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ORIGINAL ARTICLE

Long-term Deepwater Dissolved Oxygen Dynamics in a Hypereutrophic Reservoir Following Shifts in Watershed Management and Lake Warming

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Abstract

Long-term declines in lake hypolimnetic dissolved oxygen (DO) have been attributed to eutrophication, reduced water clarity, or rising temperatures. DO dynamics in human-made reservoirs may also be influenced by their distinct characteristics (for example, hydrology) and by the high levels of watershed inputs (suspended sediments, nutrients) these systems may receive, particularly in agricultural landscapes. We used a 31 year dataset in a reservoir that has experienced agricultural land management change to ask: (1) What are the long-term trends in two hypolimnetic DO metrics (DO concentration in early summer and summer anoxic factor), and (2) what are the key drivers of these metrics?. We used linear regressions to assess temporal trends, and exhaustive variable selection to identify drivers. Potential drivers included metrics of watershed discharge, temperature, stability, and potential productivity (chlorophyll, non-volatile suspended sediments; NVSS). We found that deepwater early summer DO concentrations decreased, but there was no temporal trend for anoxic factor. Deepwater DO was best predicted by surface temperature, with warming temperatures related to lower DO. However, the top five models performed similarly, and all included a temperature or stratification metric. Higher stability was related to lower DO. For anoxic factor, the top two models performed similarly with stability, surface temperature, and NVSS identified. Anoxic factor increased with higher surface temperature, lower NVSS, and higher stability. Our findings suggest that DO dynamics were linked to previously recognized drivers (for example, temperature), as well as NVSS, a driver that is rarely acknowledged and may reflect land use and management within the watershed.

Key words: Agriculture; anoxia; climate; suspended sediments; dissolved oxygen; lakes; reservoirs; temperature.

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Highlights

- Long-term changes in deepwater dissolved oxygen only occurred in the early summer.
- Suspended sediments in water column mediated reservoir dissolved oxygen dynamics.
- Deepwater dissolved oxygen metrics at different timescales aid long-term analysis.

Introduction

Dissolved oxygen (DO) is a fundamental property in lakes that reflects productivity and is widely used as a measure of water quality, particularly hypolimnetic DO which can reach hypoxic or even anoxic concentrations due to decomposition of organic matter (Wetzel 2001). Long-term studies across many geographic locations and lake types reveal that hypolimnetic DO concentrations are decreasing over time, and the extent and duration of anoxia are increasing (Foley and others 2012; North and others 2014; Jenny and others 2016; Jane and others 2021). These shifts can have detrimental effects on lake water quality and ecosystem function because low DO increases internal nutrient loading from sediments (Mortimer 1942; Søndergaard and others 2003), amplifies greenhouse gas emissions via methane production (Encinas Fernández and others 2014; Beaulieu and others 2019), and limits the habitat available for cold-water fish species that require high-DO and low-temperature conditions (Jacobson and others 2010; Woolway and others 2022).

Long-term declines in hypolimnetic DO have been linked to reduced water clarity (via eutrophication) or increasing dissolved organic matter (DOM) via lake 'browning' and rising lake temperatures (Foley and others 2012; North and others 2014; Jenny and others 2016; Knoll and others 2018; Jane and others 2021). Mechanistically, warmer water temperatures reduce the solubility of DO, although long-term trends over the past several decades show that temperature increases are restricted to shallower water depths in many lakes, whereas hypolimnetic temperatures show no consistent trends (Winslow and others 2015; Pilla and others 2020). Rising surface temperatures can also increase the strength and duration of thermal stratification (Richardson and others 2017; Woolway and others 2021), thereby minimizing DO diffusion from the mixed layer to deeper depths or prolonging the period of DO consumption in the hypolimnion (Jane and others 2023). Increases in phytoplankton biomass or DOM can influence DO dynamics through multiple mechanisms. Limnologists recognize that eutrophication leads to increased DO consumption in the hypolimnion as sinking organic matter is decomposed (Wetzel 2001). DOM can also reduce hypolimnetic DO by fueling microbial respiration within the water column (Solomon and others 2015), strengthening thermal stratification (Fee and others 1996; Solomon and others 2015; Pilla and others 2020), and restricting productivity to shallower depths (Karlsson and others 2009).

DO dynamics in human-made reservoirs, in comparison with natural lakes, may be mediated by additional factors (Bukaveckas and others 2025) given their distinct morphometry, hydrology, and tighter terrestrial–aquatic linkages with high inputs of watershed-derived subsidies (that is, nutrients or sediments) (Thornton and others 1991; Doubek and Carey 2017; Hayes and others 2017). Furthermore, many reservoirs are actively managed for human uses such as drinking water (for example, water withdrawal at various depths, oxygenation) or hydropower (Beutel and Horne 1999; Hayes and others 2017). Thus, the physical features of reservoirs, along with their management strategies, may render long-term DO patterns more complex in these systems. Although past studies have explored whether thermal properties are changing in reservoirs, often considering the unique role of dam withdrawal or inflowing waters (Moreno-Ostos and others 2008; Lewis Jr and others 2019), fewer have simultaneously examined long-term dissolved oxygen trends in reservoirs. Of these, deepwater dissolved oxygen trends often varied by reservoir mixing characteristics (that is, stratified, unstratified) or broad land use type (Detmer and others 2021; Smucker and others 2021; Bukaveckas and others 2025). However, these multireservoir studies did not explore a full suite of potential drivers that may help to explain oxygen trends in reservoir systems (for example, hydrology, external subsidies). Assessment of the drivers of long-term DO dynamics in reservoirs is thus a conspicuous knowledge gap.

Oxygen dynamics in reservoirs may be influenced by watershed characteristics because these ecosystems tend to have large watershed area to lake area ratios (Doubek and Carey 2017) and therefore may receive relatively large subsidies of nutrients and terrestrial sediments (Thornton and others 1991; Knoll and others 2014). It has long been recognized that watershed-derived materials can serve as ecosystem subsidies to aquatic systems. Nutrients, such as dissolved nitrogen or phosphorus or those contained in suspended sediments, may stimulate primary producers (Smith 2003; Vanni and others 2006; Dodds and Smith 2016). On the other hand, suspended sediments may decrease phytoplankton production by shading out light (Knowlton and Jones 2000; Pilati and others 2009; Kelly and others 2019), and reservoirs in agricultural landscapes can receive large inputs of suspended sediments from their watersheds due to soil erosion (Dodds and Whiles 2004). Thus, watershed subsidies may stimulate (that is, dissolved nutrients, nutrients bound to sediments) or depress (that is, sediment-caused shading) primary producers with potentially opposing effects on hypolimnetic DO in reservoirs. Reservoirs found in agricultural landscapes may also experience shifts in agricultural management. For example, in some areas of the Midwestern United States (location of the present study), conservation tillage, a farm management practice aimed at reducing soil erosion (Holland 2004), increased in the 1990s (Peterson 2005), and has remained in practice at varying levels to the present day (Wade and others 2015; Plastina and others 2024). In some systems, these trends have been associated with declines in suspended sediments in runoff (Tiessen and others 2010) and streams (Renwick and others 2008, 2018). However, it remains unclear the extent to which changing levels of watershed-derived suspended sediments may influence oxygen dynamics in agricultural reservoirs.

Reservoir hydrology can also impact thermal structure and potentially dissolved oxygen via several mechanisms. First, reservoirs tend to have short residence times that can vary from several hours during large runoff events to over a year during dry conditions (Thornton and others 1991). Although inflow inputs can bring large pulses of watershed subsidies that may alter physical and chemical conditions due to changes in vertical light distribution and nutrient supply (Vanni and others 2006), storm events may also bring a large influx of water from the watershed. High discharge events (that is, high influx of water in a short period of time) may disrupt the thermal stratification structure (Wang and others 2012; Li and others 2015; Lewis Jr and others 2019) or flush oxygen-producing phytoplankton from the ecosystem (Klug and others 2012). For example, in a stratified eutrophic reservoir, precipitation from a large storm event led to thermal stratification disruption and increased dissolved oxygen in the bottom of the reservoir (Li and others 2015). In addition, many reservoirs are dammed rivers, and horizontal movements of water along the former riverbed can affect thermal stratification, with the impact varying based on external water inputs (Hayes and others 2017). Thus, year-to-year variability in hydrology may influence hypolimnetic DO by affecting the strength and duration of thermal stratification, as well as phytoplankton production and biomass.

Here we use a 31 year dataset for Acton Lake, a hypereutrophic reservoir in southwest Ohio, USA, to explore the importance of climate, watershed, and internal lake drivers in predicting hypolimnetic DO dynamics. Specifically, we ask: (1) what are the long-term trends in two hypolimnetic DO metrics (DO concentration early in the summer and anoxic factor—the spatial extent and duration of anoxia), and (2) what are the key drivers of these DO metrics in a productive reservoir with land use dominated by agriculture?. Generally, we predicted that both climate and watershed variables would affect these DO metrics. Specifically, we first predicted that we would observe rising surface water temperatures, and concomitant increases in the strength of thermal stratification. Second, we anticipated that shifts in agricultural management (specifically, conservation tillage) in the watershed would influence the balance between phytoplankton and suspended sediments in the reservoir and, in turn, mediate hypolimnetic DO.

Methods

Study Site

Acton Lake is a relatively shallow (mean depth = 3.9 m, maximum depth = 8 m) hypereutrophic reservoir located in southwest Ohio, USA (39.561422, −84.738952). The lake was constructed in 1956 and has a surface area of 2.32 km^2. The watershed is large relative to the lake area (~ 111:1; watershed area 257 km^2) and is dominated by agriculture (~ 80% of watershed area; Figure 1), primarily as soy and corn cropland (Vanni and others 2001; Renwick and others 2008, 2018). The lake is dimictic or warm monomictic in years without ice cover, with seasonal stratification primarily occurring toward the dam outlet where the depth is the deepest (Nowlin and others 2005). The rest of the lake (~ 60–70% of lake surface area) does not typically stratify due to the shallower depths (Kelly and others 2018). The dam has an uncontrolled spillway outlet, meaning that once water rises above the spillway, water is discharged from the reservoir. The dam also has a release structure deeper in the water column, but it is not actively used. Acton is productive with annual

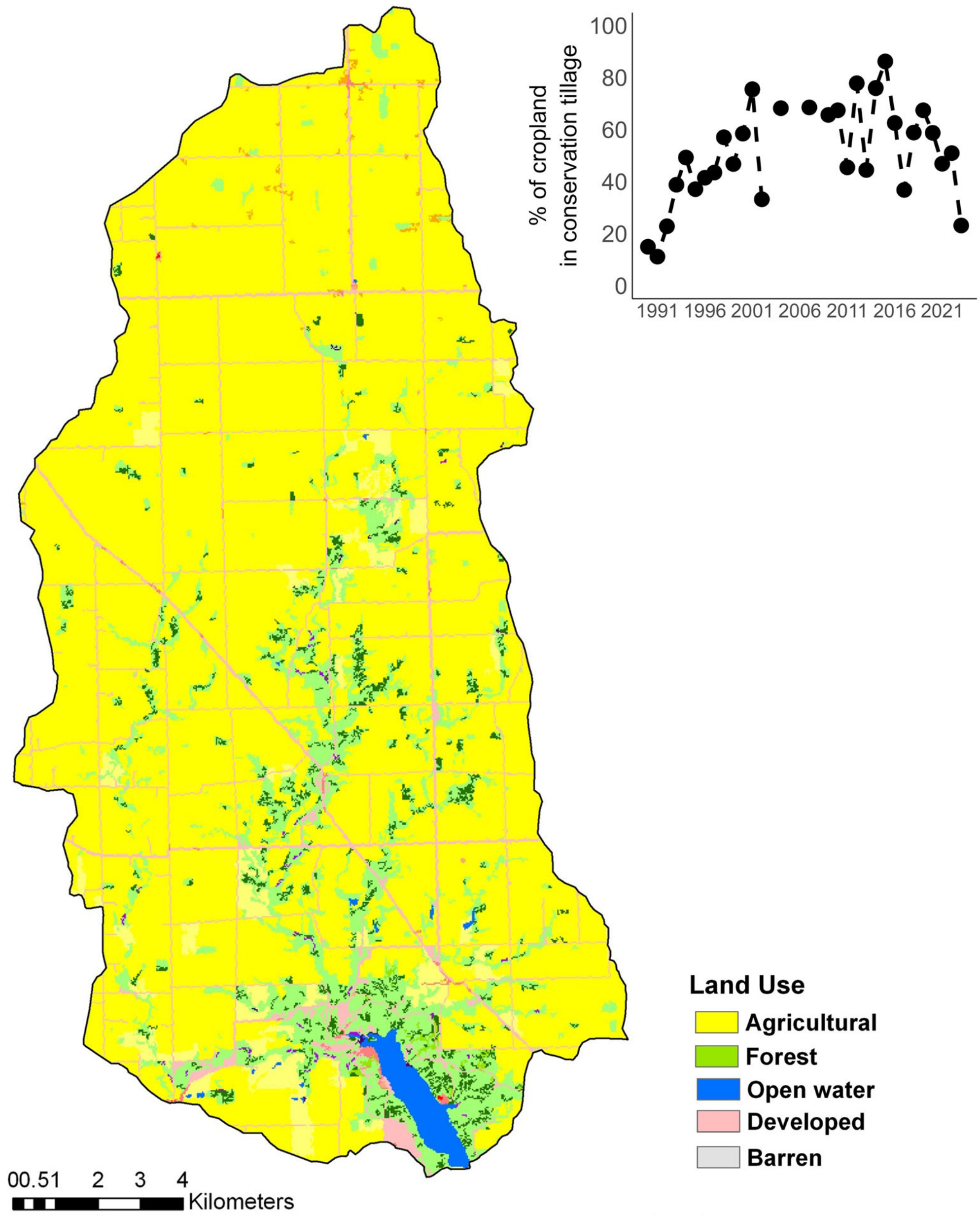


Figure 1. Watershed land use map for Acton Lake. The inset is the time series of annual cropland in conservation tillage within the watershed.

summer chlorophyll concentrations generally ranging from 40 to 70 mg L^{-1} (Kelly and others 2018), with diatoms dominating in the spring and cyanobacteria dominating in the summer (Hayes and others 2015; Hayes and Vanni 2018). The lake is turbid with high amounts of phytoplankton and inorganic sediment; thus, benthic primary producers and macrophytes make a very small contribution to the autochthonous production in the lake (Babler and others 2011).

In the early 1990s, an erosion control plan was developed for Acton's watershed (USDA-Soil Conservation Service 1992) to reduce sedimentation rates in the reservoir, which led to an increased proportion of agricultural land in conservation tillage, particularly between the late 1990s and mid-2000s (Renwick and others 2008, 2018). In more recent years, the proportion has leveled off, although recent observations suggest a decreasing trend in the last few years (Figure 1). Trends in conservation tillage in the Acton watershed generally reflect those at the regional scale (Jarvie and others 2017; Conservation Technology Information Center 2023). Between 1994 and 2006, the concentrations of soluble reactive phosphorus, ammonium, and suspended sediments draining into Acton Lake from its main inflow streams decreased (Renwick and others 2008). However, subsequent trends are more complex. Beginning in the early 2000s, the decline in suspended sediments and ammonium concentrations slowed, soluble reactive phosphorus concentrations remained static, and nitrate contractions began to drop rapidly (Renwick and others 2018).

Lake Sampling Regime and Potential Productivity Metrics

Acton Lake was sampled at the deepest location near the dam outflow from 1993 to 2023. The maximum depth of the site can vary based on water level, which is driven by precipitation and stream water inputs. Generally, the maximum sampled depth was 8 m, but on some dates in extremely dry years, the maximum sampled depth was as shallow as 6 m. Routine sampling typically occurred weekly between late April and early October. However, in some years, the sampling regime in the early and late months was less consistent. Thus, for this study, we restricted dates to those between mid-May and the end of August to ensure consistency among years. These dates capture the typical summer stratified period in Acton Lake, which generally encompasses the end of May or beginning of June until early September (Kelly and others 2018).

On each sampling date, temperature and dissolved oxygen profiles were taken at either 0.5 m or 1 m intervals. In early years, profiles were taken with a Clark polarographic electrode meter (Yellow Springs International models 57, 58, 55). In more recent years, profiles were collected using optical-based oxygen sensors (YSI ProODO).

The euphotic zone depth (depth at which photosynthetically active radiation, PAR, is 1% of surface PAR) was calculated from light profiles taken at 0.5 m increments (LI-COR underwater spherical PAR sensor). Integrated water samples were collected for nonvolatile suspended sediments (NVSS) and phytoplankton biomass (as chlorophyll-*a,* hereafter chlorophyll) from the euphotic zone. NVSS concentration represents the nonvolatile inorganic particles suspended in the lake water column (for example, clay and silt) and thus represents a measure of suspended sediments in the water column. This can serve as a proxy for productivity potential because NVSS may influence primary productivity via shading phytoplankton or by providing a subsidy of nutrients bound to the sediments. For chlorophyll analysis, euphotic zone water was filtered onto glass fiber filters (Pall A/E, 1.0 mm pore size), frozen, extracted with cold acetone or cold ethanol (both methods provided identical results), and analyzed with a fluorometer (Turner model TD-700). NVSS concentrations were quantified by filtering euphotic zone water through pre-ashed, pre-weighed glass fiber filters (Pall A/E). The filters were then dried and reweighed for total suspended solids, followed by ashing (550 °C) and reweighing to obtain NVSS (Knowlton and Jones 2000).

Watershed Discharge Metrics

Discharge from the watershed was quantified for the three main streams draining into Acton Lake (Four Mile Creek, Little Four Mile Creek, and Marshall's Branch) from 1995 to 2023. These streams collectively drain 86% of the watershed drainage (Vanni and others 2001; Renwick and others 2008). For each stream, stage was recorded every 10 min via pressure transducers and data loggers. Then, hourly discharge was calculated using standard rating curve techniques (Vanni and others 2001; Renwick and others 2008; Knoll and others 2013). Hourly discharge for each of the three streams was then summed and scaled to the entire watershed (that is, summed hourly discharge divided by 0.86).

Temperature and Stratification Metrics

We calculated volume-weighted temperature in the surface waters (0–2 m) and deep waters (bottom 2 m of the lake) for each year. We used bathymetric data and hypsographic curve estimates to calculate volume-weighted mean temperatures for these two zones in the lake. Schmidt stability was calculated as a measure of lake stratification strength (Idso 1973). Temperature profiles were linearly interpolated to 0.1 m increments from the surface to bottom of the lake. Weekly profiles were then interpolated to the daily timescale (Akima and others 2022). Schmidt stability was then calculated using the R package ''rLakeAnalyzer'' using the schmidt.stability() function (Winslow and others 2014). Higher Schmidt stability values indicate that more energy is required to mix the water column (that is, the lake is more strongly thermally stratified).

Oxygen Metrics

We chose to focus on DO concentrations early in the summer (mid-May–end of June) rather than including mid- to late summer because the hypolimnion is anoxic in those later dates in all years. Thus, hypolimnetic DO concentrations in the latter half of the summer are expected to be below 1 mg L^{-1} and to remain unchanged over the entire time series. However, over the summer, anoxia duration may be prolonged and may extend into shallower depths. Therefore, we used anoxic factor (Nürnberg 1995) as a metric to assess oxygen trends over the entire summer period. We quantified these two deepwater oxygen metrics to assess temporal changes and also aimed to identify the most important predictors of these metrics. Volume-weighted dissolved oxygen concentrations in the deep waters (bottom 2 m) were estimated for each year by using bathymetric data and hypsographic curve estimates (as for temperature). Volume-weighted dissolved oxygen concentrations were assessed for early summer (mid-May–end of June; day of year 140–182, hereafter, deepwater DO_{EARLY_SUMMER}).

We also calculated anoxic factor for each summer (mid-May–end of August; day of year 140–244). This metric quantifies the spatiotemporal extent of anoxia (Nürnberg 1995). Anoxic factor (units: days $summer^{-1}$) was calculated using dissolved oxygen concentration profiles at 1.0-m increments that were linearly interpolated to the daily timescale (Akima and others 2022) and lake bathymetric data as:

$$\text{anoxic factor} = \frac{\sum_{i=1}^{n} t_i a_i}{A_0}$$

where A_0 is the lake surface area in m^2, t_i is the period of anoxia in days, and a_i is the corresponding hypolimnetic area in m^2. For a stratum to be considered anoxic, the dissolved oxygen concentration for that day had to be < 1 mg L^{-1}.

Data Analysis

For DO_{EARLY_SUMMER} and anoxic factor, we calculated a mean for each year. For each driver variable, we calculated an early summer mean (mid-May–end of June; day of year 140–182) and a full summer mean (mid-May–end of August; day of year 140–244). These two scales were used because effects on oxygen metrics could be mediated more by early season dynamics (for example, stratification onset) or full summer dynamics (for example, stratification variability due to storm events).

We used a simple linear regression to assess temporal trends for each of the driver variables and oxygen response variables at a significance level of 0.05. We then performed an exhaustive variable selection on all main effects models to identify the driver variables that best explained the variation in DO_{EARLY_SUMMER} or anoxic factor. Driver variables included watershed discharge, lake temperature, lake stratification, and lake productivity potential (Table 1). As it is well known, there is no *best* mechanism for choosing models in a regression setting (Aho and others 2014); we used the Bayesian information criteria (BIC) as it is recognized to select simpler models, as compared to model selection using Akaike information criteria or adjusted R-squared (James and others 2013). Before considering any inference, a residual analysis was performed on each selected model assessing the standard regression assumptions and looking for any serial correlation (Fisher and Gallagher 2012). For each oxygen metric, we report the five models with the lowest BIC values. In addition to the BIC score and variables selected, we also report the standard regression parameters (estimated coefficients, standard errors, *t*-test values, *p*-values), the variance inflation factor for predictor variable multicollinearity, from the ''car'' package in R (Fox and Weisberg 2019), and the adjusted R-squared value of the model. We also present additional simple linear regressions to facilitate interpretation of the exhaustive search model selection results. Specifically, for each of the driver variables in the top performing models, we used linear regression to visualize the relationship between the driver variables and the oxygen metrics. All analyses and figures were completed in R (R Core Team 2022) using ggplot2 (Wickham 2016).

Results

Temporal Trends of Driver Variables

Long-term temporal trends in water temperature varied by season and stratum. Early summer surface water temperature significantly increased over the 31 years (Table 2, Figure 2A; $p < 0.004$), while over the entire summer, surface water temperature trends suggested a marginally significant increase (Table 2, Figure 2A; $p < 0.07$). Annual average surface water temperature in the early summer increased from ~ 22 °C in the mid-1990s to ~ 24 °C in the early 2020s. There was no significant temporal pattern in deepwater temperature over the early ($p = 0.45$) or full summer (Table 2; Figure 2B; $p = 0.16$).

Watershed discharge in the early summer and over the entire summer did not change over the 31 year dataset (Table 2; Figue 2C; $p = 0.58$, $p = 0.60$, respectively). However, watershed dis-

Table 1. Potential Predictor Variables Used in Model Selection for DO Metrics

Response variable	Potential predictor variable	Potential mechanism(s)
Deepwater DO_{EARLY_SUMMER}		
	Watershed $discharge_{EARLY\_SUMMER}$	Water temperature, stratification, subsidies, flushing
	Surface water $temp_{EARLY\_SUMMER}$	Stratification
	Deepwater $temp_{EARLY\_SUMMER}$	Stratification, DO solubility
	Schmidt $stability_{EARLY\_SUMMER}$	Stratification
	$NVSS_{EARLY\_SUMMER}$	Shading phytoplankton, subsidy
	CHL_{EARLY_SUMMER}	Phytoplankton decomposition
	CHL_{PRIOR_SUMMER}	Phytoplankton decomposition
Anoxic factor		
	Watershed $discharge_{EARLY\_SUMMER}$	Water temperature, stratification, subsidies, flushing
	Watershed $discharge_{FULL\_SUMMER}$	
	Surface water $temp_{EARLY\_SUMMER}$	Stratification
	surface water $temp_{FULL\_SUMMER}$	
	Deepwater $temp_{EARLY\_SUMMER}$	Stratification, DO solubility
	Deepwater $temp_{FULL\_SUMMER}$	
	Schmidt $stability_{EARLY\_SUMMER}$	Stratification
	Schmidt $stability_{FULL\_SUMMER}$	
	$NVSS_{EARLY\_SUMMER}$	Shading phytoplankton, subsidy
	$NVSS_{FULL\_SUMMER}$	
	CHL_{EARLY_SUMMER}	Phytoplankton decomposition
	CHL_{FULL_SUMMER}	
	CHL_{PRIOR_SUMMER}	

Dissolved oxygen response variables were volume-weighted deepwater dissolved oxygen concentration in the early summer (deepwater DO_{EARLY_SUMMER}) and anoxic factor. Time periods considered were either early summer (mid-May to end of June) or full summer (mid-May to end of August). Surface water indicates 0–2 m and deepwater indicates the bottom 2 m of the lake.

charge varied substantially, revealing high year-to-year variability in stream water inputs on both summer timescales.

There were no significant shifts in Schmidt stability in the early ($p = 0.31$) or full summer (Table 2; $p = 0.58$) over the time series. However, average annual Schmidt stability varied considerably between years suggesting high variability in stratification strength year-to-year (Figure 2D).

We used two measures of productivity potential, chlorophyll concentration, and NVSS concentration. There was no significant change in chlorophyll over the entire time series at the early or full summer timescale (Table 2; $p = 0.24$, $p = 0.26$, respectively). Although no significant trends were found over the 31 year dataset, annual chlorophyll concentrations in the lake increased from ~ 1993 to the early 2000s, but then leveled off through 2014 (Kelly and others 2018; Fisher and others 2022). In more recent years (that is, after 2014), the time series suggests a slight decrease in chlorophyll concentrations (Figure 2E). On the other hand, NVSS concentrations decreased significantly over the entire time series in both early summer ($p < 0.002$) and the full summer (Table 2; $p < 0.02$), but much of that decrease occurred over the first half of our study (Figure 2F), coinciding with the increase in chlorophyll (Kelly and others 2018).

Temporal Trends of Oxygen Metrics

Deepwater (bottom 2 m) volume-weighted dissolved oxygen concentrations for early summer (deepwater DO_{EARLY_SUMMER}) significantly decreased over time (Table 2; $p < 0.04$). Early in the dataset, deepwater DO_{EARLY_SUMMER} concentrations were ~ 2 mg L^{-1}, but concentrations in the early 2020s were ~ 0.5 mg L^{-1} (Figure 2G). In the past 15 years, mean deepwater DO_{EARLY_SUMMER} was never above ~ 1.5 mg L^{-1}, whereas it was common for concentrations to be higher than that in earlier years. While anoxic factor varied considerably year-to-year (Figure 2H), there was no long-term trend over the time series (Table 2; $p = 0.26$). Anoxic factor varied between 36 and 103 days per summer (that is, mid-May–end of August).

Drivers of Deepwater Dissolved Oxygen Metrics

Based on the regression model variable selection, deepwater DO_{EARLY_SUMMER} was best predicted by

Table 2. Range, Mean, and Temporal Trends of the Potential Predictor Variables and Oxygen Metrics

Variable	Mean (range)	*p* value	R^2	Trend direction
Discharge metrics				
Watershed discharge$_{EARLY_SUMMER}$ (m^3 yr^{-1}, May–June, $n = 29$)	1.54×10^7 (2.7×10^6–3.51×10^7)	NS	0.01	
Watershed discharge$_{FULL_SUMMER}$ (m^3 yr^{-1}, May–August, $n = 29$)	2.16×10^7 (3.21×10^6–7.11×10^7)	NS	0.01	
Temperature metrics				
Surface water temp$_{EARLY_SUMMER}$ (°C, May–June, $n = 29$)	22.9 (19.8–25.7)	0.004	0.27	+
Surface water temp$_{FULL_SUMMER}$ (°C, May–August, $n = 29$)	25.1 (23.8–26.5)	NS	0.12	
Deepwater temp$_{EARLY_SUMMER}$ (°C, May–June, $n = 29$)	15.8 (11.9–20.2)	NS	0.02	
Deepwater temp$_{FULL_SUMMER}$ (°C, May–August, $n = 29$)	17.9 (13.2–21.5)	NS	0.07	
Stratification metrics				
Schmidt stability$_{EARLY_SUMMER}$ (J m^{-2}, May–June, $n = 29$)	33 (19–52)	NS	0.04	
Schmidt stability$_{FULL_SUMMER}$ (J m^{-2}, May–August, $n = 29$)	35 (23–59)	NS	0.01	
Productivity potential metrics				
NVSS$_{EARLY_SUMMER}$ (mg L^{-1}, May–June, $n = 30$)	5.3 (1.6–13)	0.0016	0.30	−
NVSS$_{FULL_SUMMER}$ (mg L^{-1}, May–August, $n = 30$)	3.9 (1.4–8.3)	0.018	0.18	−
CHL$_{EARLY_SUMMER}$ (mg L^{-1}, May–June, $n = 31$)	49 (23–80)	NS	0.05	
CHL$_{FULL_SUMMER}$ (mg L^{-1}, May–August, $n = 31$)	56 (21–81)	NS	0.04	
Oxygen metrics				
Deepwater DO$_{EARLY_SUMMER}$ (mg L^{-1}, May–June, $n = 29$)	1.20 (0.09–4.48)	0.033	0.16	−
Anoxic factor (days $summer^{-1}$, $n = 29$)	66 (36–103)	NS	0.08	

Surface water temperature represents 0–2 m means, and deepwater temperature or dissolved oxygen concentrations represent means from the bottom 2 m of the lake. For each variable (excluding anoxic factor), we calculated an early summer mean (mid-May to end of June) and a full summer mean (mid-May to end of August). Means and ranges represent annual values. The p-values and R^2 for long-term annual trends in physical, chemical, and biological variables are also shown. The direction of significant long-term trends is shown with a + or − symbol. Mean annual values were used for linear regressions.

surface water temperature in the early summer (Table 3; adj. $R^2 = 0.19$, $p = 0.027$). However, the top five models had BIC scores that were within 0.5 of each other. The lowest BIC was 68.5058 (model 1), and the highest BIC was 68.93802 (Table 3; model 5). Thus, all models performed similarly and explained deepwater DO$_{EARLY_SUMMER}$ at a comparable level. In all of these models, a stratification or temperature metric was included, highlighting the importance of physical conditions in mediating deepwater DO$_{EARLY_SUMMER}$. Both early summer surface water temperature and Schmidt stability in the early summer had a negative relationship with deepwater DO$_{EARLY_SUMMER}$, while early summer deepwater temperature displayed a positive relationship (Table 3). This suggests that during the early summer, warmer surface waters or stronger stratification were linked to lower deepwater DO$_{EARLY_SUMMER}$ (Figure 3). On the other hand, in the early summer, our models propose that warmer deep waters were associated with higher deepwater DO$_{EARLY_SUMMER}$, although the relationship was weak (Figure 3). In two of the five best models, chlorophyll concentration in the prior summer was also included. In these two models, prior summer chlorophyll concentration had a negative relationship with deepwater DO$_{EARLY_SUMMER}$, suggesting that higher phytoplankton biomass in the prior summer led to lower deepwater DO concentrations in the early summer of the subsequent year, although the relationship was relatively weak (Figure 3).

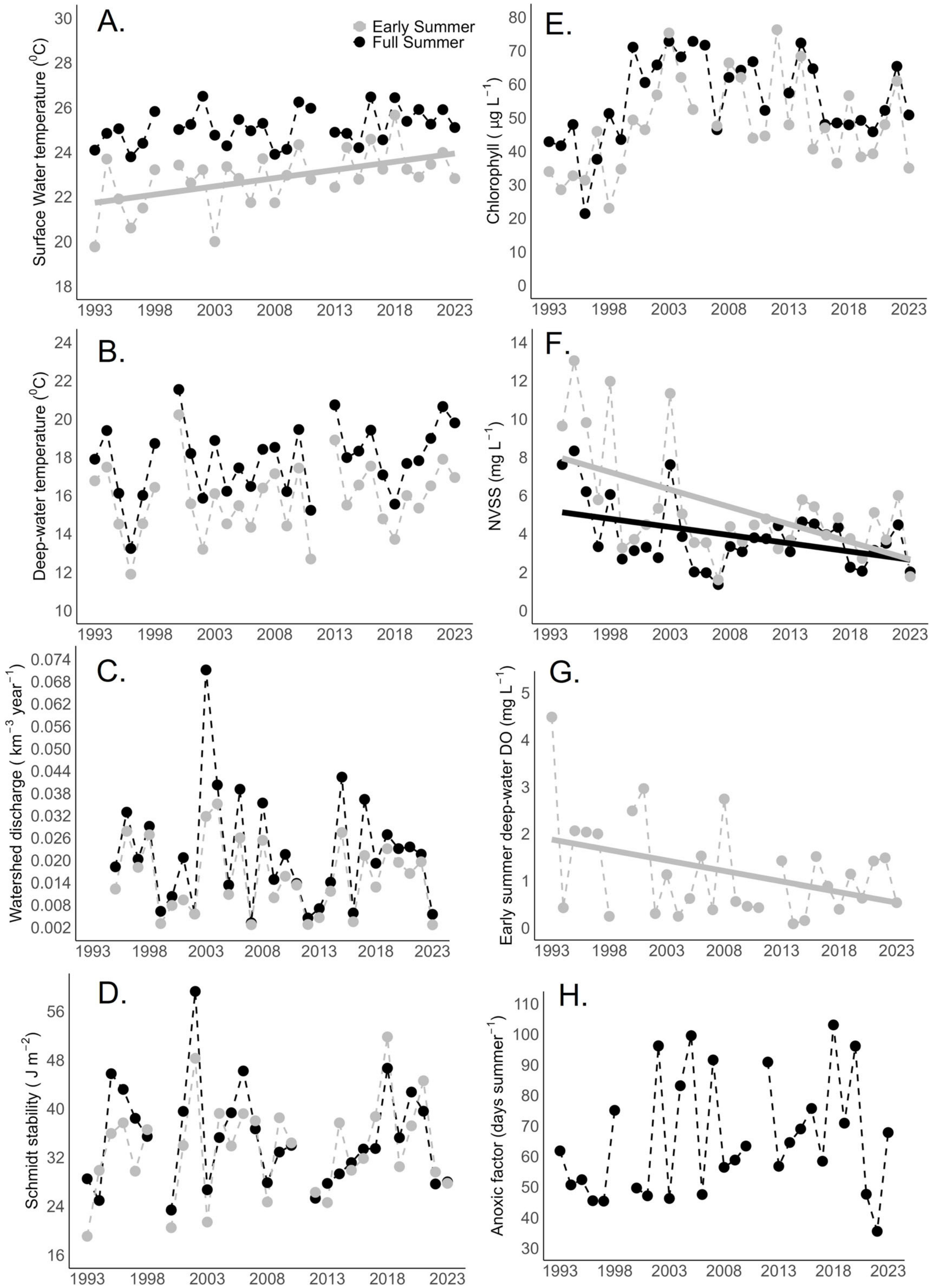
For anoxic factor, our model selection revealed that the top two models performed similarly (Table 4; BICs 227.21, 227.53). However, the BICs of the next 3 models were more than 1 unit away from the BIC score of the top model. Thus, we focus on the top two models for further exploration. The model with the lowest BIC score showed that the best predictors of anoxic factor in Acton Lake were Schmidt stability during the full summer and surface water temperature in early summer (Table 4; adj. $R^2 = 0.34$, $p = 0.003$). The second best model included NVSS concentration in the summer, surface water temperature in the summer, and deepwater temperature in the summer (Table 4; adj. $R^2 = 0.38$, $p = 0.003$). Both summer NVSS concentration and summer deepwater temperature had a negative relationship with anoxic factor, suggesting less anoxic conditions when suspended sediments in the water column were elevated or deepwater temperature were higher (Figure 4). Summer surface water temperature (early or full summer) and summer Schmidt stability displayed a positive relationship with anoxic factor (Figure 4). Thus, these models indicate that lower suspended sediments, stronger stratification, or warmer surface waters (early or full summer) were associated with increased anoxic conditions.

Discussion

Both eutrophication and warming water temperatures have been identified as key drivers of the long-term decline in deepwater dissolved oxygen concentrations over the past several decades (Foley and others 2012; Jane and others 2021). We observed significant decreases in early summer deepwater dissolved oxygen concentrations in Acton Lake over the past 31 years (1993–2023) that were also associated with warming surface water temperatures. Further, although no temporal pattern was detected for anoxic factor over the entire summer, we found that in addition to temperature and stratification metrics, the concentration of nonvolatile suspended sediments (NVSS), which measures the amount of suspended inorganic sediments in the water column, was correlated with anoxic factor. As NVSS concentrations increased, anoxia decreased. Although quantifying suspended sediments in reservoirs is relatively common, especially in systems with high terrestrial inputs (Jones and others 2020), relationships between suspended sediments and oxygen are rarely studied. Thus, our results demonstrate the importance of considering both standard limnological drivers (for example, temperature, stratification) and metrics more strongly associated with reservoirs (for example, suspended sediments, hydrology) as potential drivers of deepwater oxygen dynamics.

The oxygen metrics and potential drivers showed variable patterns over the past 31 years in Acton Lake. In particular, while deepwater DO concentrations decreased over time with greater variability earlier in the dataset, anoxic factor did not exhibit a long-term pattern. Further, of the drivers, both chlorophyll and NVSS concentrations appeared to change more dramatically over the first ~ 8–10 years. Indeed, prior research in Acton Lake (1994–2014) showed that chlorophyll increases were largely restricted to early years in the dataset (Kelly and others 2018). This was attributed, in part, to corresponding increases in conservation tillage in the watershed and decreased NVSS concentrations in the lake. Declines in NVSS concentrations were also found early in the dataset in the inflowing streams, again linked to the increase in conservation tillage in the 1990s and early 2000s (Renwick and others 2008; 2018). A noted plateauing of conservation tillage through 2015 largely tracked NVSS and chlorophyll trends (Kelly and others 2018; Renwick and others 2018). In more recent years, conservation tillage trends suggest a dip in implementation by farmers. Over this time period, NVSS in the lake has remained low while chlorophyll concentrations have either remained static, or are possibly starting to make slight declines. These shifts in conservation tillage, and hence, patterns in some of the potential drivers, may have made it more difficult to detect temporal oxygen shifts (for example, anoxic factor) or to explain a larger amount of the variation in the oxygen metrics with our predictive models. Additional years of data may help to further tease apart the links between conservation tillage and oxygen dynamics, particularly if the decrease in this tillage practice persists into future years.

Several mechanisms may account for the disparate long-term trends in anoxic factor versus volume-weighted deepwater dissolved oxygen concentrations in the early summer (deepwater DO_{EARLY_SUMMER}). First, these metrics assess different aspects of dissolved oxygen. While deepwater DO_{EARLY_SUMMER} only considers volume-weighted oxygen concentrations of the bottom two meters of the lake, anoxic factor is an integrative metric taking into account both the duration of anoxia and its spatial extent (Nürnberg 1995). Thus, DO concentrations could decrease in the bottom waters, but shifts may not extend to the


A.
Early Summer
Full Summer
Surface Water temperature (⁰C)
B.
Deep-water temperature (⁰C)
C.
Watershed discharge (km⁻³ year⁻¹)
D.
Schmidt stability (J m⁻²)
E.
Chlorophyll (µg L⁻¹)
F.
NVSS (mg L⁻¹)
G.
Early summer deep-water DO (mg L⁻¹)
H.
Anoxic factor (days summer⁻¹)

◀**Figure 2.** Time series of annual **A** surface water temperature (0–2 m), **B** deepwater temperature (bottom 2 m), **C** watershed discharge, **D** Schmidt stability, **E** chlorophyll concentration in the euphotic zone, and **F** NVSS concentration in the euphotic zone, **G** annual volume-weighted deepwater dissolved oxygen concentration in the early summer (mid-May to end of June; day of year 140–182), and **H** annual anoxic factor (mid-May to end of August; day of year 140–244). Black symbols and black dotted lines represent the full summer (mid-May to end of August) and gray symbols and gray dotted lines represent early summer (mid-May to end of June). Solid black or gray lines indicate significant linear regression trends at $p < 0.05$.

duration or extent of anoxia in the water column. Second, of the four temperature metrics assessed, only early summer surface water temperatures significantly increased over the 31 year dataset. This suggests that the association between increasing water temperatures and DO dynamics may be more pronounced in early summer months (that is, May, June) than later months (that is, July, August). A recent study in 20 reservoirs in the same geographic region as Acton found similar patterns in water temperature. Surface water temperature increases across reservoir types were more common in May and June than in July and August (Smucker and others 2021). These authors also found less consistent deepwater temperature

Table 3. Model Comparisons for Deepwater DO Concentration in the Early Summer

Model	Predictor variable	Estimate	SE	t value	p value	vif	Adj. R^2	BIC
1. Deepwater DO_{EARLY_SUMMER}					**0.027**		0.19	68.50580
	Intercept	8.03	2.94	2.73	**0.012**			
	Surface water $temp_{EARLY\_SUMMER}$	−0.30	0.13	−2.35	**0.027**			
2. Deepwater DO_{EARLY_SUMMER}					**0.028**		0.19	68.56500
	Intercept	2.80	0.73	3.83	**0.001**			
	Schmidt $stability_{EARLY\_SUMMER}$	−0.04	0.02	−2.33	**0.028**			
3. Deepwater DO_{EARLY_SUMMER}					**0.023**		0.22	68.65175
	Intercept	3.92	0.96	4.10	**0.001**			
	Schmidt $stability_{EARLY\_SUMMER}$	−0.05	0.02	−2.52	**0.019**	1.00		
	CHL_{PRIOR_SUMMER}	−0.02	0.01	−1.73	0.098	1.00		
4. Deepwater DO_{EARLY_SUMMER}					**0.018**		0.27	68.79462
	Intercept	7.51	2.82	2.66	**0.014**			
	Deepwater $temp_{EARLY\_SUMMER}$	0.16	0.08	1.92	0.068	1.08		
	Surface water $Temp_{EARLY\_SUMMER}$	−0.34	0.12	−2.81	**0.01**	1.06		
	CHL_{PRIOR_SUMMER}	−0.02	0.01	−1.75	0.09	1.02		
5. Deepwater DO_{EARLY_SUMMER}					**0.027**		0.21	68.93802
	Intercept	6.92	2.93	2.37	**0.027**			
	Deepwater $temp_{EARLY\_SUMMER}$	0.14	0.09	1.63	0.118	1.06		
	Surface water $Temp_{EARLY\_SUMMER}$	−0.35	0.13	−2.74	**0.012**	1.06		

Deepwater DO concentration in the early summer is indicated as deepwater DO_{EARLY_SUMMER} (n = 26 years). Predictors for deepwater DO_{EARLY_SUMMER} that were considered for model selection are shown in Table 1. The top five models with the lowest BIC scores are shown. The top line for each model displays the overall model p value, adjusted R^2, and BIC score. All variance inflation factor values were below 1.09 indicating a low level of multicollinearity. Significant p values are bolded.

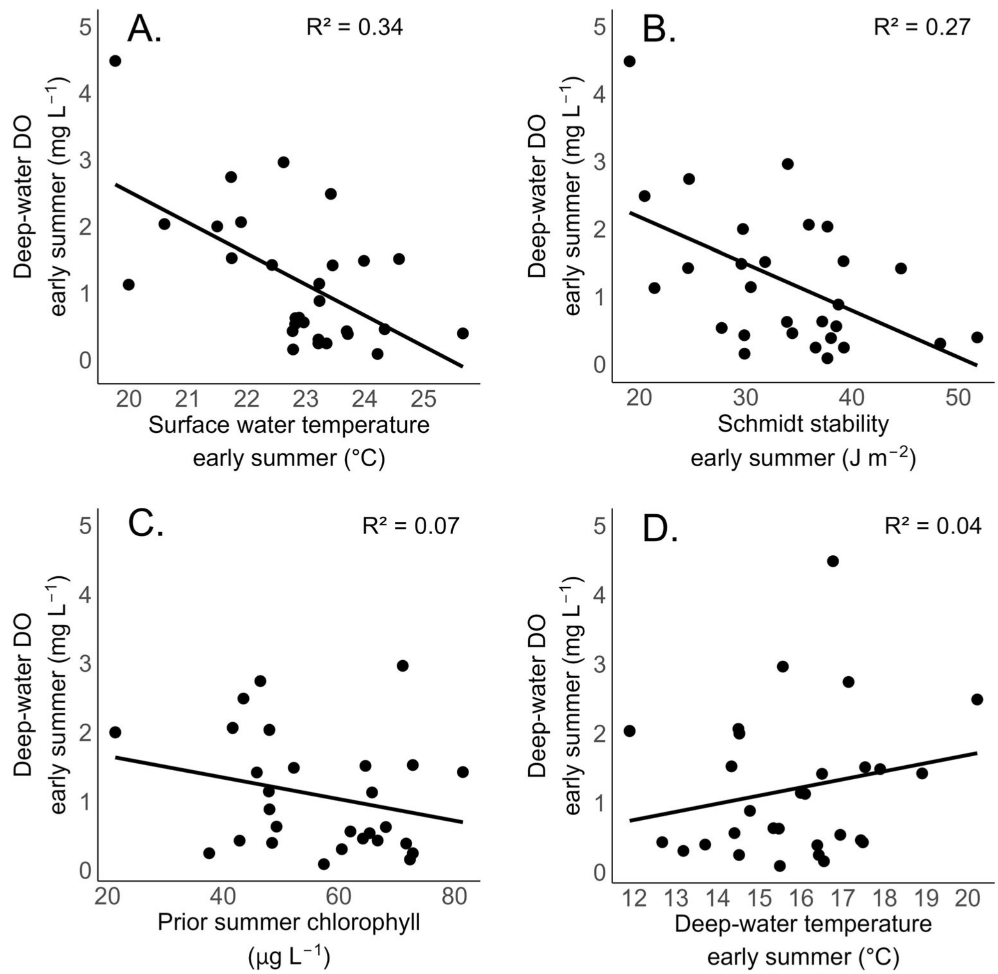


Figure 3. Linear regressions between annual volume-weighted deepwater dissolved oxygen concentration in the early summer (mid-May to end of June; day of year 140–182) and the potential drivers identified in model selection.

warming across reservoir types than surface waters. Further, across the Midwest region, air temperatures in the spring are warming faster than those in the summer (Crimmins and others 2023). Thus, our results demonstrate the importance of considering DO dynamics in early summer months. Additionally, in hypereutrophic systems like Acton Lake, long-term changes in DO concentrations may be most evident earlier in the summer because mid- to late summer deepwater DO concentrations would likely be anoxic over the past several decades, thereby limiting the ability to detect shifts over time.

The absence of a long-term trend in anoxic factor may also be explained in part by Acton's morphometry. Acton Lake is relatively shallow for a dimictic waterbody, and therefore, it typically displays weak stratification that is more prone to wind disturbance than deeper lakes. In past years, periodic deepening of the thermocline occurred over the summer depending on physical conditions (Nowlin and others 2005). The high year-to-year variability in Schmidt stability that we found likely reflects variations in wind over the time series. We lack long-term wind data to explore the relationship between wind and Schmidt stability, but it is commonly accepted that higher winds disrupt stratification (Wetzel 2001). Schmidt stability was correlated with anoxic factor in Acton Lake; greater stability was associated with increased anoxic factor. Others have found similar results, even in deeper lakes with more pronounced thermal stratification (Foley and others 2012; Ladwig and others 2021). Deepwater temperatures in Acton over the summer were also negatively associated with Schmidt stability ($r = -0.70$) suggesting periodic erosion of the thermocline during less stable summers in Acton mixes warmer, oxygen-rich surface waters with the cooler, low-oxygen deep waters. Further, the anoxic zone (DO < 1

Table 4. Model Comparisons for Predicting Anoxic Factor

Model	Predictor variable	Estimate	SE	*t* value	*p* value	vif	Adj. R^2	BIC
1. Anoxic factor					**0.003**		0.34	227.21
	Intercept	−144.25	61.15	−2.36	**0.027**			
	Schmidt stability$_{FULL_SUMMER}$	0.95	0.39	2.41	**0.025**	1.00		
	Surface water temp$_{EARLY_SUMMER}$	7.65	2.60	2.94	**0.007**	1.00		
2. Anoxic factor					**0.003**		0.38	227.53
	Intercept	−157.03	101.31	−1.55	0.14			
	NVSS$_{FULL_SUMMER}$	−4.04	1.84	−2.20	**0.038**	1.05		
	Surface water temp$_{FULL_SUMMER}$	12.15	4.07	2.99	**0.007**	1.11		
	Deepwater temp$_{FULL_SUMMER}$	−3.79	1.69	−2.24	**0.036**	1.08		
3. Anoxic factor					**0.005**		0.36	228.39
	Intercept	−141.17	103.87	−1.36	0.19			
	NVSS$_{FULL_SUMMER}$	−4.12	1.87	−2.20	**0.039**	1.06		
	Surface water temp$_{FULL_SUMMER}$	11.08	4.05	2.73	**0.012**	1.07		
	Deepwater temp$_{EARLY_SUMMER}$	−3.57	1.75	−2.03	0.054	1.04		
4. Anoxic factor					**0.005**		0.36	228.46
	Intercept	−158.28	61.07	−2.59	**0.017**			
	Schmidt stability$_{FULL_SUMMER}$	1.00	0.39	2.57	**0.017**	1.01		
	CHL$_{PRIOR_SUMMER}$	0.30	0.22	1.33	0.197	1.02		
	Surface water temp$_{EARLY_SUMMER}$	7.43	2.56	2.90	**0.008**	1.00		
5. Anoxic factor					**0.006**		0.35	228.75
	Intercept	−99.76	70.55	−1.41	0.171			
	Schmidt stability$_{FULL_SUMMER}$	0.91	0.39	2.31	**0.031**	1.01		
	NVSS$_{FULL_SUMMER}$	−2.48	2.03	−1.23	0.233	1.23		
	Surface water temp$_{EARLY_SUMMER}$	6.19	2.84	2.18	**0.040**	1.22		

Anoxic factor considered the time period from mid-May to the end of August (n = 26 years). Predictors for anoxic that were considered for model selection are shown in Table 1. The top five models with the lowest BIC scores are shown. The top line for each model displays the overall model p value, adjusted R^2, and BIC score. All variance inflation factor values were below 1.24 indicating a low level of multicollinearity. Significant p values are bolded.

mg L^{-1}) in Acton Lake regularly extends from the lake bottom to 3 or 4 m. This shallow upper depth means that wind-driven disturbances may easily influence the areal extent of anoxia. Therefore, we anticipate that the high year-to-year variability in Schmidt stability, combined with the link between stability and anoxic factor in this weakly stratified lake, prevented the long-term impacts of surface water warming from translating into sustained effects on anoxic factor over time.

Lake productivity is well established as a driver of hypolimnetic oxygen conditions, whereby excessive phytoplankton production leads to increased DO consumption in the deep waters after phytoplankton cells sink below the euphotic zone. Indeed, long-term analyses indicate that increasing chlorophyll (that is, eutrophication) may help to explain decreasing deepwater DO trends (Foley and others 2012). This study considered shallow water chlorophyll and deepwater DO within the same season. However, in Acton Lake, we found that DO$_{EARLY_SUMMER}$ was more associated with chlorophyll in the prior summer rather than within the same year (that is, selected in two of the top five models). This lag effect has been noted by others. A recent study found that a 1 year lag in chlorophyll often positively correlated with volumetric hypolimnetic oxygen depletion rates (Lewis and others 2024). Interestingly, these authors found the lag effect was most pronounced in lakes with long residence times and the effect diminished in lakes with residence times less than ~ 100 days. Short residence times may cause the flushing of phytoplankton biomass before the next summer, reducing the amount of organic matter that settles into the hypolimnion and onto lake sediments. For example, in lakes and reservoirs in Northeastern United States and Canada, the potential effects of Tropical Cyclone Irene were manifold, including flushing of primary producers particularly in the systems with high potential volume replacement during this extreme event (Klug and others 2012). As a reservoir with large inputs of stream water during storm events, Acton's residence time can be much lower than 100 days when precipitation rates are high, especially in winter and spring when runoff is high (Williamson and others 2021). However, given Acton's hypereutrophic status, a

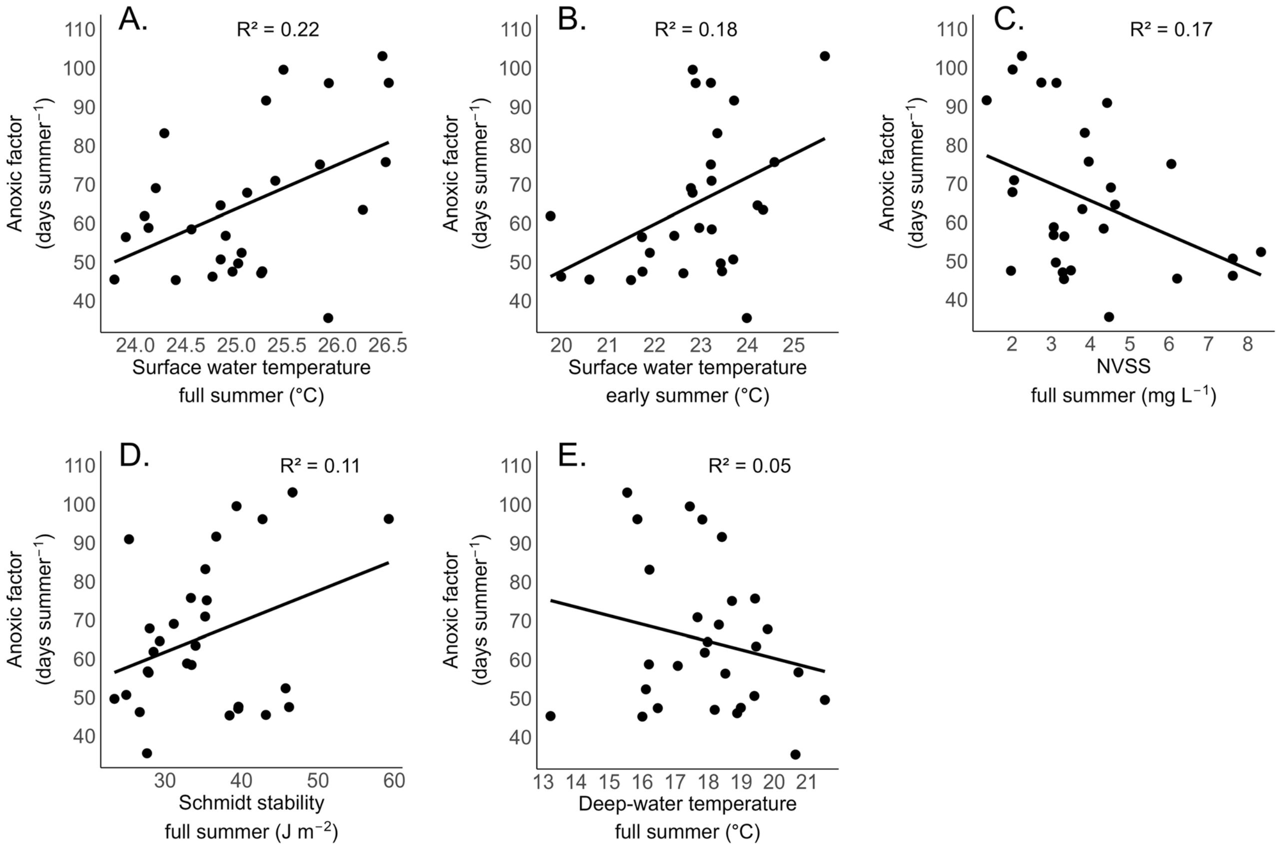


Figure 4. Linear regressions between annual anoxic factor (mid-May to end of August; day of year 140–244) and the potential drivers identified in model selection.

substantial amount of the organic matter from the prior season may fall and remain at the sediment–water interface at the start of the subsequent summer particularly in years with limited flushing between growing seasons. Taken together, these results suggest that in some lakes, the organic matter associated with the prior summer is critical in fueling DO consumption and early summer deepwater oxygen concentrations, although future research should explore the link more fully.

While phytoplankton biomass is known to influence oxygen consumption, few studies have identified suspended sediments in the water column as a potential driver of oxygen dynamics. Suspended sediments in the water column may cause a shading effect, potentially reducing phytoplankton biomass (Knowlton and Jones 2000; Pilati and others 2009; Kelly and others 2018) and thereby decreasing the organic matter available for oxygen consumption. Alternatively, others have found that suspended sediments may supply particulate-bound nutrient subsidies and stimulate phytoplankton growth (Pilati and others 2009). Our results suggest that the effect of NVSS concentration (that is, the inorganic particles in the lake that are nonvolatile like clay and silt) on anoxic factor was more tightly coupled to shading rather than nutrient subsidies. Specifically, in years with higher summer NVSS concentrations, anoxic factor was lower. Interestingly, our models did not identify chlorophyll concentrations in the current summer as a predictor of anoxic factor despite strong negative associations between suspended sediments and chlorophyll (or light availability) typically found in Acton Lake within a year (Vanni and others 2006; Kelly and others 2018) and other Midwestern United States reservoirs (Knowlton and Jones 2000). Indeed, NVSS and VSS (volatile suspended sediments) concentrations control light transparency in many Missouri reservoirs more than algal biomass does (Jones and Knowlton 1993), and NVSS attenuated more light than chlorophyll early in Acton's dataset (Kelly and others 2018). It is possible that NVSS concentrations in surface waters are a more integrative metric of lake conditions than chlorophyll. For example, elevated NVSS concentrations may reflect both high storm-associated external watershed loads and increased internal sediment resuspension during storms/windy periods. In reservoirs like Acton, storms may disrupt stratification through flushing or wind-driven mixing events, or by delivering large pulses of sediment-laden, cold stream water into the reservoir; all of which are predicted to reduce anoxic factor. Within our dataset, NVSS concentrations in the summer were more strongly associated with summer watershed discharge ($r = 0.47$) than Schmidt stability ($r = -0.19$) suggesting NVSS concentrations may have been more influenced by external inputs than by mixing events. Furthermore, prior research in Acton suggests that lake and inflowing stream NVSS concentrations may be associated with the amount of conservation tillage in the agricultural land of the watershed (Renwick and others 2008, 2018; Kelly and others 2018). Thus, our results suggest a potential link between agricultural land management practices and anoxic factor via erosion of agricultural sediments into downstream waters. It is possible that the predicted increase in precipitation in parts of the USA (Crimmins and others 2023) may influence DO dynamics in agricultural watersheds susceptible to soil erosion by elevating reservoir NVSS concentrations, even in areas with high conservation implementation rates. Thus, further insight into the extent to which large discharge events affect long-term dissolved oxygen trends is needed to better address how changing precipitation patterns influences water quality in reservoirs.

Lake productivity can clearly influence lake oxygen dynamics, and our results also highlight the importance of other drivers. The top models for both anoxic factor and DO_{EARLY_SUMMER} consistently included at least one physical predictor variable (for example, lake temperature, stability). In general, we found that warmer surface waters or higher Schmidt stability was associated with lower DO_{EARLY_SUMMER} or increased anoxic factor. These results are not surprising because stronger (or prolonged) stratification or warmer waters can increase hypolimnetic anoxic conditions in lakes (Foley and others 2012; North and others 2014; Knoll and others 2018; Jane and others 2021, 2023). Warmer waters hold less oxygen, stronger stratification minimizes DO diffusion from surface waters into deeper waters, and longer periods of stratification can increase the duration of oxygen consumption at depth in a lake (Wetzel 2001). Furthermore, warming surface waters or reductions in water clarity (for example, browning, eutrophication) can also lead to shallower thermocline depths (Fee and others 1996; Read and Rose 2013; Pilla and others 2018), potentially modifying dissolved oxygen metrics via altered hypolimnetic volumes. Accurate estimation of Acton Lake's hypolimnetic volume is difficult due to fluctuating water levels (that is, variation in precipitation and spillway discharge) because it is a relatively shallow reservoir with weak stratification. Thus, we did not explore the link between warming, hypolimnetic volumes, and oxygen dynamics, but suggest it is an area for future study, particularly in deeper systems. We also found that warmer deepwater temperatures were associated with higher DO_{EARLY_SUMMER} or lower anoxic factor, which was unexpected since warmer waters would be predicted to have lowered oxygen solubility and higher decomposition rates. Although it is unclear why we found this trend, it is possible that years with warmer deepwater temperatures coincided with later stratification onset (that is, due to wind or air temperature patterns). In a shallow, weakly stratified system like Acton Lake, delayed stratification may result in warmer deep waters, as the cooler springtime water temperatures have a longer period to increase. Further, a delay in stratification onset would likely cause a shortened season for oxygen consumption. Unfortunately, with our dataset, we cannot assess stratification onset over the entire time series because of sporadic early season sampling, nor were we able to incorporate wind speed into our models.

Reservoirs are ubiquitous across the USA (Doubek and Carey 2017; Hayes and others 2017), and many are in agriculturally dominated landscapes like Acton Lake (Vanni and others 2005; Knoll and others 2015). Our findings suggest that deepwater oxygen dynamics in a hypereutrophic reservoir were linked to climate, watershed, and internal lake drivers. Importantly, we found that infrequently sampled driver variables, like suspended sediments in the water column, should also be considered when assessing anoxia in a reservoir system. Specifically, in Acton Lake, suspended sediment concentrations reflected farming management practices (that is, the proportion of land in conservation tillage), and our results indicate that decreased watershed-derived inputs of sediments were associated with higher anoxic factor values. Even though our results suggest that lower NVSS leads to more anoxia, conservation tillage is likely still beneficial in the long run because it will decrease nutrients and sedimentation rates. For example, keeping the lake as deep as possible means a larger hypolimnetic volume and perhaps less anoxia. Taken together, our results underscore the complexity in identifying climate-related long-term deepwater oxygen trends in a weakly stratified, productive reservoir where interannual variability in environmental conditions (for example, wind, precipitation) or land management practices (for example, conservation tillage) may play a dominant role in determining oxygen dynamics.

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DATA AVAILABILITY

Data are available at EDI: https://doi.org/10.6073/pasta/0605f7afa8f8cff7bcbc8dcb4e832000.

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