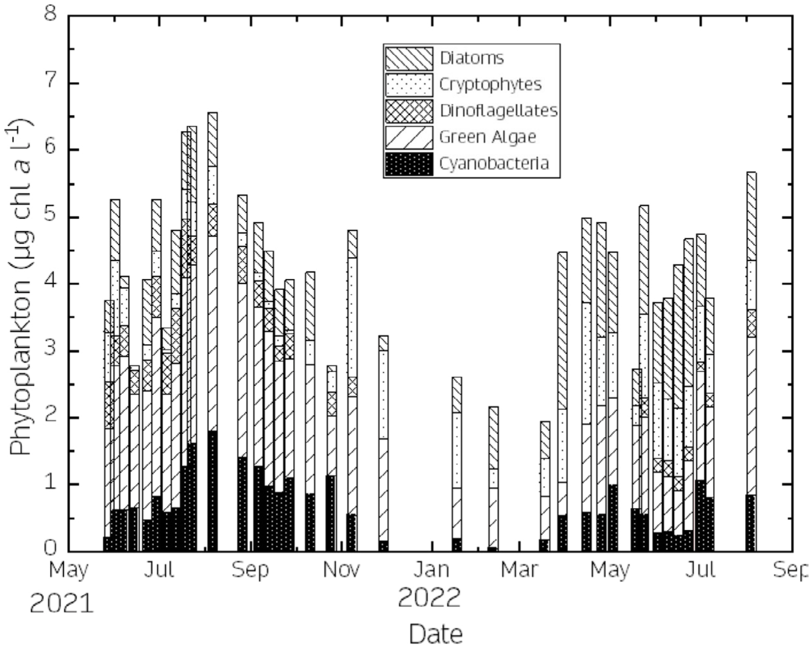


**Figure 2.** Stacked bar chart for phytoplankton group concentrations. Paired data for surface and bottom (4 m) were pooled for each sampling date.

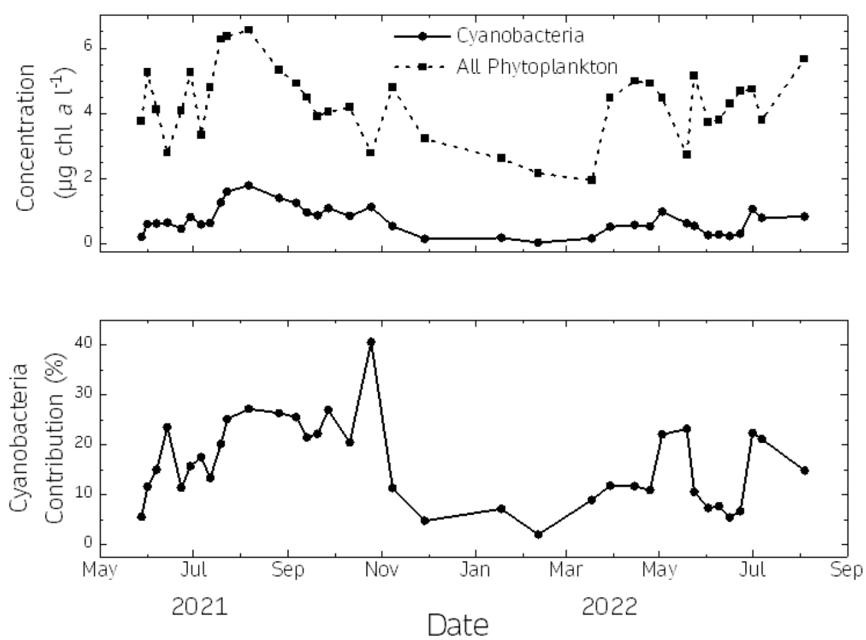


**Figure 3.** Total phytoplankton and cyanobacteria concentrations and the percent contribution of cyanobacteria to total phytoplankton biomass (chl *a*).

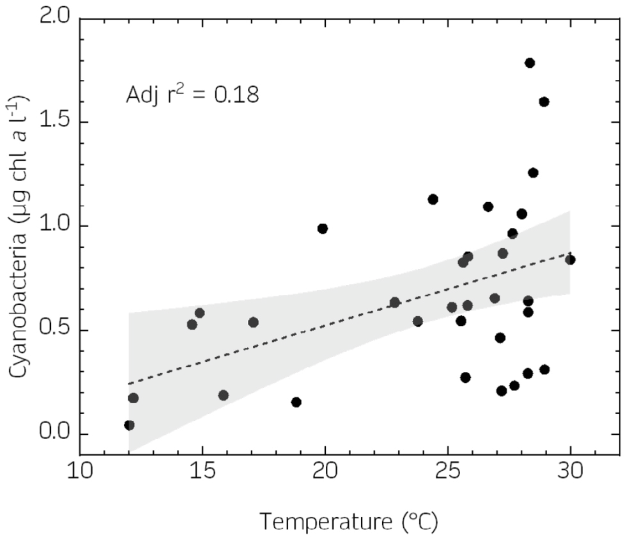


**Figure 4.** Scatterplot and regression of cyanobacteria concentration vs. water temperature. Shaded area is the 95% confidence interval.

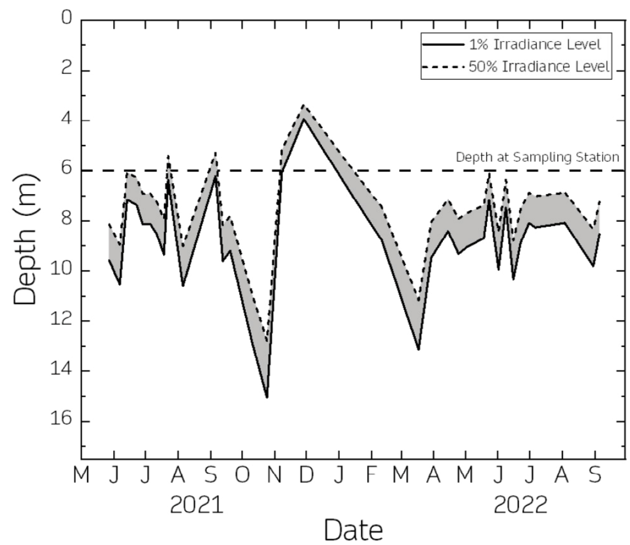


**Figure 5.** Depth of the photic zone calculated from $k_d$ measurements.

The diffuse attenuation coefficient ($k_d$) for PAR was determined using a linear regression of the log10 transformed values. Values of $k_d$ ($m^{-1}$) ranged from 0.10–1.17 with a mean of 0.54 (sd = 0.16). The average depth of the euphotic zone (1% of surface PAR) was calculated for each sampling date using the equation $I_z = I_0e^{-kz}$, where Iz is the calculated irradiance (µmol photons $m^{-2}$ $s^{-1}$), I0 is the surface irradiance, k is the diffuse attenuation coefficient ($m^{-1}$) and z is depth (m) (Fig. 5). The euphotic zone ranged from 3.9 to 15.0 m depth and averaged 8.8 (± 2.1 SD, median = 8.7, n = 35) m. Scatterplots of cyanobacterial concentrations and percent contribution to total phytoplankton biomass indicated no significant relationship with $K_d$, the diffuse attenuation coefficient for PAR (water clarity) (Fig. 6).

Nutrient concentrations were only determined for March–June 2022 (Fig. 7). Dissolved inorganic phosphorus concentrations were below the limits of detection (< 0.1 µM $PO_4^{3-}$). Total dissolved inorganic nitrogen (DIN as $NO_2^-$ + $NO_3^-$ + $NH_4^+$) concentrations ranged from 5.1–32.4 µM N, with a mean of 13.8 (SD = 7.2) and a median of 11.0.

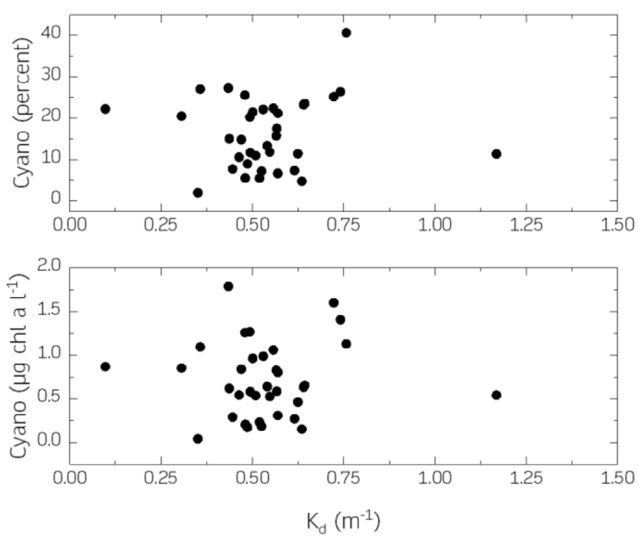


**Figure 6.** Scatterplots cyanobacteria concentrations and percent contribution of cyanobacteria to total phytoplankton biomass vs. diffuse attenuation coefficient ($k_d$).

## DISCUSSION

The phytoplankton community in Lake Murray was composed of a diverse assemblage of primarily green algae, diatoms, cyanobacteria, cryptophytes, and dinoflagellates. Community structure varied seasonally and annually. Though there were significant differences in surface and bottom concentrations for many of the phytoplankton groups, differences were so small there is likely no ecological relevance. The general trend showed bottom concentrations were slightly higher than surface concentrations, potentially indicating photoacclimation at bottom depths or photoinhibition at the surface. Further studies would need to be performed to confirm either mechanism. Total phytoplankton biomass remained below 7 µg of chl *a* $l^{-1}$ and never reached "bloom" proportions (e.g., > 40 µg of chl *a* $l^{-1}$). Planktonic cyanobacteria were present year-round in the lower reaches of Lake Murray and comprised 5–40% of the total phytoplankton biomass. Peaks in cyanobacteria

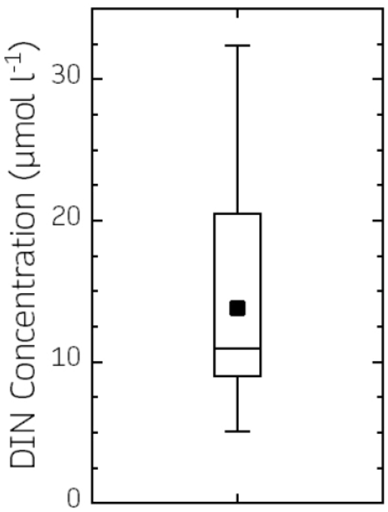


**Figure 7.** Boxplot for dissolved inorganic N (DIN) for the period March–June 2022. The line in the box is the median, the black square is the mean, the box shows the 25th and 75th percentiles, and lines indicate the 5th and 95th percentiles.

abundance occurred during the late summer months. Even at the peak in August 2021, concentrations were low (1.79 μg chl *a* $l^{-1}$). Over annual cycles, cyanobacteria had a median chl *a* concentration of 0.63 μg $l^{-1}$ and a median contribution of 14.9%.

Cyanobacterial abundance was weakly (but significantly) correlated with water temperature. The warm summer months are typically the optimal time for cyanobacterial blooms in temperate lakes (O'Neil et al. 2012; Chorus and Welker 2021). In contrast, cyanobacterial abundance was not correlated with turbidity or the depth of light penetration. The lack of correlation is unusual, as cyanobacteria concentration relative to other phytoplankton species tends to increase with increasing turbidity due to the buoyancy of cyanobacterial cells (Grobbelaar 2009; Wurtsbaugh et al. 2019). However, total phytoplankton biomass was too low to significantly affect turbidity. Limited nutrient sampling suggests P may be a limiting nutrient for phytoplankton growth in lower Lake Murray (Tilman et al. 1982). Cyanobacteria are highly competitive for low concentrations of dissolved inorganic phosphorus (DIP) but are also capable of using dissolved organic phosphorus (DOP) (Anderson et al. 2002; O'Neil et al. 2012). Utilization of DOP may infer a competitive advantage when DIN concentrations are high, as seen in our study (Tilman et al. 1982; Anderson et al. 2002).

In 2006, South Carolina Electric and Gas (SCE&G) undertook an extensive study of water quality in Lake Murray (SCE&G 2006). The primary parameters of interest in the study were pathogens, temperature, dissolved oxygen, nutrients, chlorophyll a, and water clarity. The lower region of Lake Murray near the dam had very low total phosphorus (TP) concentrations (< 0.02 mg $l^{-1}$) and have been declining since 1947. However, chl *a* concentrations have remained nearly constant (ca. 7 μg $l^{-1}$) over the past 50 years. The results of the current study found that chl a concentrations near the Lake Murray dam ranged from 2–7 μg $l^{-1}$ and suggest that total phytoplankton abundance in this region of the lake are stable under the current conditions. Secchi depth in the SCE&G (2006) study was reported at 2.7 m, or an approximate diffuse attenuation coefficient ($k_d$) of 0.6 (Castillo-Ramirez et al. 2020). Likewise, the $k^d$ of 0.54 m-1 determined in our study suggests that water clarity has also remained nearly constant. A recent two-dimensional water quality model (CE-QUAL-W2) for Lake Murray was developed to better understand causal mechanisms for low dissolved oxygen concentrations and eutrophication in the upper region of the lake (REM 2006). Model runs indicated that water quality issues could only be addressed reasonably using phosphorus reduction in the watershed.

This study surveyed a single location in a very large lake. Clearly, other regions of Lake Murray experience very different conditions. The intent is that our sampling location serve as a "sentinel" site for the lower lake region near the dam. Unlike multiple other studies, both published and in the gray literature, we focused our efforts on quantitatively assessing temporal variations in phytoplankton community composition. Although we were unable to identify any specific causal mechanisms for the fluctuations in cyanobacterial biomass, we demonstrated that cyanobacteria are a consistent component of the phytoplankton community in lower Lake Murray. Our results provide a valuable baseline for determining conditions of good water quality. Departures from the norm, especially during the summer and early fall, may signal the beginning of a cyanobacterial (or other algal group) bloom and provide an early warning for recreational users and municipal water intakes (Kibuye et al. 2021).

Lake and regulatory managers have the difficult task of recommending strategies for preventing nuisance and/or harmful algal blooms in lake systems (Rastogi et al. 2015; Huisman et al. 2018). In addition, they are responsible for setting mitigation targets for the restoration of good water quality. Both tasks require knowledge of "normal conditions" prior to experiencing the perturbation event (O'Neil et al. 2012; Rastogi et al. 2015). Baseline measurements of water quality parameters as well as phytoplankton community composition provide invaluable data essential for establishing criteria for early prediction of bloom events and evaluating the effectiveness of mitigation strategies (Srivastava et al. 2013; Paerl and Huisman 2008; Huisman et al. 2018; Wurtsbaugh et al. 2019).

## CONCLUSION

The cyanobacterial contribution to total phytoplankton biomass in the surface waters of the lower region of Lake Murray averaged 15% in 2021–2022 but ranged from 2 to 41%. Cyanobacterial biomass ranged from near 0 to 1.8 µg of chl *a* $l^{-1}$, with a median annual value of 0.63 µg $l^{-1}$. We were unable to attribute cyanobacterial abundances with any of the measured water quality parameters. Assessments of phytoplankton community composition during "good" water quality conditions provide invaluable baseline data for evaluating the effectiveness of mitigation strategies following harmful algal bloom events. Further studies of cyanobacterial concentrations in Lake Murray should explore the relationship between cyanobacterial concentrations and nutrient limitation, specifically P limitation. Additionally, nearby lakes should be sampled in conjunction with Lake Murray to determine how water management strategies may change in aquatic ecosystems in temperate regions.

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## REFERENCES

Anderson D, Glibert P, Burkholder J. Harmful algal blooms and eutrophication: Nutrient sources, composition, and consequences. Estuaries. 2002;25:704–726.

Buelo C, Pace M, Carpenter S, Stanley E, Ortiz D, Ha D. Evaluating the performance of temporal and spatial early warning statistics of algal blooms. Ecological Applications. 2022;32:e2616.

Castillo-Ramírez A, Santamaría-del-Ángel E, González-Silvera A, Frouin R, Sebastiá-Frasquet M-T, Tan J, Lopez-Calderon J, Sánchez-Velasco L, Enríquez-Paredes L. A new algorithm to estimate diffuse attenuation coefficient from secchi disk depth. Journal of Marine Science and Engineering. 2020;8:558.

Chorus I, Welker M. Toxic cyanobacteria in water. 2nd edition. Boca Raton (FL): CRC Press; 2021.

Coffer M, Schaeffer B, Darling J, Urquhart E, Salls W.Quantifying national and regional cyanobacterial occurrence in US lakes using satellite remote sensing. Ecological Indicators. 2020;111:105976.

Coffer M, Schaffer B, Foreman K, Porteous A, Loftin K, Stumpf R, Werdell P, Urquhart E, Albert R, Darlling J.Assessing cyanobacterial frequency and abundance at surface waters near drinking intakes across the United States. Water Research. 2021;201:117377.

Eaton AD, Clesceri LS, Rice EW, Greenberg AE.. Standard methods for the examination of water and wastewater. 21st edition. Washington (DC): American Public Health Association; 2005.

EPA. Recommended human health recreational ambient water quality criteria or swimming advisories for microcystins and cylindrospermopsin. EPA. 2019;822-R-19-001.

Grobbelaar JU. Turbidity. In: Likens GE, editor. Encyclopedia of inland waters. Amsterdam (NL): Elsevier Inc.; 2009. p. 699–704.

Higgins H, Wright S, Schlüter L. Quantitative interpretation of chemotaxonomic pigment data. In: Roy S, Llewellyn CA, Egeland ES, Johnsen G, editors. Phytoplankton pigments. New York: Cambridge University Press; 2011.

Huisman J, Codd G, Paerl H, Ibelings B, Verspagen J, Visser P. Cyanobacterial blooms. Nature Reviews Microbiology. 2018;16:471–483.

Jetoo S, Grover V, Krantzberg G. The Toledo drinking water advisory: Suggested application of the water safety planning approach. Sustainability. 2015;7:9787–9808.

Kibuye F, Zamyadi A, Wert C. A critical review on operation and performance of source water control strategies for cyanobacterial blooms: Part II–mechanical and biological control methods. Harmful Algae. 2021;109: 102119.

Lee T, Rollwagen-Bollens G, Bollens S. The influence of water quality variables on cyanobacterial blooms and phytoplankton community composition in a shallow temperate lake. Environmental Monitoring and Assessment. 2015;187:315.

Mantzouki E, Visser P, Bormans M, Ibelings B. Understanding key ecological traits of cyanobacteria as a basis for their management and control in changing lakes. Aquatic Ecology. 2016;50:333–350.

Mustapha S, Tijani J, Ndamisto M, Abdulkareem A, Shuaib D, Mohammed A. A critical review on geosmin and 2-methylisoborneol in water: Sources, effects, detection, and removal techniques. Environmental Monitoring and Assessment. 2021;193:204.

O'Neil J, Davis T, Burford M, Gobler C.. The rise of harmful cyanobacterial blooms: The potential roles of eutrophication and climate change. Harmful Algae. 2012;14:313–334.

Paerl H, Huisman J. Blooms like it hot. Science. 2008;320:57–58.

Paerl H, Pinckney J. A mini-review of microbial consortia: Their roles in aquatic production and biogeochemical cycling. Microbial Ecology. 1996;31:225–247.

Pinckney J, Millie D, Howe K, Paerl H, Hurley J.. Flow scintillation counting of 14C-labeled microalgal photosynthetic pigments. Journal of Plankton Research. 1996;18:1867–1880.

Pinckney J, Richardson T, Millie D, Paerl H.. Application of photopigment biomarkers for quantifying microalgal community composition and *in situ* growth rates. Organic Geochemistry. 2001;32:585–595.

Rastogi R, Madamwar D, Incharoensakdi A. Bloom dynamics of cyanobacteria and their toxins: Environmental health impacts and mitigation strategies. Frontiers in Microbiology. 2015;6:1254.

Sawyer A, Ruane R. Calibration of the CE-QUAL-W2 model for Lake Murray. REM (Reservoir Environmental Management, Inc.). [2006; accessed 2023 Mar 28]. https://www.saludahydrorelicense.com/documents/LakeMurrayW2Report-12-06Final.pdf.

SCE&G (South Carolina Electric & Gas). Saluda project (FERC No. 516) Lake Murray water quality report. [2006; accessed 2023 Mar 28]. https://www.saludahydrorelicense.com/documents/LakeMurrayWaterQualityReport.pdf.

Srivastava A, Singh S, Ahn C-y, Oh H-M, Asthana R. Monitoring approaches for a toxic cyanobacterial bloom. Environmental Science and Technology. 2013;47:8999–9013.

Tilman D, Kilham S, Kilham P. Phytoplankton community ecology: The role of limiting nutrients. Annual Review of Ecology and Systematics. 1982;13:349–372.

Wurtsbaugh W, Paerl H, Dodds W. Nutrients, eutrophication and harmful algal blooms along the freshwater to marine continuum. WIREs Water. 2019;1373.