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REVIEW

Historic and recent trends of cyanobacterial harmful algal blooms and environmental conditions in Clear Lake, California: A 70-year perspective

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Clear Lake is a large, natural lake in northern California, USA, with many beneficial uses but also substantive environmental issues. The lake has a long history of water quality problems including mercury contamination, pesticide usage, invasive species, and high rates of primary production. In recent years, an increase in cyanobacterial harmful algal blooms (cyanoHABs) has been documented in the lake, adding to the environmental issues faced by aquatic species present in the lake and the local community. Extensive observations of various physical, chemical, and biological parameters in Clear Lake began in the mid-1900s. The most pertinent of these data sets and findings have been reviewed and analyzed with the intent of improving our understanding of the causes and drivers of cyanoHABs, toxin production, and identifying data gaps. Several parameters including average annual water temperature have remained relatively constant over the past 70 years, although the seasonally averaged water temperatures have shifted in a manner that may now favor cyanobacterial dominance. Clear Lake has also witnessed recent changes in several environmental variables such as total phosphorus concentrations that might contribute to blooms. An analysis of lake conditions prior to and following the enactment of a total maximum daily load (TMDL) for phosphorus in 2007 indicates little measurable influence on total phosphorus concentrations in Clear Lake. The present trajectory of lake chemistry suggests that additional research and management efforts will be needed to address the recurrence of cyanoHABs in the future. Future lake management strategies should include consideration of the role of internal nutrient loads to lessen cyanoHABs. Furthermore, a better understanding of cyanobacterial community interactions and top-down effects on bloom formation within the lake can help guide future cyanoHAB management strategies.

Keywords: Clear Lake, Cyanobacteria, Harmful algal blooms, Cyanotoxins, Eutrophication

1. Introduction

Freshwater lakes worldwide are facing increasing impacts from climatic and anthropogenic stressors including droughts, increasing temperatures, anthropogenic nutrient inputs, and hydromodifications (Smith, 2003; Paerl et al., 2018; Plaas and Paerl, 2021). Many lakes today are experiencing increasing eutrophication, particularly in regions where agriculture is intensive, or human occupation is high (Hobaek et al., 2012; Withers et al., 2014). There are multiple effects of eutrophication in these ecosystems that include reductions in dissolved oxygen concentrations, elevated pH, and reductions in water clarity (Smith et al., 1999). Additionally, recent increases in harmful algal blooms, particularly those caused by cyanobacteria (cyanobacterial harmful algal blooms [cyanoHABs]) have become a major concern for the health and safety of inland waters (Brooks et al., 2017).

Cyanobacteria are collectively capable of the production of a wide array of toxic compounds (cyanotoxins) with physiological effects including hepatotoxic, neurotoxic, or other cytotoxic effects. The ecological functions of these compounds are still poorly characterized but may involve allelopathic activities, grazer deterrence, or extracellular signaling (El-Shehawy et al., 2012). Regardless of their purpose, cyanotoxins are hazardous to humans, domestic

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animals, and wildlife through the ingestion of water and aquatic plants or animals, direct contact with water or the inhalation of aerosolized toxins in the air near contaminated water bodies (Backer et al., 2008; Carmichael and Boyer, 2016; Figgatt et al., 2017).

Our knowledge of the existence of toxins produced by marine and freshwater phytoplankton is more than a century old (Carmichael, 2008), but recent reviews have documented their expanding distributions, frequency, and severity during the past few decades (Pearson et al., 2016; Olson et al., 2020). This new understanding of cyanoHABs is due in part to our improved ability to recognize and detect these events, as well as increases in their accounts in public media (Pick, 2016), but there is also ample information to support the case for their recent global expansion (Huisman et al., 2018; Ho et al., 2019; Svirčev et al., 2019). Natural and increasingly anthropogenically mediated eutrophication of inland waters has been implicated as the major factor promoting the global expansion of cyanoHABs, exacerbated by drought and increased temperature which tend to promote the dominance of cyanobacteria in natural phytoplankton communities (Paerl and Paul, 2012; Paerl and Otten, 2013; Brooks et al., 2017). Given present climate change scenarios, cyanoHABs are projected to continue to increase in extent and magnitude (Paerl and Huisman, 2009; O'Neill et al., 2012; Paerl and Otten, 2013).

1.1. Clear Lake background

Clear Lake is the largest natural freshwater lake (177.2 km^2) located completely within the state of California with a shoreline length of 160 km (**Figure 1**). It is located at an elevation of 400 m among the Clear Lake Volcanic Field (Richerson et al., 1994; De Palma-Dow et al., 2022). The lake is naturally eutrophic and paleoecological studies have indicated it has been a shallow, productive system since the last ice age (Bradbury, 1988). Clear Lake has a distinctive basin morphology with 3 major Arms (**Figure 1**). Clear Lake is one of the oldest lakes in North America, formed approximately 2.5 million years ago through volcanism, seismic activity, and erosion (Richerson et al., 1994; De Palma-Dow et al., 2022). The Upper Arm (western lobe) is the oldest and largest basin of the lake at roughly 127 km^2. The Oaks Arm (the northeastern

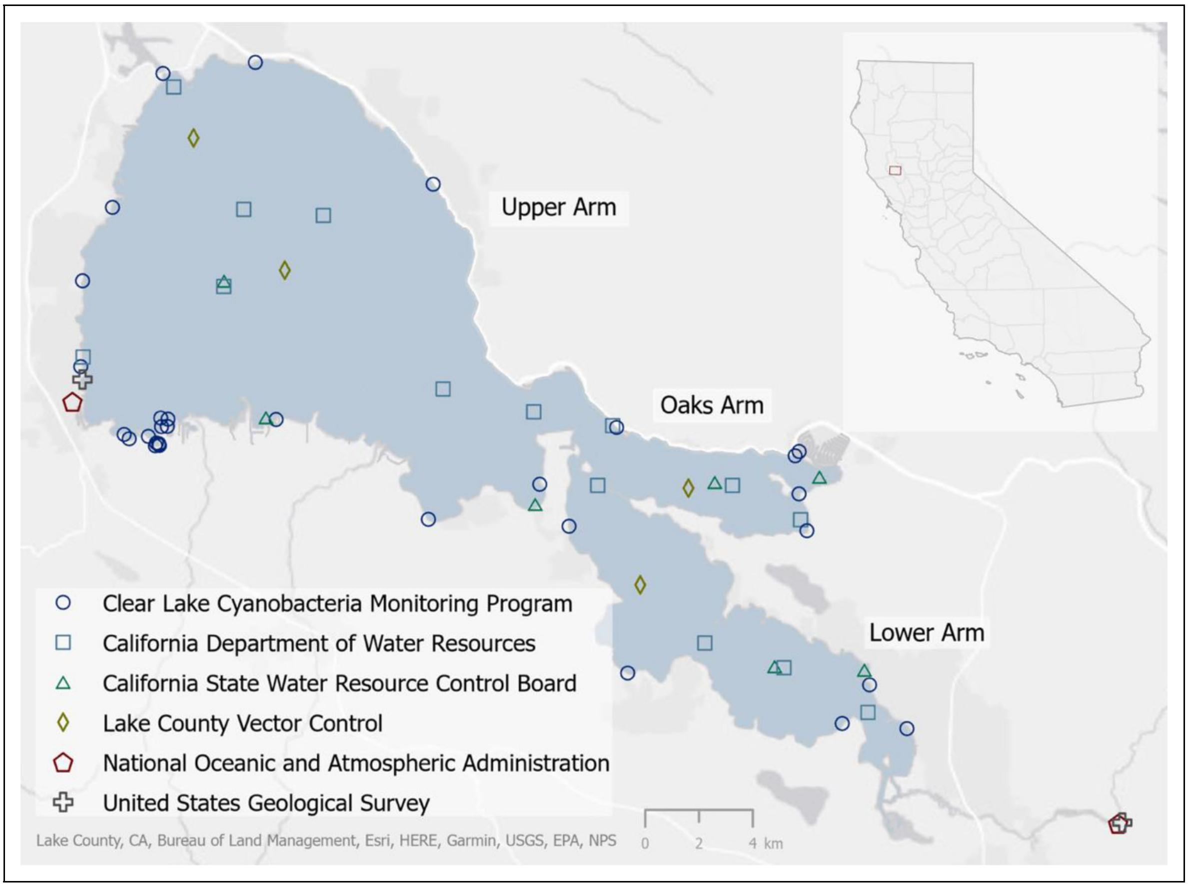

Figure 1. Map of historical and ongoing sampling and monitoring stations in Clear Lake, CA. Map of sampling stations included in the master database at which 20 or more observations have been made between 1951 and 2019. The shape of the location indicates the primary entity that has collected data from that station (see legend for entity identifications). Inset in the upper right shows the location of Clear Lake in California (identified with red box). All stations represent locations of water sampling except the National Oceanic and Atmospheric Administration stations and United States Geological Survey stations. The National Oceanic and Atmospheric Administration stations are the 2 weather stations from which precipitation data were obtained. The United States Geological Survey stations were where historical gauge height (located in the northwestern shore of the Upper Arm) and lake discharge (located in the Cache Creek, east of the Lower Arm) were measured at the United State Geological Survey stations.

lobe) and Lower Arm (the southeastern lobe) are smaller at 37.2 and 12.5 km^2, respectively. Clear Lake is a relatively shallow lake, with maximal depths of approximately 18 meters in the Oaks and Lower Arms, and 12 meters in the Upper Arm (Richerson et al., 1994). Lake depth is affected by seasonal rain and runoff, human use which includes agricultural irrigation and drinking water and is controlled by a dam erected in 1914 at the southeastern end of the Lower Arm. Clear Lake is polymictic throughout the year due to its shallow depth, large surface area, and the strong winds that result in frequent and thorough water column mixing. Short-term water column stratification sporadically occurs, particularly during hot summer periods if the wind is calm.

Early scientific studies of biological processes in the lake characterized the magnitude and seasonal patterns of primary productivity in Clear Lake. High levels of planktonic primary production and high standing stocks of phytoplankton in Clear Lake have been documented in the scientific literature for many decades (Winder et al., 2010), and Richerson et al. (1994) noted reports that indicated that the lake has been highly productive since at least the 1870s. High productivity was documented in the early 1960s, and followed a pattern that was positively correlated with light and water temperature, and inversely correlated with turbidity which decreased light penetration (Goldman and Wetzel, 1963). A "red tide" caused by a massive accumulation of the dinoflagellate *Peridinium pernardii* was documented in 1970 (Horne et al., 1971) but large cyanobacterial blooms were not reported at that time. Nonetheless, nitrogen fixation was substantial in the lake even then, constituting >40% of the yearly nitrogen flow into the lake (Horne and Goldman, 1972). The nitrogen fixing cyanobacterial taxa *Aphanizomenon* and *Anabaena* were implicated as the causative agents.

Although these studies indicate that the lake has long been productive, eutrophication in Clear Lake has also been accelerated by human activities, which have been extensive around the lake over the last century (Suchanek et al., 2002). Extensive development began in the 1850s, and modification and impacts to the lake became much more significant during that period (see figure 3.7 in Richerson et al. [1994] for a timeline). A major impact on the lake was the establishment of the Sulphur Bank Mine on the southeast edge of the Oaks Arm in the late 1850s, which produced primarily sulfur and mercury for nearly 100 years (Hammack et al., 2002). The mine site was eventually designated an Environmental Protection Agency (EPA) superfund site due to high levels of mercury and arsenic in lake sediment, ground water, and surface water. Other major watershed modifications included the construction of Clear Lake Dam along Cache Creek by the Yolo Water and Power Company in 1914 (U.S. Army Corps of Engineers, 2002) to limit flood (Gopcevic decree, Superior Court of Mendocino County, 1920) and drought impacts (Solano Decree, Superior Court of the State of California, 1978). Extensive and repeated modifications to Rodman Slough at its northwestern end also affected lake water quality (Kim, 2003).

The timings of these major changes in the Clear Lake watershed are generally consistent with the inception of massive phytoplankton blooms in the lake. Analyses of sediment cores from the lake have revealed increased rates of sedimentation in the 1930s and 1980s owing in part to changes in the Rodman Slough watershed which resulted in increased flow and the transport of silt, clay, and organic particles into the lake (Kim, 2003). A separate analysis of sediment cores from the lake documented increased rates of sedimentation during the 1920s, attributed largely to the use of extensive earth-moving equipment and open-pit practices at the Sulphur Bank Mercury Mine (Richerson et al., 2008). These findings highlight that the timing of major changes in erosional inputs into Clear Lake, or effects on water movement, coincided with the timing of blooms and accumulations of excessive phytoplankton biomass.

Clear Lake provides a variety of beneficial uses for recreation, agricultural irrigation, drinking water, and habitat for fish and wildlife. Most notably, it is important for the California Native American Tribes and provides Tribal Beneficial Uses, which include uses of the water that support tribal cultural, spiritual, and ceremonial uses and Tribal subsistence fishing. Due to the adverse impacts to beneficial uses by cyanoHABs, Clear Lake was added to the Clean Water Act Section 303(d) List of Impaired Water Bodies due to nutrient impairments. More recently, Clear Lake has also been listed on the 303(d) list due to impairments caused by microcystins.

1.2. Blooms and cyanotoxins in Clear Lake

High abundances of cyanobacteria were reported in Clear Lake beginning in the 1970s (Richerson et al., 1994; Mioni et al., 2011). Cyanobacteria cause a variety of water quality issues for the lake including decreased water quality, increased strain on water treatment facilities, and the expansion of anoxic events and noxious smells. A variety of toxigenic cyanobacterial taxa have been reported in the lake over the last decade including *Anabaena, Aphanizomenon, Dolichospermum, Gloeotrichia, Lyngbya, Woronichinia*, and *Microcystis* (Mioni et al., 2011; Kurobe et al., 2013; Moore et al., 2016). More recently, Clear Lake has also experienced cyanoHABs associated with extreme concentrations of cyanotoxins (Winder et al., 2010; Mioni et al., 2011). Several cyanobacterial blooms in Clear Lake have been associated with extremely high concentrations of microcystins during the period examined in this study, reaching up to 16,920 μg/L, which is more than 840 times, 2,800 times, and 20,000 times the California "danger" (20 μg/L), "warning" (6 μg/L), and "caution" (0.8 μg/L) recreational guidelines for microcystins, respectively (California Cyanobacterial and Harmful Algal Bloom Network [CCHAB], 2016). Cyanotoxins in the water pose a threat to residents and visitors to the lake, as well as Tribal cultural and subsistence fishing uses that may overlap in time and place with toxic events. At least one dog death has been linked to the presence of cyanotoxins in the lake (Moore et al., 2016), and adverse effects of these toxins on aquatic organisms is suspected but presently not well understood (Mehinto et al., 2021). Recent concerns in other geographic areas in the United States over potential exposure through aerosolization of toxins has also raised human health concerns (Backer et al., 2008; Facciponte et al., 2018; Olson et al., 2020). Finally, the decrease in water quality has reduced tourism and fishing-related revenue to the community.

Phosphorus concentrations have been singled out as the major factor leading to excessive cyanobacterial growth in Clear Lake. Mioni et al. (2011) highlighted that phosphorus availability can influence the abundance of certain cyanobacterial species, although they also pointed out that variables such as temperature and nitrogen affect some species. Studies have also identified important roles for other nutrients in contributing to phytoplankton production and shifts in overall community composition. Additions of nitrate and sulfate, for example, were shown to increase carbon fixation of the natural phytoplankton assemblage of the lake at certain times of year during the mid-1900s (Goldman and Wetzel, 1963). Therefore, a variety of elements, or imbalances in nutrient ratios, may be important in the timing, magnitude, and composition of phytoplankton blooms in Clear Lake.

These findings have resulted in various proposals and actions to decrease nutrient loading into the lake. Most significantly, the State of California Central Valley Regional Water Quality Control Board (CVRWQCB) adopted a control program that included a TMDL and Control Program to limit the amount of phosphorus entering the lake (Webber, 2006; CVRWQCB, 2007). The total maximum daily load (TMDL) targeted a phosphorus load reduction of 87,100 kg per year, representing a roughly 40% reduction in average annual loading. Additionally, the TMDL identified a target chlorophyll *a* concentrations target of 73 μg/L for the lake. To date, some dischargers have met the load allocations of the TMDL while others continue to work toward the reduced phosphorus load allocations (CVRWQCB, 2021).

1.3. Purpose and goals

Data from the various Clear Lake monitoring programs and scientific studies that have been conducted since the mid-1900s have been compiled here to create a comprehensive data set to enable analysis of water quality and cyanobacterial related trends, with a focus on incorporating the last decade of information. These efforts have been vital in furthering our understanding of the long-term changes that have taken place in the lake, and some of the processes that may be stimulating the chronic reoccurrence of cyanoHABs. The last major review of the lake was published in 2010 (Winder et al., 2010), and since then many changes occurred in the local environment including drought, several major fires, and more than a decade of TMDL implementation. The goals of this review were to determine changes in lake conditions over time, to identify seasonal and annual trends in water quality within the lake, as well as assess seasonality and spatial heterogeneity within the lake. This review focused on cyanobacteria with the aim of identifying trends in the overall occurrence and magnitude of blooms and possible putative drivers of toxin-producing blooms. This review also examined the results of the TMDL developed for the lake to determine if overall water quality has improved following its implementation. Lastly, we identified data gaps that prevent predictive understanding of bloom dynamics and developed recommendations for ongoing and future research and monitoring to fill these gaps.

2. Data and methods

2.1. Data sources and dataset assembly

Basic climatological and hydrologic data have been collected near and around Clear Lake as early as the 1910s by the U.S. Geological Survey (USGS) and National Oceanic and Atmospheric Administration (NOAA). Multiple agencies have conducted both routine and intermittent monitoring of chemical and physical parameters on Clear Lake since the 1950s, although routine and consistent collection of biological monitoring data began more recently within the last 2 decades. The Department of Water Resources, the California State Water Resource Control Board, and Lake County Vector Control District have monitored several water quality parameters beginning in the 1950s. In 2014, 2 Tribal Nations, the Big Valley Band of Pomo Indians, and the Elem Indian Colony, developed the Clear Lake Cyanobacteria Monitoring Program (CLCMP: https://www.bvrancheria.com/clearlakecyanotoxins) which includes water quality parameters along with cyanobacterial-specific parameters such as cyanotoxins, phycocyanin, and cyanobacterial species identifications via microscopy.

For this study, the aforementioned databases were synthesized to create a master database of 50 lake and climatological parameters (∼217,000 individual data points) from the period of 1920 to mid-2020 of environmental parameters within and surrounding the lake (Supplemental Table 1). Since the data set was assembled from multiple sources, the methodologies used over time were queried and parameters were combined and converted to a single metric unit across data sources where appropriate. Included sampling sites were limited to locations for which a minimum of 20 sampling events were conducted. A total of 63 sampling locations were thus identified (**Figure 1**), although the timeframe and parameters sampled at each station varied. The master database was refined to a subset of specific parameters that were selected based on their possible roles in bloom formation and toxin production, and for continuity across the focal period in analytical methodology and repeated sampling over time, resulting in a narrower data set of 19 lake parameters covering a period ranging from 1951 to 2019 that were the focus of the statistical analyses (**Table 1**). The sample collection and analytical approaches applied to collect these parameters are summarized in the Supplemental Materials and Supplemental Table 2.

Observations of precipitation, maximal and minimal air temperature, gauge height (estimate of lake level), and lake discharge were made on daily to weekly timescales. Annual precipitation was estimated from 2 NOAA weather stations (USC00041806 and USC00044701) that offered the most consistent data collection (**Figure 1**). Years with >90 missing days of rain gauge observations were omitted

Table 1. Summary of data included in this study

Parameters Type	Parameter	Reporting Agency	Years Measured	Specific Range(s)
Climatology	Maximal air temperature	NOAA	80	1940–2007; 2009–2020
Climatology	Minimal air temperature	NOAA	80	1940–2007; 2009–2020
Climatology	Precipitation	NOAA	100	1920–2007; 2009–2020
cyanoHABs	Anatoxin-a	CSWRCB, CLCMP	5	2011; 2015–2017; 2019
cyanoHABs	Microcystin-LA, -LR, -RR, -YR	CSWRCB, CLCMP	3	2011; 2014–2015
cyanoHABs	Total microcystins	CSWRCB, CLCMP, DWR	7	2011; 2014–2019
cyanoHABs	Phytoplankton relative abundance	CLCMP	5	2015–2019
cyanoHABs	Sensed phycocyanin	CLCMP, DWR	4	2016–2019
Hydrology	Gauge height	USGS	70	1949–1981; 1984–2020
Hydrology	Lake discharge	USGS	72	1949–2020
Water Quality	Sensed chlorophyll *a*	CLCMP, DWR	14	2007–2020
Water Quality	Dissolved oxygen	CLCMP, LCVCD, DWR	67	1951–1955; 1957–1965; 1968–2020
Water Quality	Total hardness	USGS, DWR, LCVCD	70	1951–2020
Water Quality	Total Kjeldahl nitrogen	DWR, CLCMP	37	1965; 1974–1991; 1991–2003; 2005–2017
Water Quality	Dissolved nitrate + Nitrite	DWR	37	1978–1991; 1998–2020
Water Quality	pH	USGS, DWR, CLCMP, LCVCD	70	1951–2020
Water Quality	Total phosphorus	DWR, CLCMP	48	1965; 1968–1991; 1998–2020
Water Quality	Dissolved orthophosphate	DWR	56	1959–1991; 1998–2020
Water Quality	Secchi depth	DWR, CLCMP, LCVCD	36	1985–2020
Water Quality	Specific conductance	USGS, DWR, CLCMP, LCVCD	62	1951–1990; 1999–2020
Water Quality	Water temperature	DWR, CLCMP, LCVCD	70	1951–2020

Table includes the parameters, the data source, and date range for which data were available. cyanoHABs = cyanobacterial harmful algal blooms; USGS = U.S. Geological Survey; DWR = Department of Water Resources; CLCMP = Clear Lake Cyanobacteria Monitoring Program; CSWRCB = California State Water Resources Control Board; NOAA = National Oceanic and Atmospheric Administration; LCVCD = Lake County Vector Control District.

since these instances were likely to provide a false indication of annual precipitation. In instances where precipitation values were available from both weather gauges for a given year, the stations were averaged together. Monthly and yearly averages were calculated for the temperature maxima and minima from the same NOAA weather stations. Yearly and monthly averages were calculated for gauge height and lake discharge observations from USGS stations 11450000 and 11451000, respectively. Gauge height observations were collected on near daily intervals except in 1976, 1977, 1981, and 1984 where observations were sporadic, and no observations were made in 1982–1983.

Outliers in the database were identified using a 2-step process. All parameters were plotted and manually inspected for extreme values. It was expected that some parameters such as chlorophyll *a* and cyanotoxins might yield extreme values due to biological variability. However, parameters with observations that were either beyond reasonable limits (e.g., off-scale pH values) or were rare, extreme observations were also identified. In those cases, z scores were calculated for the parameters. Data points which were 3 standard deviations from the mean were removed. Although many of the parameters of interest follow a log-normal distribution, estimates of z-scores provided similar identification of outliers for log-transformed variables. This procedure ensured that only extreme values that likely resulted from data entry or measurement errors were removed. The following parameters had outliers removed: water temperature, air temperature, dissolved oxygen, oxygen saturation, dissolved orthophosphate, dissolved hardness, total hardness, pH, salinity, specific conductance, total dissolved solids, turbidity, and minimal air temperature. For all parameters, outliers represented less

Table 2. Annual and monthly trends in water quality parameters with sufficient data density between 1951 and 2019 with the slopes indicating the magnitude and direction of the trend

Parameter	Annual	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Average gauge height (m)	**−0.004**	−0.008	−0.007	−0.003	0.000	−0.001	−0.003	−0.003	−0.003	−0.003	−0.003	**−0.004**	**−0.006**
Lake discharge ($m^3\ s^{-1}$)	0.000	0.000	−0.002	−0.001	−0.036	0.015	−0.007	−0.004	−0.011	−0.008	0.002	**0.001**	0.001
Dissolved oxygen (mg/L)	**−0.022**	**−0.032**	**−0.024**	**−0.029**	**−0.029**	**−0.028**	−0.014	−0.008	−0.010	−0.006	−0.012	**−0.027**	**−0.022**
pH	–	0.003	0.000	0.000	0.002	**0.002**	**0.005**	**0.008**	**0.010**	**0.011**	**0.008**	**0.007**	0.002
Daily maximal temp (°C)	–	**0.055**	0.031	**0.041**	0.016	0.008	−0.004	−0.007	−0.006	0.001	0.019	**0.040**	**0.041**
Daily minimal temp (°C)	–	0.012	0.004	**0.020**	0.014	**0.025**	**0.025**	**0.036**	**0.029**	**0.023**	**0.022**	0.001	0.001
Total hardness (mg/L $CaCO_3$)	**−0.075**	0.151	**−0.306**	−0.049	0.013	−0.008	−0.059	−0.012	−0.150	−0.043	−0.104	**−0.414**	0.040
Precipitation (cm)	–	−0.001	**0.005**	**0.004**	0.002	0.000	0.000	0.000	**0.000**	0.000	0.000	0.001	0.006
Water temperature (°C)	–	0.013	0.004	**0.021**	**0.036**	**0.046**	**0.036**	0.013	−0.001	−0.014	**−0.025**	−0.007	−0.014

Annual trends were assessed using Seasonal Mann–Kendall tests and monthly trends were assessed using Mann–Kendall tests. Significant trends ($P < 0.05$) are indicated in bold. Annual trend estimates that did not meet the heterogeneity assumptions for the test are indicated with a dash.

than 1% of the total number of observations of a given analyte except for dissolved orthophosphate, where 3.3% of the observations were identified as outliers.

In some cases, samples appeared in duplicate within the assembled data set due to duplicate entries across queried databases. In all cases where the values for the duplicated parameter were exact matches, duplicated entries were removed. In a subset of the duplicated entries, the parameter values of the duplicates did not match. In these instances, the Relative Standard Deviation between these samples was determined and if it was above 20% the values were removed from the data set. For samples with a relative standard deviation below 20%, the samples were averaged and recorded as one value.

2.2. Statistical analysis

The assembled data set, while wide-ranging, had several key limitations that limited the types of analyses that could be conducted. Data set limitations included a lack of co-occurring measurements for many parameters. Most parameters were observed across variable and irregular spatial and temporal scales, with many parameters measured at differing time steps and intermittent gaps in observations (**Table 1**). Additionally, most of the parameters followed non-normal distributions. Such situations are typical when assessing multidecadal time series measurements. Because of these limitations, a descriptive exploratory analysis of concordance between parameters over time was conducted to develop a general understanding of driving factors of eutrophication and cyanoHABs. Nonparametric statistics were also used to assess status and trends of individual parameters and correlations between parameters following conventional approaches that are common in the analysis of long-term water quality data. All statistical analysis was performed in the R software environment (R Core Team, 2022).

Annual and interannual variations in water quality were investigated by plotting each parameter against sampling date/time and constructing boxplots of monthly and yearly distributions of each parameter. Box and whisker plots were used to indicate the interquartile range (IQR; top of the rectangle was the 75th percentile and the bottom was the 25th percentile). The median value were depicted as horizontal lines within each box. Whiskers were 1.5× the IQR. Black circles showed outliers (values > or < than 1.5× the IQR). Monthly and yearly boxplots were also grouped by Arms of the lake (Upper, Oaks or Lower Arm) in to examine spatial heterogeneity between the Arms. This series of initial analyses was used to narrow the larger data set to that shown in **Table 1**.

Annual and monthly trends in water quality parameters were investigated using the nonparametric Mann–Kendall approach in the R EnvStats package (Millard, 2013), which tests for monotonic trends of a given water quality or climatic parameter. Trends were estimated over the 70-year period of 1951–2019 using only parameters with few gaps in temporal coverage. All observations from a given month and year were used to calculate a mean value for each parameter for each month of each year. Individual monthly trends were estimated using the Mann–Kendall test. This test detects trends by calculating differences in signs between earlier and later time points and determines if there is a consistent increase or decrease in sign values over the time series for each individual month or across years. Annual trends in this same monthly series were estimated using the Seasonal Mann–Kendall test to account for seasonality across months (Hirsch et al., 1982). The Seasonal Mann–Kendall test follows the same principles of the Mann–Kendall test, but can take monthly data observations into account when considering a given year as a whole.

Correlative relationships between water quality and cyanoHAB indicators were explored using non-parametric Spearman cross-correlation functions in the R Hmisc package (Harrell, 2022) for all parameters shown in **Table 1**. Significant correlations were defined as parameters with a positive or negative Spearman's correlation coefficient (ρ) with a $P < 0.05$. This analysis was conducted with all parameters that co-occurred in space and time, and significant correlations were plotted. Time-lagged correlations were also examined between gauge height (a crude indicator of lake water residence time) and relevant water quality parameters and harmful algal bloom indicators. The monthly averages of the relevant parameters were lagged behind the corresponding lake discharge values 1 month at a time up to a year and then a Spearman cross-correlation was performed to determine the strength of the lagged relationships.

The CLCMP data set included microscopic identification of the cyanobacterial genera present in most of their monitoring samples beginning in 2015. Between 2015 and 2019, a total of 1072 samples were collected, although 305 samples were not analyzed. Water sample observations were conducted via microscopy and the dominant taxa were identified. If a mixed community was observed, multiple taxa were reported. Relative abundance data was coded as an individual cyanobacterial genus observation per record for whatever taxa were reported in the sample. Samples dominated by taxa other than cyanobacteria (e.g., diatoms, unidentified species) or no cells were detected were not shown ($n = 157$). Observations were summed to calculate the number of observations per cyanobacterial genus during the monitoring period.

In September of 2007, the TMDL and Control Program was implemented to reduce the input of phosphorus into Clear Lake. The effectiveness of this action was evaluated in the present study by grouping key water quality parameters from the complete data set into 2 smaller groups representing 10 years prior to (1997 to 2007) and 10 years after enactment of the TMDL (2007 to 2017). Analysis was limited to parameters with roughly an equal number of datapoints in the 10 years prior to and after the TMDL. Probability density functions (PDFs) were calculated for these parameters for data before and after the implementation of the TMDL and Control Program. PDFs describe the probability of a given parameter's value (*x*-axis) within each data set given the data's distribution. Higher *y* values indicate a higher probability that a sample falls in the area below it on the *x*-axis. Boxplots were also generated from

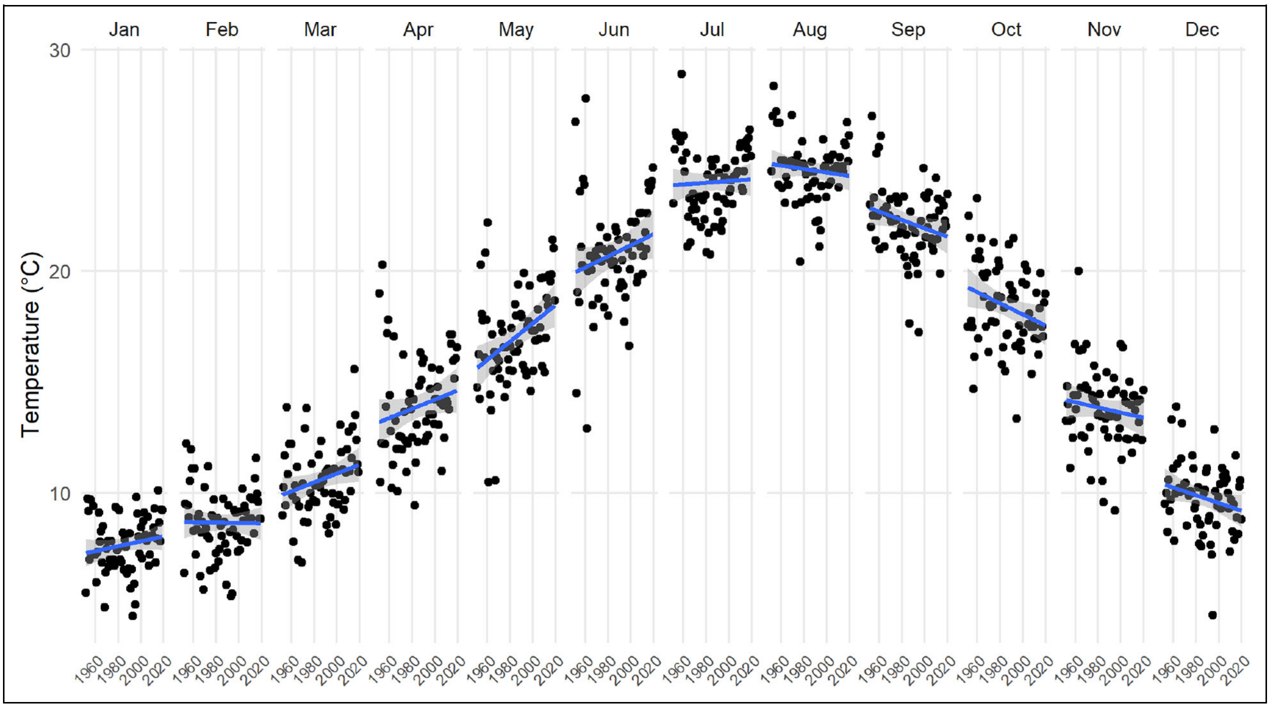

Figure 2. Historic records of lake water temperature collected during water quality sampling events made between 1951 and 2019. A plot of mean monthly water temperature faceted by month. The mean temperature of all observations collected within a given month each year is plotted as a black circle, showing the typical annual cycle of temperatures observed at Clear Lake. The linear trend in temperature for each month is shown as a blue line, with the directionality of the line indicating if the average temperature in a given month has shown an increase or decrease over the last 70 years.

the summed data sets for each period. Non-parametric Wilcoxon rank-sum tests were performed to test for significant differences (significance defined as $P < 0.05$) in each parameter's median value between years prior to and following the TMDL and Control Program enactment. Effect size tests were also conducted to estimate the magnitude of the effects, with *r* values varying from 0, indicating no effect to 1 indicating a large effect (Cureton, 1956).

3. Results and discussion

3.1. Historical trends and relationships among Clear Lake stressors

A complex set of interacting environmental stressors affect lake dynamics and cyanoHAB development in Clear Lake. Devising approaches for mitigating recurring cyanoHABs and preventing future blooms is predicated on understanding those stressors and their effects on primary production, biomass accumulation, and community composition. Both historical and more recent perspectives on land and water use are critical to this understanding.

3.1.1. Environmental stressors and correlations

Environmental parameters observed within and around Clear Lake for varying durations over the past 70 years were investigated to characterize long-term changes, and identify which might relate to the increase of cyanoHABs (**Figures 2**, **3**; Supplemental Figures 1–5). Among these, water temperature is considered a primary driver of cyanoHABs in the presence of sufficient nutrients to support growth. Water temperature in Clear Lake for the past 70 years has followed an expected seasonal pattern, with warmest water temperatures occurring in the summer months of July and August, and coolest temperatures in January and February (**Figure 2**). Averaged annually, water temperature has not changed significantly or directionally during this period (**Table 2**). Similarly, minimal and maximal air temperatures have not changed dramatically or directionally (**Table 2**; Supplemental Figure 1). Mean water temperature has been marginally, but not significantly, higher during the past 5 years, and largely coincided with or followed extreme, prolonged drought conditions in the region that occurred 2014–2016 (**Figure 3A**; National Drought Mitigation Center [NDMC], 2020).

Relatively unchanging average water temperature over nearly 7 decades of observation in Clear Lake was an unexpected finding, since warming climate has received much attention as a promotor of cyanobacterial blooms in water bodies globally. A study of 137 lakes across Europe in 2015 revealed a strong relationship between temperature and the distribution of cyanobacterial toxins with nutrients, surprisingly, playing a secondary role (Mantzouki et al., 2018). This would suggest that temperature is a major determinant of toxin distributions, at least at large geographic scales. Yet our finding is in agreement with the observation by Richerson et al. (1994) who reported no substantial variation in water temperature

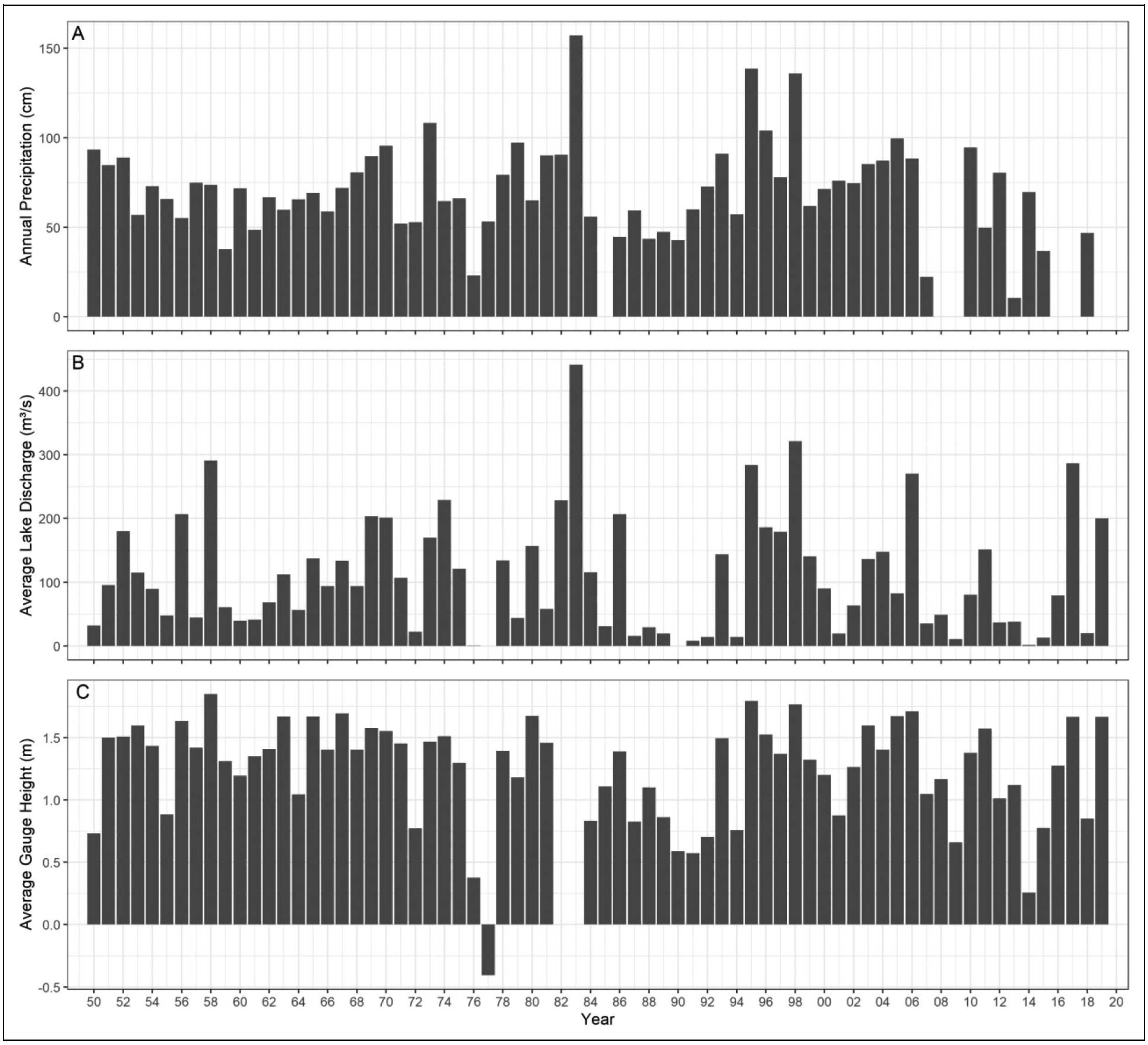

Figure 3. Historic records of annual hydrologic conditions in and around Clear Lake. Total annual precipitation (A), annual average lake discharge (B), and annual average gauge height (C) between 1950 and 2019 are plotted. If no or insufficient data were available for a given year, data were not plotted. Precipitation, lake discharge, and gauge high observations were collected at the National Oceanic and Atmospheric Administration stations and United States Geological Survey stations indicated on the map in **Figure 1**. Gauge height was measured as meters above Zero Rumsey (equivalent to 1,318.25 feet above sea level: National Geodetic Vertical Datum of 1929).

maxima or minima in Clear Lake from year to year over a 24-year period. On a much larger temporal scale, deviations of lake water temperature based on pollen data from the sediments of Clear Lake have indicated that water temperature in the lake has experienced relatively minor variations over the past several thousand years (Adam and West, 1983). Thus, increased frequency or magnitude of cyanoHABs in recent years are difficult to attribute to an increase in average annual water temperature in the lake.

While average annual lake water temperature did not change appreciably over nearly 70 years in Clear Lake, statistically significant monotonic changes in monthly water temperatures were apparent for several months (**Figure 2**). Specifically, average water temperatures in the lake examined over multiple decades increased in March–June, while significant decreases occurred in October (**Figure 2**; **Table 2**). That is, monthly water temperatures in recent decades have increased more rapidly during spring and decreased more rapidly during fall relative to the 1950s, although summer temperature maxima and winter minima have remained relatively unchanged, the latter observation in line with relative constancy of water maximal and minimal temperatures observed by Richerson et al. (1994). This coincides with a similar increase in minimal air temperatures during that same period that likely contributed to the observed shifts in average monthly water temperatures (**Table 2**).

We speculate that the more rapid increase in water temperature in the spring during recent years has expanded the season of favorable growing conditions for cyanobacteria. This influence has taken place despite the lack of an increase in annually averaged lake water temperatures and provides a competitive advantage for cyanobacteria over eukaryotic algae within the phytoplankton community. Visser et al. (2016) noted that earlier onset and longer duration of stratified water column conditions may provide a competitive advantage for buoyant cyanobacteria relative to many eukaryotic algae. Clear Lake experiences intermittent periods of water column stratification and mixing on time scales ranging from 1 to several days (Rueda et al., 2003). Even minor shifts in the timing and/or duration of changes in water column stability may be contributing to cyanobacterial growth and community dominance in present day Clear Lake.

Total annual precipitation, lake discharge, and resulting lake height have also varied considerably in Clear Lake although, as for water and air temperature, a clear directional trend through time was not apparent for these parameters (**Figure 3**; **Table 2**). Precipitation data were obtained from 2 different stations, one in the Upper Arm of the lake and one near Cache Creek. However, the lake is 20 miles along the major axis and as such data from these stations may not be completely representative of the amount of rainfall over the entire lake. Given this caveat, total precipitation has exhibited cyclical fluctuations and greater variability during the past few decades (**Figure 3A**).

Similarly, average annual lake discharge through Cache Creek has been highly variable (**Figure 3B**). Note that total annual precipitation and annual lake discharge have not always been correlated due to variable and multiple uses of lake water (i.e., not all water entering the lake is discharged through the dam) although expectedly, years of low discharge have been during periods of low precipitation. Lake height (indicated by gauge height; **Figure 3C**) can indicate the effect of various water inputs to the lake (precipitation and runoff) and removal (discharge and various uses of lake water). The lake height is measured in feet above "Zero Rumsey," which is 401.8 m above mean sea level. Current regulations specify that the lake level must be maintained between Zero Rumsey and 2.3 m above Zero Rumsey. Lake height has varied significantly but not directionally over the past 7 decades. Gauge height, together with discharge information, provides a crude measure of residence time of water in the lake, which in turn affects biological use of available nutrients and therefore overall productivity in the lake.

Lowest lake levels have been consistently observed in Clear Lake during fall, attesting to the seasonality of precipitation in the region. Accordingly, lake discharge is maximal during the winter and spring with minimal discharges recorded during late summer and fall. The relationship among these 3 parameters results in increased water temperatures and reduced flushing during the summer and early fall. Such environmental conditions do not necessarily lead to cyanoHABs, but they are consistent with conditions that are generally conducive to cyanobacterial growth and dominance (Paerl and Huisman, 2008; Gobler et al., 2016).

Fluctuations in pH and dissolved oxygen have varied widely, even on very short temporal scales, throughout the past 70 years (Supplemental Figure 2A, B). Measurements of each of these parameters have been conducted by multiple agencies using multiple approaches, which likely introduced some level of variability. Nonetheless, observations of pH have shown strong seasonal variation which presumably are related to high rates of primary production and respiration in the lake (Supplemental Figure 2A). In particular, pH fluctuations during the last decade have been very large, with maximal values exceeding 10 and minimal values approaching 6, likely related to the magnitude of recent phytoplankton blooms.

The significance of hypoxic and anoxic events in lakes for nutrient release from sediments is well established (Mortimer, 1941). These events are common in Clear Lake where they may constitute an important but largely unstudied mechanism for releasing phosphorus and nitrogen from the sediments into the water column where phytoplankton can utilize them. Dissolved oxygen concentrations in Clear Lake measured throughout the water column have ranged from saturated or supersaturated conditions to anoxic conditions since the 1960s (Supplemental Figure 2B) although, overall, annual averages of dissolved oxygen concentrations have decreased significantly over time (left column, **Table 2**). The wide variances in dissolved oxygen reflect the eutrophic nature of the lake, while the relatively rapid onset and termination of these events can presumably be explained by short-term changes in wind/weather conditions and their effects on water column stability and mixing. The wind regime in the Clear Lake basin is notable for its diurnal periodicity (Rueda et al., 2003), with periods of quiescence generally occurring during the night. Richerson et al. (1994) noted that oscillations in dissolved oxygen were typical in Clear Lake at seasonal, daily, and sub-daily time scales, with decreasing oxygen in deep, cooler waters during periods of low water column turbulence driven by lower winds, returning to a well-mixed water column with increasing winds. Stratification events lasting days due to prolonged periods of calm weather also occurred. These events can be highly ephemeral and difficult to observe and model (Cortés et al., 2021), however, given the significance of hypoxic/anoxic events in Clear Lake, the release of these internal loads of sediment nutrients as catalysts for cyanoHABs is a fruitful topic for future study.

Specific conductance is employed as an indirect measurement of total dissolved solids in the lake. Specific conductance has varied seasonally and interannually since the 1950s but has also exhibited directional changes across multiple years (Supplemental Figure 2C; Total Hardness, **Table 2**). A steady increase in values occurred beginning in 2012 and peaking in 2015, with a subsequent decreasing trend to values more consistent with historical values. Unsurprisingly, exceptional high values observed 2013–2016 coincided with extreme drought conditions. Seasonal cycling of specific conductance was discussed by Goldman and Wetzel (1963) who noted a strong seasonality in the ionic composition of the lake that was largely attributed to the effect of winter precipitation and summer evaporation. Cycling of this parameter prior to, during, and following extreme drought years supports their claim.

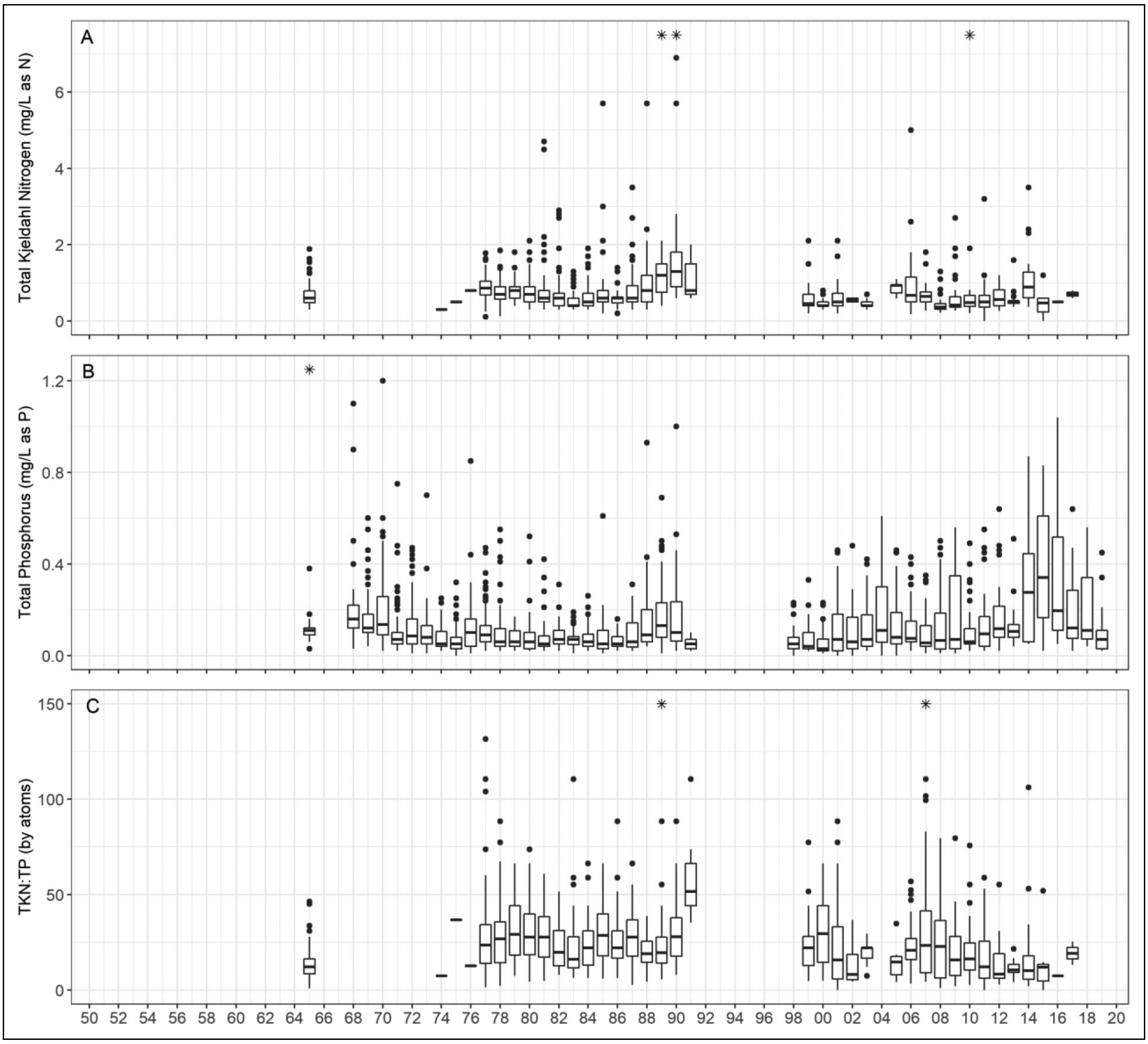

Figure 4. Historic records of nutrient measurements in Clear Lake between 1965 and 2019. Boxplots of total Kjeldahl nitrogen (A), total phosphorus (B), and the ratio of Kjeldahl nitrogen to total phosphorus (TKN:TP, by atoms; C) for all instances where there were co-occurring observations. Asterisks at the top of each figure indicate concentrations larger than 7.5 mg/L as N in Panel A, concentrations larger than 1.25 mg/L as P in Panel B, and ratios greater than 150 in Panel C.

Secchi depth has been recorded routinely in Clear Lake beginning in the mid-1980s (Supplemental Figure 2D). High water transparency, as indicated by greater Secchi depth, is expected to vary greatly with season because of particulate material carried into the lake by land runoff, seasonality associated with biological production, and wind-induced resuspension of sediment. Beyond these variances, low Secchi depth values were consistently observed during the periods 1986–1990 and 2004–2007. Additionally, a high density of low values were observed during 2014–2018 with only occasional excursions to higher water transparency, again corresponding approximately with the extreme drought period in the region.

High nutrient levels in Clear Lake indicate a state of hypereutrophication and a fundamental driving force for massive blooms in the lake. As previously noted, Clear Lake is a naturally eutrophic lake and phytoplankton blooms within the lake have been documented in the scientific literature for more than 60 years, and anecdotally well before 1900. Natural eutrophication has therefore undoubtedly played a role in the long history of algal blooms within the lake although that does not exclude anthropogenic nutrient enrichment events within the last few centuries from playing a role in the apparent rise of cyanoHABs in recent years.

A variety of nutrient measurements have been made sporadically throughout the years (**Table 1**), but total Kjeldahl nitrogen (TKN; **Figure 4A**) and total phosphorus (TP; **Figure 4B**) measurements have been made fairly consistently since the late 1960s. High median values of TKN and TP were observed between 1988 and 1991 relative to prior years, but measurements were discontinued for the next several years. Measurements were resumed in the late 1990s and reveal that median concentrations of TP have increased in the lake since 2000 with the highest values observed between 2014 and 2018, generally corresponding with the period of extreme drought (**Figure 4B**). Measurements of dissolved nitrate + nitrite and dissolved orthophosphate have also been made in the lake and showed similar trends to the total nutrient concentrations (Supplemental Figure 3) although firm conclusions for these constituents are more tenuous because the latter measurements were less consistently conducted.

Previous work has suggested that nitrogen and/or iron limitation has played a role in limiting bloom magnitude in the past, although phosphorus appears to have become increasingly important (Richerson et al., 1994). Due largely to increased TP concentrations, TKN:TP ratios in the present century have trended downward relative to values observed prior to 2001, except values in 2007–2008 which overlapped ratios observed prior to 2001 (**Figure 4C**). Most median TKN:TP values post-2001 have been at or near the Redfield ratio (16:1 N:P by atoms) relative to pre-2001 values which were above that ratio. The Redfield ratio has been used as an index of the degree of nitrogen or phosphorus limitation of the biological community in marine ecosystems (Redfield, 1958). This ratio, and variations on it, have also proven useful for investigating possible elemental limitation in freshwater ecosystems (Guildford and Hecky, 2000; They et al., 2017). Trends in TKN:TP over the past decade in Clear Lake indicate a shift in the lake toward a more nitrogen-limited biota (i.e., lower TKN:TP ratios; **Figure 4C**), mimicking trends in many eutrophic and hypereutrophic lakes globally (Liang et al., 2020; Wu et al., 2022). Such a shift could result from changes in the rates of nitrogen transformation in the lake, although nitrogen fixation rates have not been measured routinely enough to identify shifts over time (Horne and Goldman, 1972). Alternatively, increases in the delivery of phosphorus to the lake or less efficient sequestration of phosphorus in the sediments relative to nitrogen sequestration could also explain the change in TKN:TP ratios in the water column during the last decade. Regardless, increasing concentrations of TP (**Figure 4B**) and diminishing TKN:TP (**Figure 4C**) have resulted in a focus on controlling phosphorus loading to mitigate blooms in Clear Lake (Webber, 2006).

Lower lake levels, presumably resulting in longer water residence times, appear to play a role in allowing for TKN and TP concentrations to increase in the lake (Supplemental Figure 4A, B). Gauge height provides an indication of residence time with greater gauge heights indicating shorter residence times due to increased discharge at higher lake levels. Both TKN and TP exhibited weak negative correlations with gauge height, with higher total nutrient concentrations generally observed at lower gauge heights across all 3 Arms of the lake (Supplemental Figure 4A, B). TKN and TP are typically dominated by particulate nitrogen and phosphorus contained in living or detrital biomass. Therefore, increased TKN and TP concentrations associated with higher residence times of water in the lake are likely due to the additional time for phytoplankton to utilize nutrients and produce biomass.

Correlations were also investigated between the concentration of TP and lake discharge rates, with TP lagged at various monthly time increments (Supplemental Figure 4C). TP lagged by 2 months exhibited the strongest relationship with lake discharge, albeit a highly nonlinear one (Supplemental Figure 4C). TP values greater than 0.2 mg P/L were only observed at times when lake discharge was exceptionally low (<20 m^3/s). This relationship indicates the importance of water residence time in allowing TP to build to high concentrations, with approximately a 2-month lag period. Conversely, TP concentrations are low or modest when residence times are short and turnover of water in the lake is more rapid (i.e., at higher discharge rates in Supplemental Figure 4C).

Significant negative correlations between TKN or TP and Secchi depth have also been apparent when co-occurring measurements have been made (Supplemental Figure 5A, B). Spearman correlation coefficients of −0.28 and −0.37 indicate moderate negative correlations of TKN or TP with Secchi depth, respectively. The directionality of these correlations was anticipated, as greater concentrations of TKN or TP in the water would imply decreased water transparency. Correlations might be also expected between chlorophyll *a* concentration and Secchi depth, but this relationship was not examined because of the limited co-occurrence of these measurements. Additionally, other factors, such as runoff of terrigenous material and resuspended sediment, also affect water transparency. Specific conductance weakly correlated with Secchi depth in Clear Lake, although the scatter for this relationship was large (Supplemental Figure 5C). If resuspended sediments or runoff were the dominant cause of low Secchi depth, specific conductance would be expected to correlate strongly with Secchi depth. The fact that only a weak correlation exists between these parameters indicates that other factors, such phytoplankton standing stock, plays a role in controlling water transparency.

There has been considerable speculation on the effect of drought on the formation of cyanoHABs. Here, we were able to evaluate lake conditions before and after extended drought periods. Since 1950, there have been a few major drought periods effecting California including significant drought periods in 1976–1977 and 2014–2016 (Diffenbaugh et al., 2015; Stewart et al., 2020). Higher levels of TKN, TP, and specific conductance accompanied decreases in Secchi depth, gauge height, and lake discharge in Clear Lake during these periods. In general, higher nutrient levels occurred when the gauge height was low. The combination of low lake levels and low lake discharge likely resulted in higher residence times. While increased nutrient concentrations and longer residence time could theoretically increase the potential for blooms of all types of phytoplankton, cyanobacteria have been shown to outperform other phytoplankton under such conditions, particularly in turbid water (Cuker, 1987; Scheffer et al., 1997; Burkholder et al., 1998).

Along with droughts, Clear Lake has also experienced sporadic flooding. The lake is considered flooded when gauge height is greater than 2.74 m above Zero Rumsey. Since the 1950s, this has occurred 12 times: 1956, 1958, 1965, 1970, 1974, 1986, 1995, 1998, 2011, 2017, and 2019. There does not appear to be a significant change in lake conditions during these times, except for specific conductance which typically was low during flood periods (Supplemental Figure 2C). Flooding increases the input of nutrients and terrestrial material into the lake potentially increasing nutrient loading in the water column, but also potentially increasing burial of nutrients in the sediments or flushing them out of the lake due to higher discharge rates. While we did not observe a significant change in nutrients concentrations in the water column of Clear Lake during these flood periods in our data set, Richerson et al. (1994) showed that during flood periods there is indeed an increase in phosphorus absorption by the sediments in Clear Lake. Specifically, the rainy period of 1982–1986 showed increased absorption, and the drought that followed in 1987–1994 showed increased sediment release of phosphorus (Richerson et al., 1994). This highlights the connectivity between pools of nutrient elements in the water and sediments, and the importance of monitoring nutrients in the sediments as well as in the water column. Furthermore, this shows that even when external nutrient inputs are limited, there is still significant internal nutrient loading to support bloom development.

3.2. Recent biological trends and correlations

A variety of biologically relevant parameters have been collected in Clear Lake over time scales that are much shorter than the historical data set presented in the preceding section. Many of these measurements have been focused on assessing cyanobacterial blooms within the last 10–15 years. These measurements and studies provide insight, albeit limited, into the causative cyanobacterial species of blooms in the lake, their associated cyanotoxins, and ancillary information that provide clues into the cause(s) of toxic events.

3.2.1. Pigments, biomass, and toxins

Pertinent to the focus of this review on cyanoHABs are chlorophyll *a*, phycocyanin, and cyanotoxin concentrations that have been recorded in all 3 Arms of Clear Lake (**Figures 5** and **6**; Supplemental Figure 6). Chlorophyll *a* concentration, a proxy for total phytoplankton biomass, has been collected with regularity since 2007 (**Figure 5**). Strong seasonality in chlorophyll *a* concentrations has been observed in all 3 Arms of the lake, with high values observed during summer-fall in all Arms of the lake ($\geq$10 μg/L), although highest seasonal concentrations in each Arm do not always co-occur in time (**Figure 5**). Additionally, extremely high concentrations ($\asymp$1,000 μg/L) can occur in surface foams and scums in any of the Arms (**Figure 5**; note log scale on *y*-axis). These excursions to very high values are far in exceedance of the TMDL target of 73 μg/L of chlorophyll *a*.

Concentrations of the cyanobacteria pigment phycocyanin, a common proxy for cyanobacterial biomass, also exhibits strong seasonality in Clear Lake (Supplemental Figure 6). The highest concentrations of phycocyanin have been observed in summer-fall when cyanobacterial abundances typically reach their maxima, and similar to chlorophyll *a* concentrations, can be observed in any of the 3 Arms of the lake (**Figure 5**; Supplemental Figure 6). Chlorophyll *a* and phycocyanin concentrations observed in the lake indicate a eutrophic-to-hypereutrophic state for Clear Lake, at least for the past several years.

Cyanotoxins were first measured in Clear Lake in 2011 (Mioni et al., 2011) and have been routinely detected by the CLCMP since 2014 (**Figure 6A**). Microcystins have been detected in most years, with year-to-year maxima exhibiting substantial differences (note the log scale in **Figure 6A**). Concentrations of microcystins during this time interval exceeded California recreational health thresholds, including the highest "Danger" threshold in 6 of the 7 years of data (CCHAB, 2016). The highest concentrations occurred in Oaks and Lower Arms. The presence of anatoxin-a concentrations has been more sporadic than microcystins but positive detections have been reported in approximately half of the years since measurements began, with most detections in Oaks and Lower Arms (**Figure 6B**). Anatoxin-a concentrations exceeded the California recreational health thresholds (detection of anatoxin-a constitutes a "Caution" level) in most years in which anatoxin-a was analyzed but did not attain "Warning" levels.

The highest cyanotoxin concentrations in Clear Lake to date have regularly occurred in the Oaks and Lower Arms relative to Upper Arm (**Figure 6**), while chlorophyll *a* and phycocyanin concentrations do not show a clear trend among the Arms of the lake (**Figure 5**; Supplemental Figure 6). This difference indicates that factors other than bloom magnitude are controlling differences in the distribution of cyanotoxin concentrations in the lake. It is presently unclear if differences in the dominant cyanobacterial taxa among the Arms of the lake or differences in physiological condition of the cyanobacteria across the expanse of the lake (or both) are determining the distributions and concentrations of cyanotoxins in Clear Lake. This deficiency in our knowledge requires further study.

Correlations between cyanotoxins and other parameters of lake biology or chemistry are difficult to discern due to the limited amount of toxin data and scarcity of colocated observations with environmental parameters. Microcystins correlate negatively with gauge height in the lake for the available data (Supplemental Figure 7A). The Spearman correlation coefficients for the Upper, Oaks, and Lower Arms of the lake were −0.49, −0.47 and −0.31, respectively, indicating moderate correlations across the Arms between these factors. These relationships indicate that toxins are higher when the lake level is low, consistent with the negative correlations that exist between TKN or TP and gauge height in the longer time series of measurements (Supplemental Figure 4A, B), and the negative correlation between TP and lake discharge (Supplemental Figure 4C). The strength of these correlations were moderate, however, suggesting there are other factors associated with these relationships.

Significant, though moderate, correlations were observed between microcystin concentrations and chlorophyll *a* concentrations (Supplemental Figure 7B), and between microcystins concentrations and phycocyanin

Figure 5. Observations of chlorophyll *a* concentrations in Clear Lake from 2007 to 2019. Concentrations of chlorophyll *a* were collected via sonde and are plotted based on observations were made locations in the Upper Arm (green points), Lower Arm (blue points), and Oaks Arm (red points). The black line indicates the 2007 TMDL chlorophyll *a* target of 73 µg/L, with approximately 9.3% of these observations exceeding that level.

concentrations (Supplemental Figure 7C). These findings imply that other noncyanobacterial phytoplankton or cyanobacteria that are not producing toxins, respectively, make these pigment parameters imperfect proxies for the presence of microcystins. Notably, significant concentrations of chlorophyll *a* and phycocyanin have been observed in the absence of detectable microcystins (Supplemental Figure 7B, C). Interestingly, a stronger correlation exists in Clear Lake between phycocyanin and chlorophyll *a* than between each of those parameters and microcystins (Supplemental Figure 7D). Therefore, although the contribution of cyanobacteria can be crudely determined from chlorophyll *a* (or vice versa), neither parameter can be used to accurately predict microcystins.

3.2.2. Plankton community composition

The CLCMP has identified a variety of cyanobacterial taxa present at their 34 sampling sites since 2015, including numerous potentially toxic genera (**Figure 7**). At present, more than 20 planktonic and benthic cyanobacterial genera have been documented in Clear Lake with 3 genera, *Dolicospermum*, *Microcystis*, and *Anabaena*, constituting the bulk of the microscopical identifications. However, *Gloeotrichia* and *Lyngbya* have also been common and occasionally highly abundant taxa observed in the lake in recent years. Richerson et al. (1994) noted that the presence of several of these species have been recorded prior to the present century, and more recently the presence of quite a few cyanobacterial taxa have been confirmed based on DNA sequence information (Kurobe et al., 2013).

These accountings of observed cyanobacterial taxa in the lake are considerably expanded from a survey of the lake in the early 1900s that documented only a few species of cyanobacteria (Coleman, 1930), although cyanobacterial taxonomy has become considerably more complex since that early study. Therefore, it would appear that while a few cyanobacterial species have been present in Clear Lake for many decades, either more species have appeared in the lake or their abundances have increased sufficiently to make them more apparent. The 3 most commonly reported taxa reported by the CLCMP, *Dolicospermum, Anabaena*, and *Microcystis* (**Figure 7**) as well as

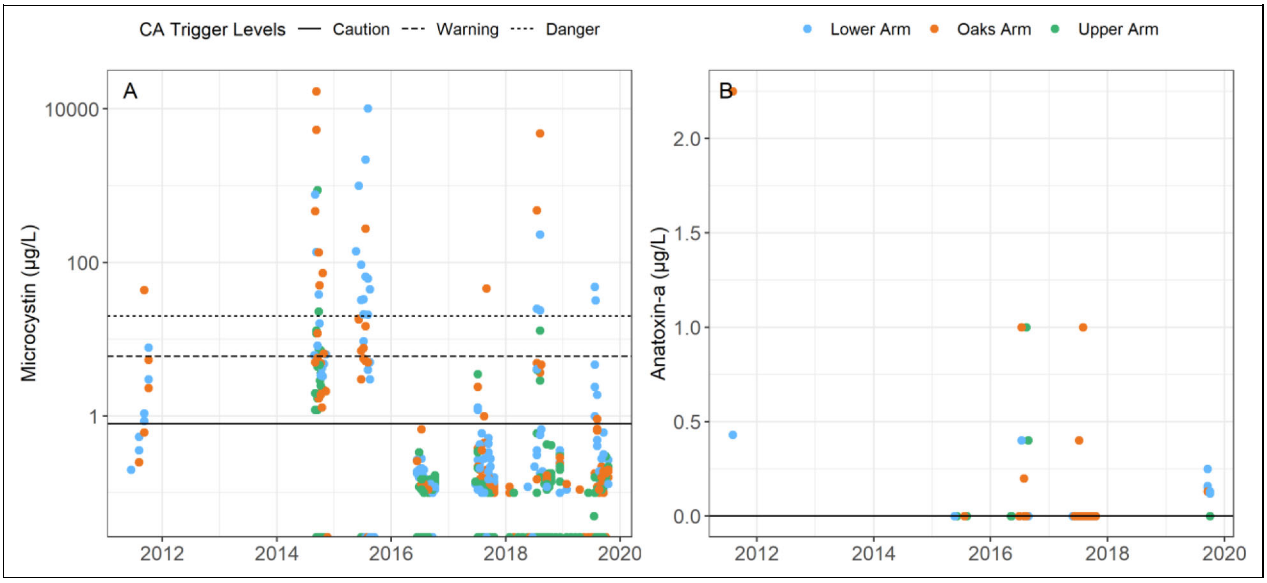

Figure 6. Annual observations of microcystins and anatoxin-a from 2011 to 2019. Microcystins (A) and anatoxin-a concentrations (B) observed in Clear Lake annually. Samples were collected from surface waters at various stations in the Upper Arm (green points), Lower Arm (blue points), and Oaks Arm (red points) from 2011 to 2019. The California "Caution" level for microcystins (0.8 μg/L), the California "Warning" level (6 μg/L), and the California "Danger" level (20 μg/L) are displayed by a solid, dashed, and dotted lines, respectively in (A). The California "Caution" level for anatoxin-a (detection) is displayed with a solid line in (B). Microcystin concentrations are plotted on a logarithmic scale.

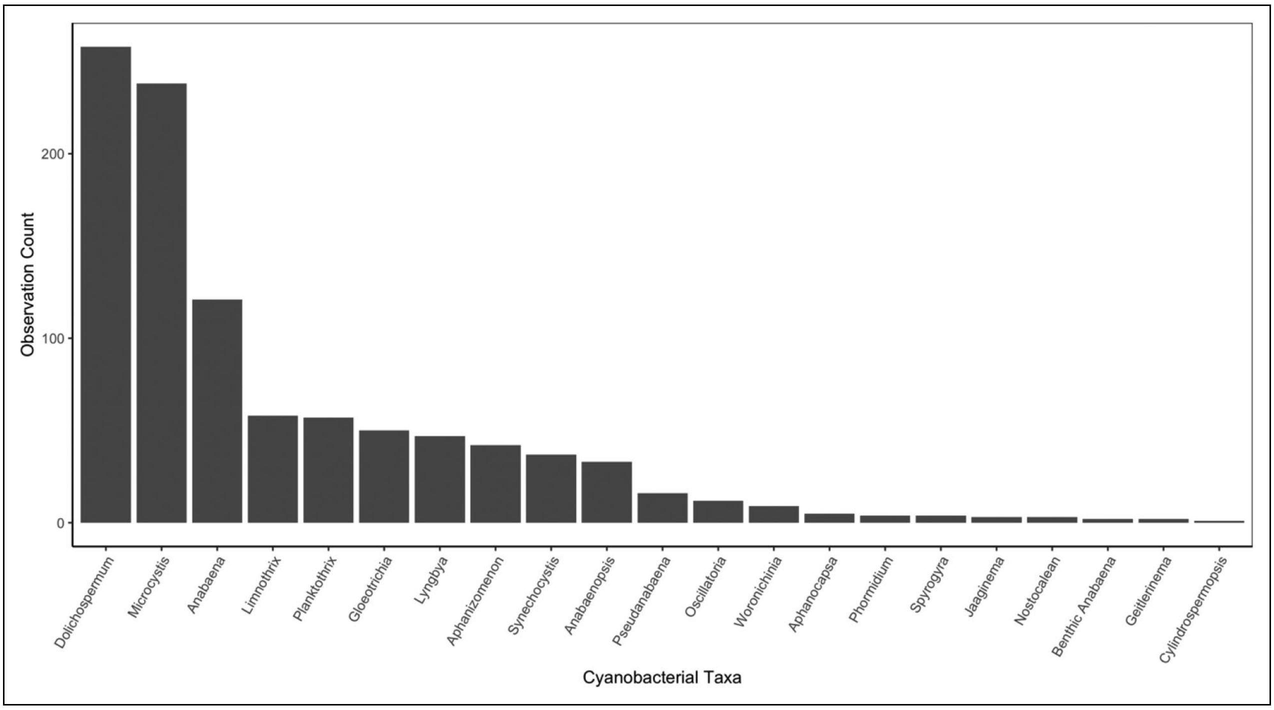

Figure 7. Recent cyanobacterial community composition in Clear Lake. Observations of cyanobacterial community composition were made 2015–2019 by the Clear Lake Cyanobacteria Monitoring Program via microscopy. Frequency indicates the number of observations (*y*-axis) where each genus (*x*-axis) was observed out of 767 samples where community composition was assessed.

many of rarer taxa, are capable of toxin production and likely account for the cyanotoxins reported from the lake. Identification of the toxin producers, and the environmental and biological factors that stimulate their growth and toxin production, are fundamental to understanding toxic events and their prevention in Clear Lake.

Species of *Microcystis*, together with *Dolicospermum*, have been a dominant component of cyanobacterial blooms in Clear Lake in recent years (**Figure 7**) but their historical presence in the lake is undocumented. Both are potential toxin producers (Harke et al., 2016; Li et al., 2016). *Microcystis* species have a cosmopolitan distribution (Harke et al., 2016), and recent evidence from the San Francisco Estuary ecosystem indicates that, once established, these species are resilient to removal by flooding and dilution (Lehman et al., 2022). The persistence of *Microcystis* in Clear Lake since its first documentation there is consistent with that suggestion. Reasons for its year-to-year dominance of the phytoplankton community are less understood.

The physiologies of the dominant cyanobacterial taxa, however, provide some insight into how lake conditions may drive both community composition and potentially toxin production. *Dolicospermum* (*Anabaena*) and *Gloeotrichia* are nitrogen-fixers, an ability that implies that nitrogen limitation may have imposed a strong control on phytoplankton community composition in Clear Lake throughout the past 5 years. *Microcystis* does not fix nitrogen, and in other nitrogen-limited systems, blooms of *Microcystis* have been shown to succeed blooms of nitrogen-fixing cyanobacteria, using nitrogen recycled from the dying bloom of the nitrogen fixers (Beversdorf et al., 2013). In several instances, the CLCMP has observed the succession of *Microcystis* after a *Dolicospermum* bloom, suggesting that nitrogen availability may be an important factor controlling the initial cyanobacterial bloom in Clear Lake, shifts in cyanobacterial dominance, and possibly toxin production.

Massive blooms of nitrogen-fixing cyanobacteria have recently become common in early summer in Clear Lake. Shifts in community structure between nitrogen fixing and non-nitrogen fixing cyanobacteria may be an important factor in bloom formation and the production of cyanotoxins (Tanvir et al., 2021). It is feasible that blooms of nitrogen fixing genera such as *Dolicospermum* or *Gloeotrichia*, which have been commonly observed in the lake (**Figure 7**) may constitute a "nitrogen loading event" that sets the stage for toxigenic blooms of *Microcystis* in the lake. Alternatively, or additionally, studies have demonstrated that *Gloeotrichia* may obtain significant amounts of phosphorus from the sediments of shallow lakes (Cottingham et al., 2015). In Lake Erken, Sweden, *Gloeotrichia echinulata* acquired most of its phosphorus requirements from the sediments, with subsequent growth in the epilimnion derived from internally stored phosphorus (Istvánovics et al., 1993). In Green Lake, Washington state, 40% of the planktonic colonies of *Gloeotrichia* were recruited from the benthos (Barbiero and Welch, 1992). Their behavior constituted a significant fraction of internal phosphorus loading from the sediments into water column. Development of the planktonic population of *Gloeotrichia* in that lake appeared to be independent of phosphorus availability in the water column. It is therefore possible that phosphorus internal loading by *Gloeotrichia* is as important as nitrogen fixation in creating conditions that support a subsequent bloom of *Microcystis* (and possibly microcystins production) in Clear Lake.

An apparent contradiction to this hypothesis is the observation of Mioni et al. (2011) who noted a positive relationship between *Microcystis* abundance and orthophosphate in Clear Lake. The authors suggested that *Microcystis* might be particularly well suited to compete for ammonium and phosphate, perhaps because of its ability to vertically migrate and capture nutrients throughout the water column. This explanation differs from the generally observed pattern that *Microcystis* blooms typically follow a nitrogen-loading event (Gobler et al., 2016), that is, a bloom of a nitrogen-fixing cyanobacterium. Clearly there is much yet to be deciphered regarding cyanobacterial succession and species–species interactions in Clear Lake.

Cyanobacterial growth and biomass accumulation are affected not only by bottom-up conditions (e.g., light, temperature, nutrient availability), but also by top-down control (grazing, viral lysis), allelopathic interactions and symbiotic relationships (mutualism, parasitism). Many monitoring and scientific studies of cyanobacterial bloom formation have focused on nutrient conditions that are conducive to cyanobacterial growth. Conversely, food web interactions and dynamics are also pivotal for understanding community composition, phytoplankton succession, and cyanotoxin production. Over the years, there have been introductions into Clear Lake of 25 non-native fish species. For example, the Mississippi silverside (*Menidia audens*) was introduced in 1967 to control gnats and cyanobacteria, although it has not been shown to be a significant control of those organisms (Moyle, 1976). The threadfin shad (*Dorosoma petenense*) was accidentally introduced and was abundant until the 1990, surged in abundance again in the 2000s but decreased again by 2011 (Moyle, 1976; Richerson et al., 1994; Thompson et al., 2013). These species are of particular significance because they prey on zooplankton larvae which can lead to a decrease in zooplankton populations, which in turn can affect phytoplankton abundance and community composition in a "trophic cascade" (Ripple et al., 2016). Winder et al. (2010) proposed that the decrease in threadfin shad populations in Clear Lake allowed increases in daphnid and rotifer populations, which in turn resulted in decreased phytoplankton standing stocks and subsequent improvements in water quality.

These largely anecdotal reports point to the potential importance of food web interactions in controlling both the magnitude, and especially the species composition of the phytoplankton community. Interactions between the phytoplankton community and submerged aquatic plants are also understudied. Aquatic plants may exert some localized control on phytoplankton community composition through a variety of mechanisms including nutrient competition, physical shading, or allelopathy (Nezbrytska et al., 2022; Bilous et al., 2023). Furthermore, many studies have reported the influence of zooplankton on phytoplankton community composition, and selective or preferential grazing by zooplankton on non-cyanobacterial species is well documented (Haney, 1987). *Microcystis* species have been reported to be a less desirable prey for many zooplankton (reviewed in Harke et al., 2016). Some copepods selectively consume algae over cyanobacteria, and when they do consume cyanobacteria, they graze preferentially on non-toxic species rather than toxigenic ones (Hong et al., 2013; Leitão et al., 2018). Such selective feeding may reduce overall phytoplankton biomass but specifically favor the growth of toxigenic cyanobacterial populations. The potential for toxins of other cyanobacterial compounds to act as allelopathic substances has also been suggested (Leão et al., 2009). Selective grazing may be a significant factor in determining phytoplankton community structure, but these interactions are still largely unexplored in cyanobacterial research. The role of competitive interactions among phytoplankton groups, particularly in a changing climate, are also not well understood. For example, a recent analysis of North American lakes suggested that in addition to eutrophication and warming temperatures, rising CO_2 may also influence phytoplankton community composition (Verspagen et al., 2022). Therefore, it is not only important to understand factors that stimulate growth, but also the role that community interactions play in shifting dominance within the phytoplankton assemblage to understand cyanobacterial blooms in Clear Lake.

3.2.3. Poorly characterized stressors: Anthropogenic influences and wildfires

While Clear Lake is a naturally eutrophic lake, there are still substantial effects from present or past mining operations, agriculture, and erosion. With increases in the number of homes and road construction in the 1970s there was higher demand for gravel, which resulted in the mining of creek beds until the late 1980s (Zalusky, 1992). According to sediment cores taken from Rumsey Slough located at the northwestern end of the Upper Arm, there was a spike in carbon, nitrogen, and phosphorus levels around 1969, which is hypothesized to be due to increased erosion and runoff from gravel mining (Kim, 2003). During that time there was also a reduction of wetlands due to agricultural uses. By 1977, 85% of the natural wetlands in the watershed were either destroyed or replaced with farms (Richerson et al., 1994; Suchanek et al., 2002). The loss of natural wetland habitat around the lake likely played an important role in the eutrophication and rise of cyanobacterial dominance in the system, but quantification is difficult due to the limited period that concerted biological measurements have been made.

The construction of the dam across Cache Creek in 1914 is another anthropogenic stressor potentially contributing to cyanoHABs in Clear Lake. Microcystin concentrations in all Arms of the lake showed negative correlations with gauge height, presumably an indication that longer residence times of water in the lake allow for the development of more extensive blooms and toxin production. Given the correlation between residence times and blooms, a relationship between the installation of the dam and intensification of blooms seems likely. The use of the dam is outlined in multiple decrees to avoid flooding, while preserving lake levels for the summer and periods of drought (U.S. Army Corps of Engineers, 2002). It is likely that water retained by the dam during summer, and particularly during periods of drought, experiences longer residence times and therefore the potential to develop substantial blooms. Although the decrees controlling the dam were created to balance the needs of the lake and the need to pull water for other purposes, reevaluating the current practices may aid in bloom management.

In the last decade, Clear Lake has experienced catastrophic fires that may affect lake ecology. Fires occur seasonally in the watershed, albeit some are more devastating than others. Some of the largest fires include the 2012 Wye-Walker and Scotts fires, the 2015 Rocky, Jerusalem, and Valley fires, the 2016 Clayton fire, the 2017 Sulphur fire, and the 2018 Ranch, River, and Pawnee fires which each collectively burned between 8.9 km^2 and 688 km^2 in and around the Clear Lake watershed (CalFire, 2020). The impacts of these events on the ecology of the lake are not well understood but are presumed significant. Unfortunately, there are limited data at present on the effects of wildfires on lake chemistry, although recent studies suggest that fires certainly can play a role in changing lake ecosystems. Those studies have found that fires can increase nutrients such as phosphorus and nitrogen in watersheds although it is not yet clear that these inputs result in significant changes in lake chemistry or phytoplankton biomass (McColl and Grigal, 1975; Tarapchak and Wright, 1986; McCullough et al., 2019). Additionally, the importance of such events for a lake as eutrophic as Clear Lake is particularly difficult to ascertain. The link to lake ecology is still largely unexplored for Clear Lake, and most lakes in general, but may play an increasingly significant role in a changing climate with increasing wildfires.

3.3. Seasonality and spatial heterogeneity

Seasonality, and year-to-year variability in seasonality, is a normal feature of lakes that contributes to temporal heterogeneity and complicates our understanding of the biological dynamics taking place within Clear Lake. Changes in the seasonality of water temperature, and its potential consequences on the length of the cyanobacterial "growing season" have already been noted (**Figure 2**). Also, strong seasonality has been noted in chlorophyll *a* and phycocyanin concentrations (**Figure 5**; Supplemental Figure 6) for the relatively few years that the latter information has been collected. Seasonality and spatial heterogeneity of other pertinent physical, chemical, and biological parameters among the Arms of Clear Lake have been observed but only a few have displayed the seasonal amplitude exhibited by temperature and phytoplankton biomass.

Strong seasonality has been observed for microcystin concentrations in Clear Lake over the past decade that they have been analyzed, with highest concentrations observed from June through November (**Figure 8**; note log scale on *y*-axis). Unsurprisingly, this finding is in agreement with seasonal maxima in chlorophyll *a* and phycocyanin concentrations (**Figure 5**; Supplemental Figure 6). It is also consistent with the general tendency of cyanobacterial community dominance during warm water

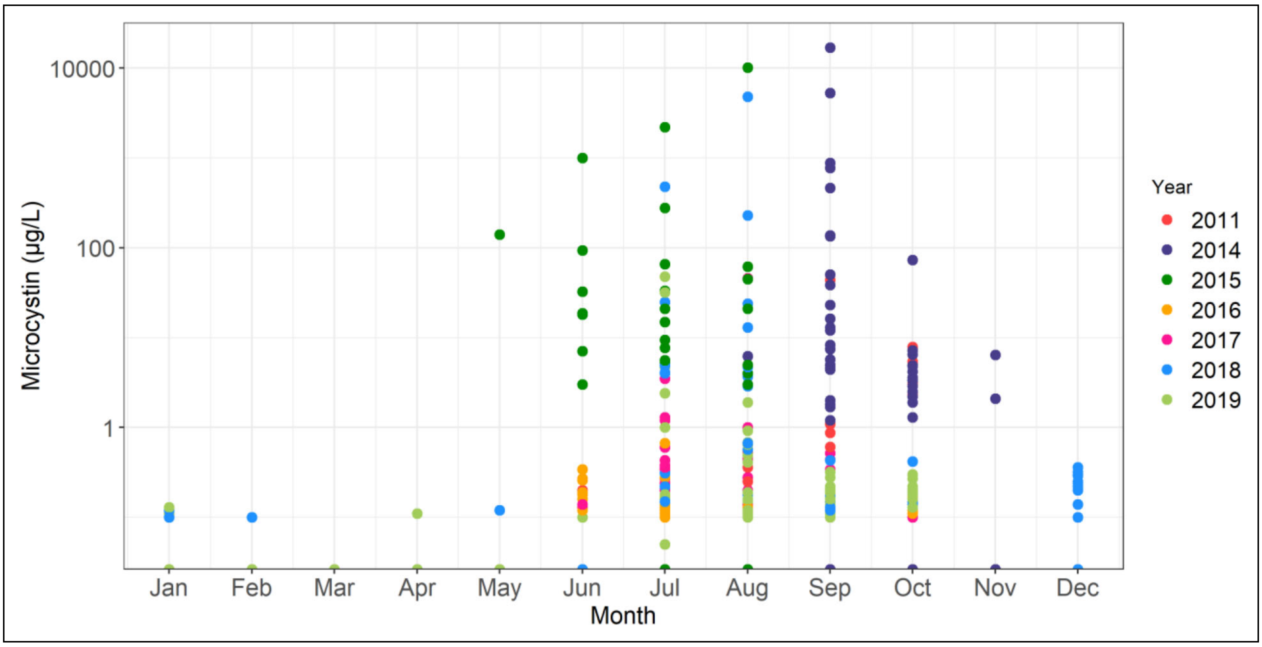

Figure 8. Monthly patterns in total microcystin occurrence and concentrations. All microcystin concentrations collected between 2011–2019 are plotted by month to evaluate seasonal patterns in occurrence. The color of the point indicates the year in which the observation was collected.

periods (Paerl and Huisman, 2008; Paerl and Otten, 2013; Mantzouki et al., 2018).

In contrast to the parameters noted above, a seasonal pattern in TKN was not readily apparent in a data set that spanned 5 decades nor was a marked difference in TKN values among the 3 Arms of Clear Lake, although summer and fall months have had more instances of very high values compared to other months (**Figure 9A**). TP values revealed minor but consistently higher median values throughout the summer and fall compared to other months, coinciding with maxima in chlorophyll *a* (**Figure 5**), phycocyanin (Supplemental Figure 6), and microcystin concentrations (**Figure 8**), as well as more instances of very high values (**Figure 9B**). Additionally, median values for TP during the summer/fall were generally different among the 3 Arms of the lake with highest values observed in the Upper Arm and lowest values in Lower Arm.

Seasonality and differences in TN and TP among the 3 Arms of Clear Lake were reflected in the TKN:TP values. The lowest ratios, generally below Redfield proportions, were observed in the Upper Arm while the highest values were observed in Lower Arm. This finding may indicate that nitrogen is generally more limiting to phytoplankton growth in the Upper Arm compared to the other Arms of the lake (**Figure 9C**), although the differences could also be a result of more efficient uptake and retention of phosphorus by phytoplankton, the selective movement of phosphorus from the sediments up into the water column by vertically migrating cyanobacteria as noted above (Barbiero and Welch, 1992; Istvánovics et al., 1993), or non-phytoplankton constituents of particulate material that preferentially retain more phosphorus than nitrogen. Teasing apart these alternate explanations of variances in TKN:TP may be key to understanding the factors driving cyanobacterial dominance in the lake, assuming these ratios are indicative of the element limiting cyanobacterial biomass. Seasonally, somewhat higher values of TKN:TP were observed during the winter and spring, relative to summer and fall, primarily driven by seasonality in TP.

Modest seasonal variances and/or spatial heterogeneity among the Arms of Clear Lake were also apparent in some of the other chemical constituents over the 70-year period that they have been observed. Specifically, seasonality was apparent in pH and dissolved oxygen that reflected the annual cycle of phytoplankton growth (Supplemental Figure 8A, B). Seasonal maxima in pH occurred during summer and fall at the time of maxima in phytoplankton production (Supplemental Figure 8A). Dissolved oxygen concentrations revealed the opposite pattern, with the probability for the lowest values during the summer and fall when bacterial oxygen demand would be expected to be maximal due to the presence of large amounts of decaying phytoplankton biomass (Supplemental Figure 8B). Little spatial heterogeneity was apparent in either pattern. Specific conductance revealed maxima during winter months, presumably reflective of inputs to the lake during periods of precipitation and therefore increased runoff (Supplemental Figure 8C).

3.4. Review of TMDL and Control Program for Clear Lake

The TMDL and Control Program for phosphorus in Clear Lake were adopted by the Central Valley Water Board in 2006, and approved by U.S. EPA in 2007 to reduce inputs of phosphorus to the lake (CVRWQCB, 2007). Reduction of external phosphorus loads was deemed beneficial for reducing the nutrient impairment driving cyanobacterial

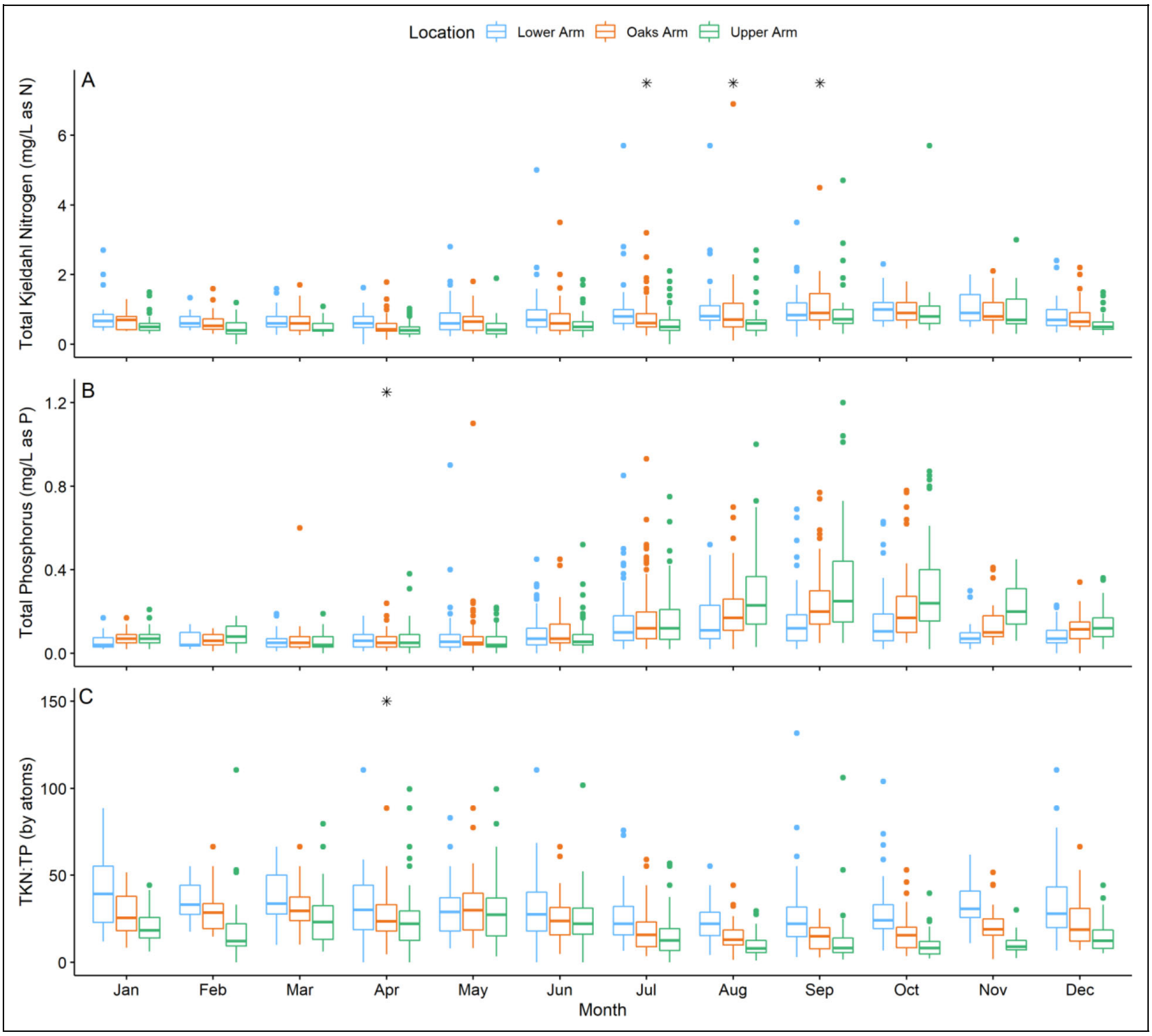

Figure 9. Seasonal patterns in total Kjeldahl nitrogen and total phosphorus concentrations and ratios. Monthly changes in total Kjeldahl nitrogen (A), total phosphorus (B), and the ratio of total Kjeldahl nitrogen to total phosphorus (TKN:P, by atoms; C) in Clear Lake. Colors indicate values in the Upper Arm (green), Lower Arm (blue), and Oaks Arm (red). Seasonal patterns in total Kjeldahl nitrogen concentrations and TKN:P ratios were summarized from data between 1965 and 2017, while data about total phosphorus concentrations were summarized from data between 1965 and 2019. Asterisks at the top of each figure indicate concentrations larger than 7.5 mg/L as N in Panel A, concentrations larger than 1.25 mg/L as P in Panel B, and ratios greater than 150 in Panel C.

blooms in the lake. The long-term data set generated in this study was used to investigate the effectiveness of these measures on altering pertinent environmental parameters by comparing 10-year periods prior to enactment and following the enactment of the TMDL and Control Program (**Figure 10**).

These analyses identified several changes that have occurred in the lake since enactment of the TMDL, as well as parameters that have shown no apparent change. In the latter case, water temperature, which was not specifically targeted by the TMDL and Control Program, has shown minimal changes in its PDF or overall magnitude and range of values (**Figure 10A, B**; $P \leq 0.0001$ $r = 0.097$). More significant shifts in TP have occurred between the 2 decadal data sets ($P \leq 0.0001$ $r = 0.271$), although these changes are not in keeping with expectations for imposing the TMDL and Control Program (**Figure 10C, D**). The PDF for TP values in the 10 years following the implementation of the TMDL indicate a decreased probability of low TP concentrations, but a higher probability of high values ($\geq$0.25 mg P/L; **Figure 10C, D**). These results indicate that the observed values of TP were greater after the TMDL and Control Program effective date compared with observed TP values beforehand. Some dischargers have met the load allocations of the TMDL and Control Program while others continue to work toward the reduced load allocations (CVRWQCB, 2021).

The source of the phosphorus contributing to the increased TP in the years since the TMDL and Control Program was imposed is unclear yet understanding that

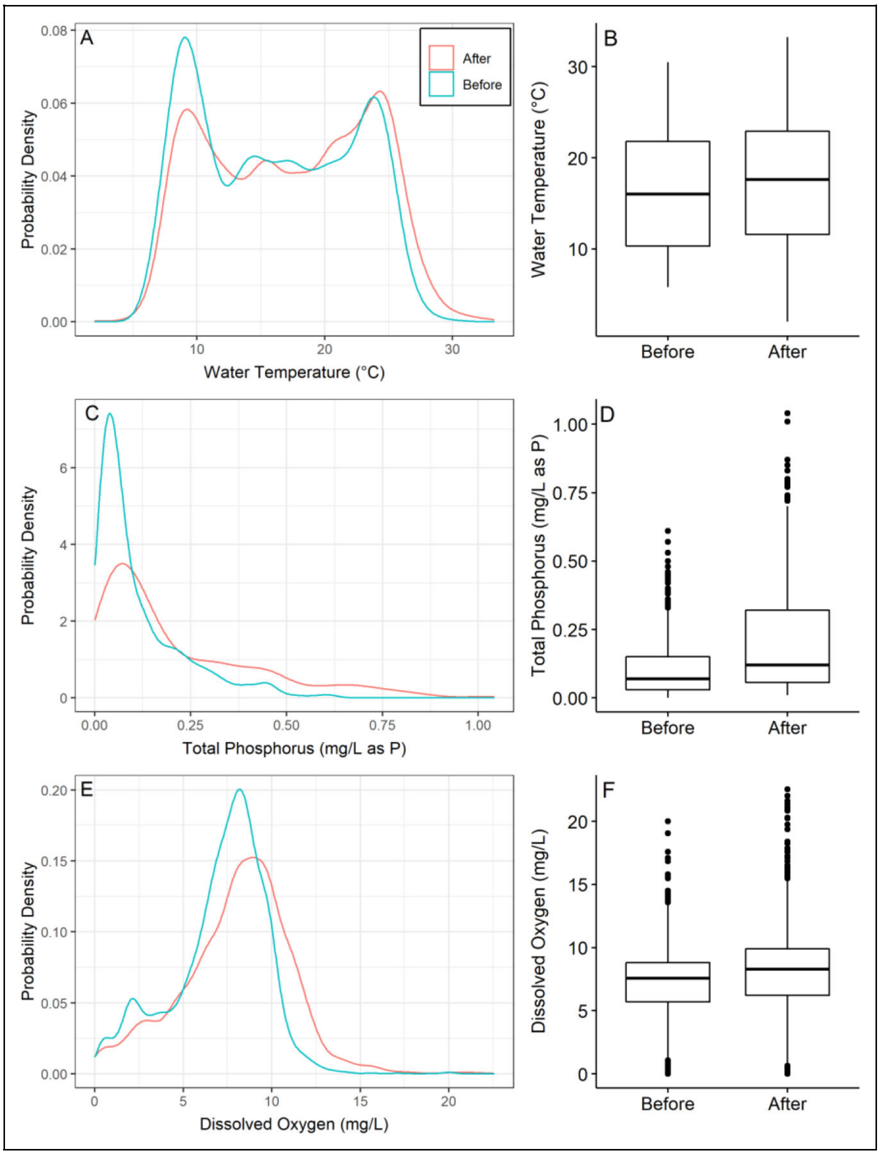

Figure 10. Evaluation of the effects of TMDL and Control Program imposed on Clear Lake. A comparison of a decade of data collected prior to enactment, and a decade following enactment of the TMDL and Control Program. Figures show probability density functions (A, C, E) paired with box plots (B, D, F). Data examined included total water temperature (A, B), total phosphorus (C, D), and dissolved oxygen (E, F). Lines representing 10 years of data before (blue) and 10 years of data after the 2007 implementation of TMDL (red). *P*-values and *r*-values from Wilcoxon rank-sum test indicating the statistical significance and effect size of the differences in the boxplots respectively are as follows: (B) Water temperature $P \leq 0.0001$ $r = 0.098$, (D) Total phosphorus $P \leq 0.0001$ $r = 0.271$, (F) Dissolved oxygen $P \leq 0.0001$ $r = 0.165$.

source is fundamental to constraining phosphorus availability for phytoplankton growth (and thus in reducing blooms) in the lake. In addition to a reduction in the external loading of phosphorus in Clear Lake, it appears clear that attention should be focused on the role of the internal loading of phosphorus in the lake, and how it becomes available to algae and cyanobacteria in the water column. Water temperature, per se, does not appear to play a major role as noted above, although an expansion of the warm water period in the lake may play a role (**Figure 2**). A relationship with drought conditions appears to be involved, as it has been reported that release of phosphorus from the sediment is enhanced in drought years (Richerson et al., 1994). That hypothesis is consistent with the fact that TP values were highest in the lake during the extreme drought years of 2014–2016 (**Figure 5B**).

The mechanism of this mobilization, however, is still not clear. One might expect that such events would coincide with hypoxic/anoxic events that could release substantial amounts of phosphorus from the sediment (Mortimer, 1941). There is little evidence of increased incidences of hypoxic or anoxic events in the 70-year time series of dissolved oxygen (Supplemental Figure 2A) but overall a negative correlation was obtained for the data set (**Table 2**). Clearly, the importance of hypoxia/anoxia as a mechanism for nutrient release from Clear Lake sediments should be evaluated. Alternatively, the potential for cyanobacterial vertical migration, and particularly the role that *Gloeotrichia* or *Microcystis* may play in moving nutrients from the sediments into the water column, as noted previously, should be determined.

Minor changes in the PDF for dissolved oxygen indicated a slightly higher probability of higher values following the TMDL and Control Program ($P \leq 0.0001$ $r = 0.165$), although the probability for very low values appears mostly unchanged (**Figure 10E, F**). That is, the lake has a higher probability of experiencing high dissolved oxygen concentrations since the enactment of the TMDL but the probability of hypoxic or anoxic events is unchanged.

3.5. Current practices and future directions

The task of improving water quality and eutrophic conditions in Clear Lake and mitigating or preventing toxic cyanoHABs in the lake will be a lengthy and difficult task. Such a goal has been deemed impossible in some other highly eutrophic lakes (Canfield et al., 2021), and it will be a formidable one in Clear Lake. Additional research and management actions are needed to improve the water quality in the lake, although it is also important to note that extensive work is currently underway. Multiple groups now regularly monitor Clear Lake for cyanoHABs and related water quality metrics. The resulting information has contributed to the data set assembled here and improved our understanding of the factors promoting cyanoHABs in the lake. Nonetheless, one of the major shortcomings of the data set continues to be a lack of co-occurring measurements of chemical, physical, and biological parameters. Such co-occurring measurements are necessary to identify relationships between the major physical/chemical features of the lake and the biological outcomes of those features (e.g., cyanoHABs). Similarly, continuous and automated monitoring (Sharp et al., 2021) would also be useful in capturing processes that occur simultaneously across the lake, as well as high-resolution dynamics on smaller spatial scales (e.g., within the 3 Arms of the lake) that may affect local nutrient availability and utilization.

The large size of Clear Lake makes it difficult to obtain good sample coverage across its extent, so collaborative relationships to collect water quality data in a coordinated and cohesive way must be prioritized. The establishment of the Clear Lake Blue Ribbon Committee in 2017 as a multistakeholder effort to rehabilitate the lake and surrounding ecosystem has fostered collaborative rehabilitation efforts. Similarly, formation of the multiagency Clear Lake Cyanobacterial Task Force is an important step in coordinating monitoring efforts between the Tribal governments with local, state, and federal agencies working in the lake. For example, a collaboration between CLCMP and Department of Water Resources began in 2018 which resulted in a cohesive data set of co-occurring physicochemical and biological measurements that will enhance future research, particularly toward understanding cyanoHAB drivers. Continued efforts toward open-data practices among agencies should also be made to streamline research efforts on the lake.

The TMDL and Control Program for Clear Lake enacted in 2007 created limits on phosphorus inputs to create a 40% load reduction. Since the residence time of the lake is approximately 4.5 years, the expectation has been that changes would be observed within a decade following the implementation of the TMDL and Control Program. Our study indicates TP levels have actually increased since 2007 (**Figure 10C, D**). While this analysis cannot conclude if the increase is due to external or continued internal loading, nor can the impact of episodic events such as drought be accurately characterized by this study, the TMDL and Control Program should be reevaluated to achieve the desired change in Clear Lake. In addition to the TMDL and Control Program, there have been other efforts in the watershed to address the impairments to beneficial uses. The goal of the Middle Creek Flood Damage Reduction and Ecosystem Restoration Project was to restore historic wetland and floodplain areas to capture phosphorus-laden sediment. The first phase of the project is to reclaim 6.7 km^2 of which they have been able to obtain rights to 0.5 km^2.

Several possible revisions to the TMDL and Control Program might be considered in light of continuing cyanoHABs in the lake. Most significantly, the TMDL and Control Program could include nitrogen in addition to phosphorus since the TKN:TP ratios were lower in the Upper Arm indicating that nitrogen may be a limiting factor. At the time the TMDL and Control Program was developed, phosphorus was the primary nutrient attributed to controlling cyanobacterial blooms in freshwater systems. Many studies since then have showed that nitrogen, as well as phosphorus, control cyanobacterial blooms and both nitrogen and phosphorus need to be included in water quality management strategies (Conley et al., 2009; Scott and McCarthy, 2010; Paerl and Otten, 2013). Moreover, early studies in Clear Lake identified nitrogen availability as an important factor in bloom formation (Horne and Goldman, 1972; Richerson et al., 1994). Therefore, revision may be needed of the TMDL and Control Program based on current scientific recommendations to address both nitrogen and phosphorus inputs as a nutrient management solution. Most significantly, our summary and review of existing data indicate that the role of the internal loading of phosphorus in the lake should be considered in the TMDL and Control Program revision. Approaches to reduce internal loads could range from fish reduction efforts (Søndergaard et al., 2008), efforts to support the growth of submerged aquatic vegetation to bind available nutrients making them unavailable to harmful algae and cyanobacteria (Zou et al., 2020) or sediment removal (Kiani et al., 2020).

A variety of special studies are needed to accurately identify the specific environmental drivers of cyanoHABs and cyanotoxin production. Multiple co-occurring and interacting factors influence Clear Lake water quality and cyanoHABs. Special studies focused on parsing out and quantifying those aspects of water chemistry, physics, and biology that are most impactful for stimulating cyanoHABs and toxins production will be necessary to properly design effective lake mitigation and management strategies to combat them. These focal areas should include:

(1) The importance of internal loading of nutrients in Clear Lake in supporting recurrent cyanoHABs. Multiple lines of evidence implicate lake sediments as a major source of nutrients fueling blooms. The importance of hypoxic/anoxic events in facilitating the flux of nutrients into the overlying waters, thereby stimulating, prolonging, or enhancing cyanoHABs should be thoroughly evaluated.
(2) The possible role of cyanobacteria themselves in moving nutrients from the sediment or deep water of the lake into the upper water column where they contribute to blooms needs investigation. The vertical migratory behaviors of *Gloeotrichia* and *Microcystis* in this process have been documented (Barbiero and Welch, 1992; Istvánovics et al., 1993; Hunter et al., 2008) but to our knowledge this behavior has not been investigated in Clear Lake.
(3) The roles and influence of co-occurring microbes in cyanobacterial dominance, succession, and cyanotoxin production. Studies focusing on characterization of microbial community diversity and interspecies communication may yield insights into the reasons for species success and dominance. Studies of the cyanoHAB microbiomes, and the role co-occurring microbes play in dominance and toxin formation is in its infancy, but preliminary studies indicate a significant role for these interactions (Cook et al., 2020).
(4) The influence of top-down effects in bloom formation and in the taxonomic composition of the bloom. The importance of trophic interactions in bloom initiation, persistence, and demise is still highly under-studied, and as one recent review indicates the outcome of such interactions is far from clear (Ger et al., 2011).

Data accessibility statement
The master database assembled for this study is published on Zenodo under the DOI: https://doi.org/10.5281/zenodo.8352065.

Supplemental files
The supplemental files for this article can be found as follows:

Supplemental Material.docx

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Wrote the manuscript: JS, EE, MDAH, DAC.

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Conducted the data acquisition and data set assembly: JS, EE, SR, AT, JG, KK, SH.

Analyzed and synthesized the data with significant contributions from MB: JS, EE, SH.

Contributed significantly to the interpretation of the data: All authors.

Approved the submitted version for publication: All authors.

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