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Key Points:

- A month-long drawdown (36% volume reduction) in a eutrophic reservoir substantially changed water quality relative to a reference year
- Coincident with drawdown, both stratification strength at the thermocline and epilimnetic nutrient concentrations increased
- A subsequent cyanobacterial bloom led to decreased surface dissolved oxygen and increases in solutes associated with bloom degradation

Supporting Information:

Supporting Information may be found in the online version of this article.

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Reservoir Drawdown Highlights the Emergent Effects of Water Level Change on Reservoir Physics, Chemistry, and Biology

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Abstract Water level drawdowns are increasingly common in lakes and reservoirs worldwide as a result of both climate change and water management. Drawdowns can have direct effects on physical properties of a waterbody (e.g., by altering stratification and light dynamics), which can interact to modify the waterbody's biology and chemistry. However, the ecosystem-level effects of drawdown remain poorly characterized in small, thermally stratified reservoirs, which are common in many regions of the world. Here, we intensively monitored a small eutrophic reservoir for 2 years, including before, during, and after a month-long drawdown that reduced total reservoir volume by 36%. During drawdown, stratification strength (maximum buoyancy frequency) and surface phosphate concentrations both increased, contributing to a substantial surface phytoplankton bloom. The peak in phytoplankton biomass was followed by cascading changes in surface water chemistry associated with bloom degradation, with sequential peaks in dissolved organic carbon, dissolved carbon dioxide, and ammonium concentrations that were up to an order of magnitude higher than the previous year. Dissolved oxygen concentrations substantially decreased in surface waters during drawdown (to 41% saturation), which was associated with increased total iron and manganese concentrations. Combined, our results illustrate how changes in water level can have cascading effects on coupled physical, chemical, and biological processes. As climate change and water management continue to increase the frequency of drawdowns in lakes worldwide, our results highlight the importance of characterizing how water level variability can alter complex in-lake ecosystem processes, thereby affecting water quality.

Plain Language Summary Changes in climate and water management are having substantial effects on the water level of lakes and reservoirs around the world. In particular, the frequency with which waterbodies experience water level drawdowns is increasing worldwide. However, the effects of drawdown on aquatic physics, chemistry, and biology remain poorly understood. Here, we intensively monitored before, during, and after a drawdown in Beaverdam Reservoir, VA, USA, during which water volume decreased by 36% over the course of 1 month. Physical changes to the waterbody during drawdown led to increased nutrient concentrations in surface water, which contributed to the formation of a substantial phytoplankton bloom. Degradation of the phytoplankton bloom then resulted in decreased dissolved oxygen and increased dissolved carbon dioxide in surface waters, among other chemical changes. Combined, our results illustrate how changes in water level can have cascading effects on coupled physical, chemical, and biological processes in lakes. As drawdowns become increasingly common, our results highlight the effects that drawdown can have on interconnected aquatic processes, with important implications for water quality worldwide.

1. Introduction

Water levels in many lakes and reservoirs are changing due to altered climate and water management practices (Kraemer et al., 2020; Wada et al., 2014; Ye et al., 2017). While global climate change is driving a general trend of decreasing water levels in lakes and reservoirs (Fergus et al., 2022; Yao et al., 2023), local human activities also cause water level changes over multiple timescales (e.g., Furey et al., 2004; Hannoun & Tietjen, 2023; Liu et al., 2019; Rimmer et al., 2011). In particular, many human-made reservoirs experience large water level fluctuations on daily to annual timescales due to management for flood control, hydropower, fish passage, irrigation, and drinking water provision (Fergus et al., 2022; Hamilton et al., 2022; Jiang et al., 2018; Keller et al., 2021; Wada et al., 2014). The seasonal variability of water level in managed reservoirs is, on average, more

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Water level drawdown can alter numerous ecosystem processes, making the emergent effects of drawdown difficult to predict

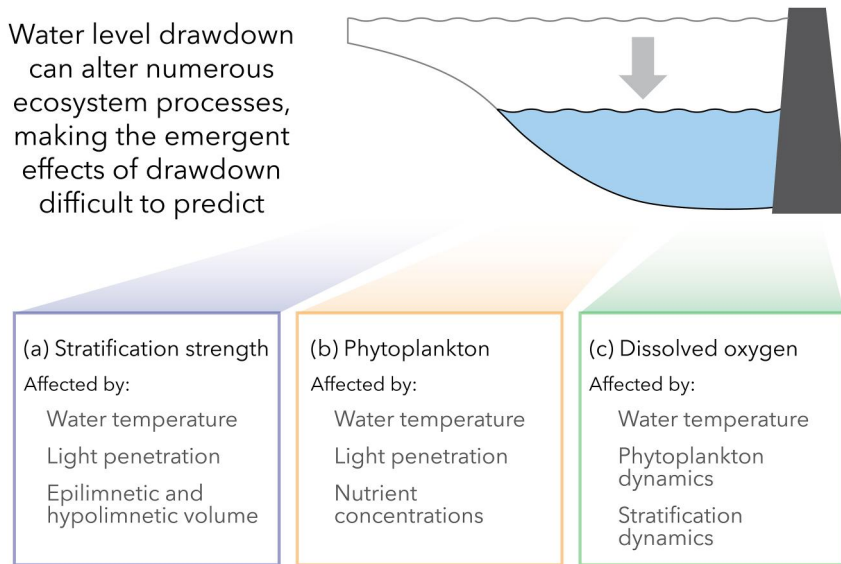


Figure 1. Hypothesized emergent responses of (a) thermal stratification strength, (b) phytoplankton biomass and depth distribution, and (c) dissolved oxygen concentrations to water level drawdown, with predominant drivers that are expected to change as a result of water level drawdown. We note that these drivers are not comprehensive, and the timeline of responses is likely to differ among emergent responses.

than four times greater than in natural waterbodies (Cooley et al., 2021), and extreme, non-seasonal water level fluctuations may also be more common in these managed systems. As just one example, water level fluctuated by ~50 m over two years in Lake Shasta, a reservoir in California, USA (Zohary & Ostrovsky, 2011). As the frequency of water level drawdowns increases due to both climate change and water management (Cooley et al., 2021; Kraemer et al., 2020; Ye et al., 2017; Zhao et al., 2022), it is critical to determine the ecosystem-level effects of water level change on the interconnected biological, chemical, and physical processes that shape water quality.

Decreases in water level can play an important role in structuring reservoir physical dynamics. Depending on the depth of water extraction, reservoirs may differentially lose volume from the epilimnion (the warmer surface water layer) or the hypolimnion (the colder bottom water layer), which could mediate the effects of drawdown on reservoir heat budgets, thermal stratification, and water quality (Nürnberg, 2007; Zohary & Ostrovsky, 2011). Decreased hypolimnetic volume may result in a warmer overall waterbody, weaker thermal stratification, and a proportionally smaller anoxic (<1 mg/L dissolved oxygen) volume in the reservoir (Barbiero et al., 1997; Li et al., 2017; Nürnberg, 2007, 2020), while decreased epilimnetic volume may result in a colder waterbody, stronger thermal stratification, and a proportionally greater volume of anoxic water (Barbiero et al., 1997; Li et al., 2017; Moreno-Ostos et al., 2008; Wang et al., 2012). Stratification strength may further be altered by changes in the light environment of a reservoir during drawdown. For example, increased light penetration to the sediments due to reduced water depth may result in increased hypolimnetic warming (Matsuzaki et al., 2023). Conversely, increased epilimnetic turbidity resulting from drawdown-induced littoral erosion may increase surface warming and decrease hypolimnetic temperatures (Jones et al., 2005; Kumagai et al., 2000). Across drawdowns, decreased water volume will be expected to decrease the resistance to full water column mixing (Wetzel, 2001), though the occurrence of mixing events and consequent effects on water quality will depend on the magnitude of drawdown and initial thermal stability of the reservoir. Ultimately, the responses of light conditions and thermal structure to drawdown is likely to differ in reservoirs of varying morphometry, which is a key driver of thermal stratification dynamics (Butcher et al., 2015; Kraemer et al., 2015; Magee & Wu, 2017), making the net effect of drawdown on stratification strength challenging to predict (Figure 1a).

Changes in reservoir physical properties due to drawdown may cascade to alter chemical and biological dynamics, but the net effects of multiple interacting ecosystem processes remain unresolved (Figure 1). If hypolimnetic water is withdrawn from the reservoir (e.g., for water quality management or downstream temperature regulation), nutrient and metal concentrations may decrease at the whole-ecosystem scale (Nürnberg, 2007,

2020). However, if epilimnetic water is withdrawn (e.g., for some drinking water, irrigation, and hydroelectric purposes), or if hypolimnetic withdrawal weakens thermal stratification, epilimnetic nutrients may increase as a result of increased entrainment from the hypolimnion (Zohary & Ostrovsky, 2011). Littoral erosion and sediment drying due to water level fluctuations may lead to inputs of nitrogen (N), phosphorus (P), and carbon (C) from littoral sediments, further increasing surface concentrations during drawdown (Klotz & Linn, 2001). Likewise, methane ebullition may increase during drawdown due to decreased hydrostatic pressure (Beaulieu et al., 2018; Deemer & Harrison, 2019; Harrison et al., 2017), potentially increasing the suspension of bottom sediments and/or increasing cyanobacterial recruitment to the water column (Deemer & Harrison, 2019; Delwiche et al., 2020; Schwarz et al., 2023). Increased nutrient concentrations can subsequently also lead to increased phytoplankton biomass (e.g., Baldwin et al., 2008; Naselli-Flores & Barone, 2005). However, the effect of increased nutrient concentrations could be tempered by expected declines in light availability resulting from increased turbidity (e.g., Perrin et al., 2000). Taken together, these divergent changes in nutrient and light availability could result in positive or negative net effects on total phytoplankton biomass (Ma et al., 2023, Figure 1b). Moreover, alteration of thermal stratification by drawdown could also alter the distribution of phytoplankton biomass throughout the water column (Leach et al., 2018; Lofton et al., 2020, 2022). Drawdown could alter biomass distributions either by inducing mixing, thereby homogenizing biomass across depths (Kasprzak et al., 2017; Planas & Paquet, 2016; Rinke et al., 2009; Wu et al., 2015), or by facilitating the formation of deep maxima of biomass if thermal stratification increases post-drawdown (Alldredge et al., 2002; Cullen, 2015; Lewis et al., 2017).

Among freshwater ecosystem variables, the net effect of drawdown on dissolved oxygen (DO) concentrations is particularly difficult to predict, as DO is modulated by interacting physical (e.g., stratification dynamics), chemical (e.g., oxygen demand by reduced solutes), and biological conditions (e.g., production and respiration; Figure 1c). DO may increase in surface waters if primary productivity increases, or decrease if primary productivity decreases (Odum, 1956). Likewise, decomposition of phytoplankton biomass and inputs of allochthonous organic carbon due to littoral erosion could potentially stimulate epilimnetic respiration, thereby decreasing DO concentrations and increasing the production of carbon dioxide (CO₂; e.g., McLaren et al., 2023; Naselli-Flores, 2003). Decreased stratification strength could cause whole-ecosystem DO concentrations to increase with mixing of well-oxygenated surface waters into the hypolimnion, or loss of oxic epilimnetic water from the reservoir could cause whole-ecosystem DO concentrations to decrease (e.g., Matsuzaki et al., 2023). Depending on the direction and magnitude of change in DO, further cascading effects on other ecosystem processes (e.g., dissolved metals concentrations, greenhouse gas production, etc.) may be expected. Overall, while the effects of drawdown on reservoir physics, chemistry, and biology are increasingly being examined (e.g., Deemer & Harrison, 2019; Matsuzaki et al., 2023), less is known about the emergent responses to drawdown that arise from changes in multiple, interconnected ecosystem processes (Figure 1). Here, we adapt the definition of “emergent” from the complex systems literature to refer to reservoir responses to drawdown that arise from multiple ecosystem interactions, which cannot be easily predicted from the dynamics of one response variable in isolation of the larger ecosystem (*sensu* Artime & De Domenico, 2022).

Characterizing the effects of management-driven drawdown events may be particularly important in small, thermally stratified waterbodies, which are common in many regions of the world (Downing et al., 2006). In the United States, over 90% of reservoirs are less than 1 km² in surface area (Figure S1 in Supporting Information S1; U.S. Army Corps of Engineers, 2021). However, previous whole-ecosystem studies examining the effects of water level changes have often focused on large lakes and reservoirs (e.g., Nakanishi et al., 2022; Ouyang et al., 2021; Table S1) or very shallow, weakly stratified or fully mixed waterbodies (e.g., Coops et al., 2003; Matsuzaki et al., 2023; Table S1). Other studies have been conducted in mesocosms that cannot encompass all interacting factors occurring on a whole-ecosystem scale (e.g., Matsuzaki et al., 2023). Moreover, much of the existing literature examining the whole-ecosystem effects of water level drawdown has focused on seasonal or drought-induced changes (see Table S1), which co-occur with changes in temperature and precipitation. Thus, as opportunities to perturb whole ecosystems and examine the couplings between lake and reservoir physics, chemistry, and biology are rare (Barley & Meeuwig, 2017), management-driven drawdowns provide an excellent opportunity for whole-ecosystem experimentation.

Here, we intensively monitored a month-long drawdown in a small eutrophic reservoir to analyze the emergent effects of water level change on reservoir physics, chemistry, and biology (Figure 1). Specifically, our study aimed to assess the effects of drawdown on three focal variables: thermal stratification strength, phytoplankton biomass and depth distribution, and DO concentrations. We expected that changes in these three focal variables

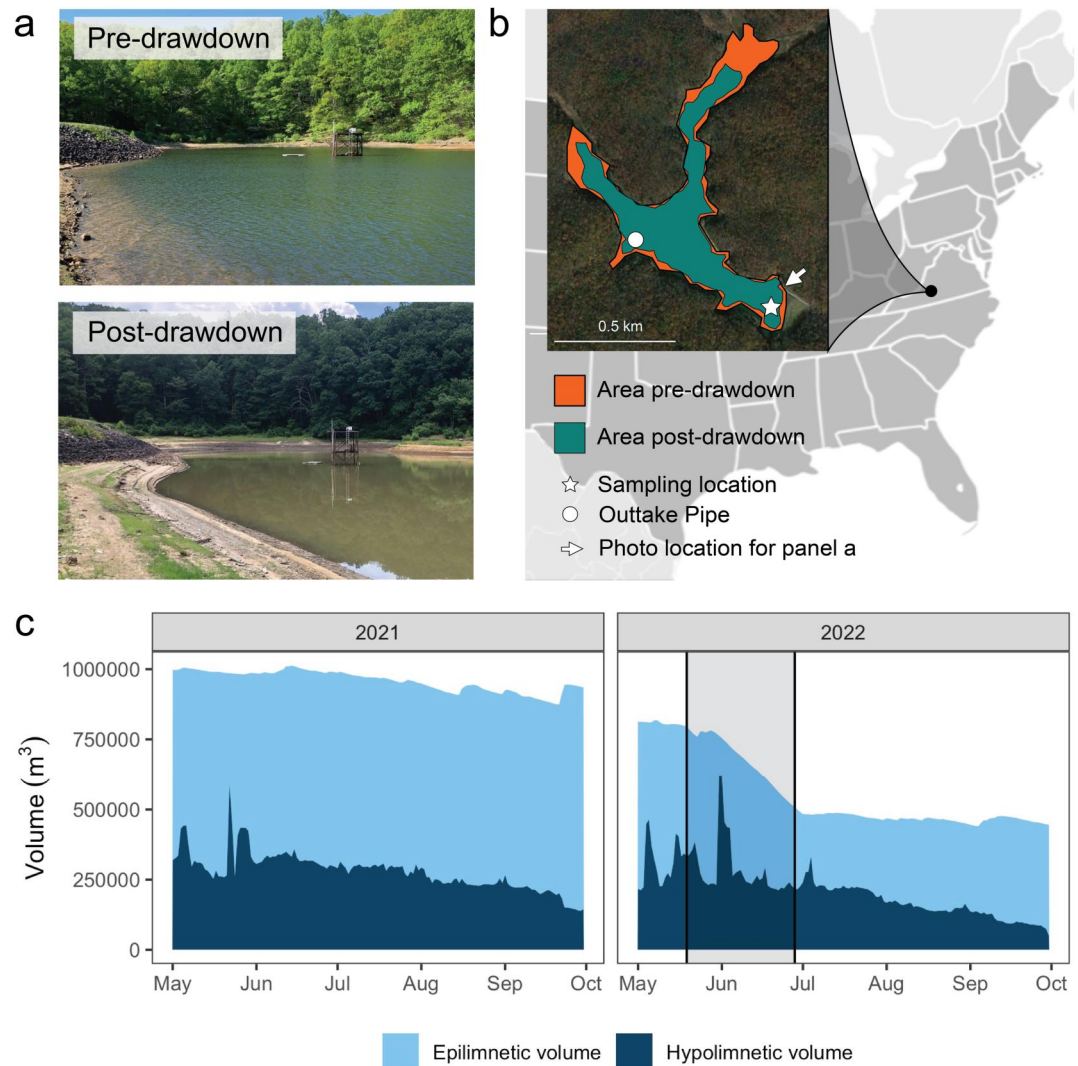


Figure 2. A drawdown in summer 2022 substantially decreased water level in Beaverdam Reservoir. (a) Photos of the reservoir before (top, 9 May 2022) and after (bottom, 5 July 2022) the month-long drawdown. (b) The spatial extent of the reservoir surface area change from pre-drawdown in May (orange) to post-drawdown in July (teal), traced from satellite imagery. The background map shows the location of the reservoir within North America. (c) Change in epilimnetic and hypolimnetic water volume in 2021 and 2022. Vertical lines indicate when the outtake pipe was opened and closed, with the shaded month noting the drawdown interval.

would be mediated by concurrent changes in water temperature, light penetration, and nutrient concentrations that result from multiple ecosystem interactions during drawdown (Figure 1).

2. Methods

2.1. Study Site

Beaverdam Reservoir is a small, dimictic reservoir located in Vinton, Virginia, USA (37.3128°N, 79.8160°W; Figure 2) that is owned and operated as a secondary drinking water source by the Western Virginia Water Authority. When the reservoir is at full pond it has a maximum depth of 13.4 m, surface area of 0.39 km², and residence time of ~0.9 years (Hamre et al., 2018). The catchment area of the reservoir is 3.69 km², and consists primarily of deciduous forest (Hamre et al., 2018). The reservoir is typically thermally stratified from May through October, and experiences hypolimnetic anoxia throughout the summer stratified period (Doubek et al., 2018).

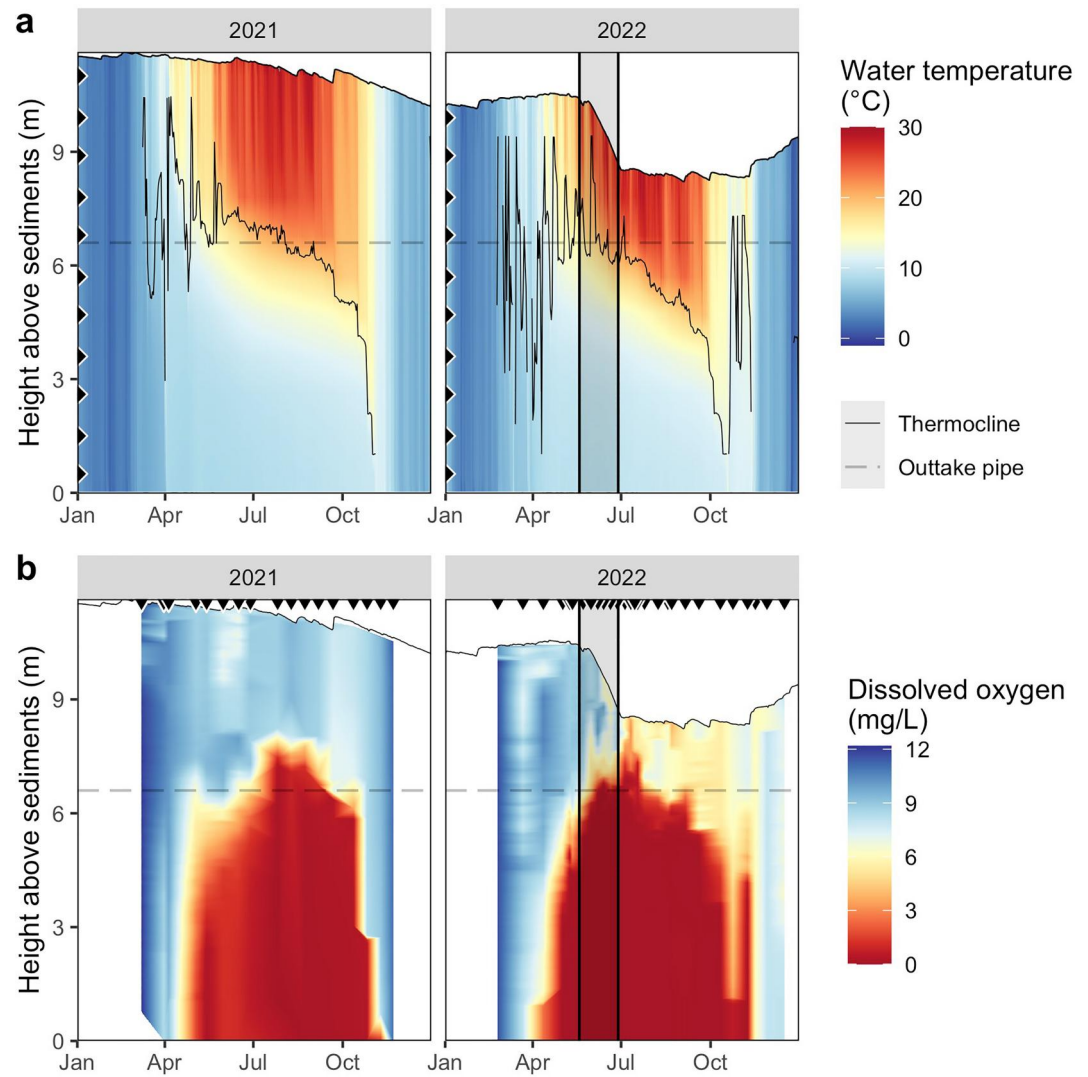


Figure 3. Drawdown decreased epilimnion thickness and increased the anoxic (i.e., dissolved oxygen concentration <1 mg/L) proportion of the water column in 2022 at Beaverdam Reservoir. (a) Contour plot of water temperature measured with in situ thermistor sensors throughout 2021 and 2022, with the thermocline depth indicated by a solid black line. Ticks at the left of each panel indicate sensor depths. (b) Contour plot of dissolved oxygen concentrations sampled using Conductivity, Temperature, and Depth (CTD) sensor profiles in 2021 and 2022. Ticks at the top of the figure indicate CTD sampling dates. We interpolated among sensor depths (panel a) and sampling dates (panel b) to create the contour plots. Shaded interval indicates the 2022 drawdown period in both panels. The depth of the outtake pipe that was opened in 2022 is marked using a dashed line.

2.2. Water Level Drawdown (2022) and Reference Year (2021)

We monitored water physics, chemistry, and biology in Beaverdam Reservoir for two years (2021–2022), which included a reference year prior to the drawdown in 2022. During the reference year (2021), water level was higher than in 2022 ($\mu = 10.7 \pm 0.4$ m SD) and relatively constant throughout the stratified period. On 19 May 2022, managers opened an outtake pipe (see Figure 2b) at Beaverdam Reservoir to lower water level for dam maintenance. At the time that the drawdown began, the maximum depth of the reservoir was 10.1 m. The outtake pipe was upstream of our sampling site and was in the epilimnion throughout a majority of the drawdown period (Figure 3a). Due to precipitation in the days following 19 May, water level did not begin to decline until several days after the pipe was opened (approximately 28 May; Figure 2c). The outtake pipe was closed on 28 June 2022. Following 28 June 2022, water level stayed relatively constant throughout the remainder of the summer stratified period ($\mu = 7.9 \pm 0.1$ m), then increased gradually throughout the fall and winter.

2.3. Monitoring Program

2.3.1. In Situ Sensors

We used a suite of high-frequency in situ sensors to continuously monitor water level and water temperature at the deepest site of the reservoir near the dam (Figure 2b). A Campbell Scientific pressure transducer (Logan, UT, USA) was fixed at 0.2 m above the sediments, and NexSens T-Node FR Temperature Sensor thermistors (NexSens, Fairborn, OH, USA) were deployed at 1 m intervals from 0.2 m above the sediments to 13.2 m above the sediments. Both the pressure transducer and temperature sensors were affixed to a metal platform and therefore did not move up or down in absolute elevation as the water level changed in the reservoir (see Carey, Breef-Pilz, Bookout, et al., 2023).

In addition to the in-water sensors, we also measured air temperature, wind speed, and precipitation using a research-grade Campbell Scientific meteorological station that collected data every minute (Carey & Breef-Pilz, 2023). The station was located at 37.3027°N, 79.8369°W, 2.17 km from the sampling site at Beaverdam Reservoir. Air temperature was measured using a HC2S3 Temperature and Relative Humidity probe by Rotronic Instrument Corp (Hauppauge, NY, USA). Wind speed was measured using a R.M. Young Wind Monitor Model 05103 (RM Young Company, Traverse City, MI, USA), which averaged wind speeds over the minute. Precipitation was measured using a TE525WS-L Rain Gage (Texas Electronics Inc., Dallas, TX, USA), which measures rainfall in 0.254 mm increments (Carey & Breef-Pilz, 2023).

2.3.2. Field Sampling

To complement in situ sensor data, we measured a suite of water quality variables weekly or fortnightly throughout the duration of this 2-year study. Field sampling methods involved both manual sensor profiles and grab samples at multiple depths.

2.3.2.1. Sensor Profiles

Full water-column profiles of DO (concentration and percent saturation), photosynthetically active radiation (PAR), and turbidity were collected using a SeaBird 19plus V2 SeaCAT Profiler Conductivity, Temperature, and Depth (CTD) profiler (Sea-Bird Scientific, Bellevue, WA, USA) (Carey, Lewis, & Breef-Pilz, 2023). These profiles were collected approximately weekly during the summer stratified periods of 2021 and 2022, and monthly during the fall, winter, and spring. A YSI ProODO Optical Dissolved Oxygen Instrument (YSI Inc., Yellow Springs, OH, USA) was used to record DO concentrations at 1 m depth intervals in the reservoir July–December 2021 during CTD maintenance (Carey, Breef-Pilz, Wander, et al., 2023); a comparison of the CTD and YSI DO sensors shows very strong correspondence (Carey, Hanson, et al., 2022).

We used a FluoroProbe (bbe Moldaenke, Schwentental, Germany) to measure phytoplankton biomass and depth distribution in the reservoir. FluoroProbes are submersible, in situ fluorometers that estimate biomass of four spectral groups using fluorescence of a suite of photosynthetic pigments (Catherine et al., 2012; Kring et al., 2014): (a) green algae, which is largely correlated with chlorophyll-*a* and chlorophyll-*b* fluorescence; (b) cyanobacteria (phycocyanin); (c) brown algae (xanthophyll, fucoxanthin, and peridinin); and (d) cryptophytes or mixed algae (phycoerythrin; Beutler et al., 2002). Biomass of the four spectral groups at each measured depth was then summed to produce depth-specific total phytoplankton biomass concentrations (Carey, Breef-Pilz, & Lofton, 2023).

2.3.2.2. Water Chemistry Grab Samples

We used a 4-L Van Dorn sampler (Wildco, Yulee, FL, USA) to collect water chemistry samples at 0.1, 3, 6, 9, and 10 m. If the water level was too low to obtain a 9 m or 10 m sample, we collected samples to all of the routine monitoring depths possible and also from ~1 m above the sediments. At each depth, subsamples were taken for dissolved CO₂, dissolved organic carbon (DOC), total and soluble N and P, and total and soluble iron (Fe) and manganese (Mn) concentrations.

Water samples for dissolved CO₂ were collected from the Van Dorn sampler and immediately sealed in 20-mL glass vials with crimped septum caps and no headspace. These samples were kept on ice, then refrigerated in the lab and analyzed within 24 hr (Carey, Lewis, Niederlehner, et al., 2023).

Samples for DOC and total and soluble N and P were collected in acid-washed polypropylene bottles. Unfiltered water samples were used for analysis of total nitrogen (TN) and total phosphorus (TP). Filtered water samples (Thomas Scientific GF/F 0.7 μm filters) were collected for analysis of DOC, ammonium (NH_4^+), nitrate (NO_3^-), and soluble reactive phosphorus (SRP). Both total and filtered nutrient and C samples were frozen for later analysis, as described below (Carey, Wander, et al., 2023).

Water samples for analysis of Fe and Mn were collected in 15-mL centrifuge tubes. Unfiltered samples were analyzed for total Fe and Mn. A separate aliquot was filtered immediately upon collection with a 0.45- μm nylon membrane for analysis of soluble Fe and Mn. Samples for metals analysis were preserved with trace metal grade nitric acid in the field to $\text{pH} < 2$ (Schreiber et al., 2023).

2.4. Laboratory Analysis

2.4.1. Dissolved Carbon Dioxide

Dissolved CO_2 concentrations were measured on a Shimadzu Nexis GC-2030 Gas Chromatograph (GC; Shimadzu, Kyoto, Japan) with a Flame Ionization Detector (FID) and Thermal Conductivity Detector (TCD) following McClure et al. (2018). Prior to analysis, a 2-mL headspace was created with Helium (He) by displacing 2-mL of sample water and equilibrated by shaking each sample at 300 rpm for 15 min. The 2-mL headspace was then injected into the GC at a temperature of 35 degrees C and a carrier gas (He) flow rate of 15 mL/min. Dissolved concentrations of CO_2 in water were calculated using the observed head-space concentrations and Henry's Law (Carey, Lewis, Niederlehner, et al., 2023; McClure et al., 2018).

2.4.2. Carbon, Nitrogen, and Phosphorus

Water column depth profiles of C, N, and P concentrations were measured following collection in the field. DOC samples were poured into glass vials which had been acid-washed and combusted at 550°C. These samples were analyzed on an Elementar vario TOC cube (Elementar Analysensysteme GmbH, Hanau, Germany) using the persulfate catalytic method (Brenton & Arnett, 1993). The detection limit for DOC was 0.76 mg/L. Samples for NH_4^+ , NO_3^- , and SRP were analyzed colorimetrically using flow injection analysis (APHA, 2012) on a Lachat Instruments XYZ Autosampler ASX 520 Series and QuikChem Series 8500 (Lachat ASX 520 Series, Lachat Instruments, Loveland, Colorado, USA). Method detection limits were 4.3 $\mu\text{g/L}$ (NH_4^+), 3.8 $\mu\text{g/L}$ (NO_3^-), and 3.0 $\mu\text{g/L}$ (SRP), determined following Carey, Wander, et al. (2023). Samples for TN and TP were digested with alkaline persulfate and then analyzed colorimetrically using flow injection analysis. Method detection limits were 56 $\mu\text{g/L}$ (TN) and 3.5 $\mu\text{g/L}$ (TP). Additional analytical methodology can be found in the data publication (Carey, Wander, et al., 2023).

2.4.3. Fe and Mn

Samples for total and soluble Fe and Mn were analyzed by ICPMS (inductively coupled plasma mass spectrometry; Thermo Electron iCAP RQ). Detection limits were 0.80 $\mu\text{g/L}$ (Fe) and 0.004 $\mu\text{g/L}$ (Mn) (Schreiber et al., 2023).

2.5. Data Analysis

2.5.1. Thermal Stratification

We calculated multiple metrics to quantify how thermal conditions changed in Beavertdam Reservoir following drawdown. Schmidt stability (Idso, 1973), a measure of total water column stability; maximum buoyancy frequency, a measure of local stability at the thermocline; and thermocline depth were calculated using the R package *rLakeAnalyzer* (Read et al., 2011) using in situ high-frequency thermistor data. Thermocline depth was calculated using a minimum density difference of 0.1 kg/m^3 (Lewis et al., 2024; following Wilson et al., 2020). For simplicity, we refer to all volume above the thermocline as the epilimnion and all volume below the thermocline as the hypolimnion. Schmidt stability was calculated with dynamic bathymetry as the reservoir volume changed during drawdown by updating the depth of each hypsometric layer of the reservoir with daily water level data (Lewis et al., 2024). We determined the date of fall turnover as the first day surface and bottom temperatures were within 1°C, following McClure et al. (2020).

2.5.2. Phytoplankton Depth Distribution Metrics

We calculated two metrics from the FluoroProbe data to characterize the depth distributions of fluorescence-based phytoplankton biomass in Beaverdam Reservoir, following Lofton et al. (2020, 2022). First, we calculated the chlorophyll maximum (C_{\max}) depth as the depth at which the maximum concentration of fluorescence-based biomass of each spectral group (green algae, brown algae, cyanobacteria, mixed algae, and total phytoplankton) was observed. Second, we calculated the width of the biomass peak (peak width) for each spectral group and for total phytoplankton biomass. To determine peak width, we identified the depths above and below the maximum observed biomass where observed biomass was nearest to the mean biomass concentration across the water column. The distance between these two depths in meters was assigned as the peak width (see Figure S2 in Supporting Information S1). While we calculated C_{\max} depth and peak width for all four spectral groups and total phytoplankton, we focus our reporting on fluorescence-based biomass of cyanobacteria and total phytoplankton, as cyanobacteria exhibited the highest biomass concentrations of any spectral group on 64% of $n = 25$ total sampling days between 1 May–1 September in 2021 and 2022.

2.5.3. Temporal Comparison

Throughout this analysis, we describe observed changes in reservoir biogeochemistry that occurred in 2021 (a reference year) and 2022 (the year when drawdown occurred). While our observational analysis did not permit statistical comparison of conditions before and after drawdown, we report the percentage difference in biogeochemical state variables (e.g., Schmidt stability, dissolved nutrients, phytoplankton depth distribution) between 2021 and 2022. Additionally, we report the timing of minima and maxima in multiple biogeochemical variables coincident with drawdown in 2022.

3. Results

Water level changed substantially during drawdown, altering Beaverdam Reservoir's physics, chemistry, and biology. From the beginning (19 May) to the end (28 June) of the 2022 drawdown, the total volume of Beaverdam Reservoir decreased by 36% (from 795,000 m³ to 508,000 m³; Figure 2c). In comparison, during the same time period in the reference year (2021), water volume was relatively constant (0.2% increase from 989,000 m³ to 991,000 m³), exhibiting typical seasonal fluctuations in the reservoir's water budget (Figure 2c). Drawdown in 2022 resulted in a loss of 69,000 m² of reservoir surface area and reduced maximum reservoir depth by 1.7 m, from 10.4 to 8.7 m (Figures 2a and 2b).

Due to epilimnetic water extraction, the majority (61%) of the observed change in the reservoir's volume during the drawdown resulted from a loss of epilimnetic water (Figures 2c and 3a). Total epilimnetic volume decreased by 37% (from 462,000 m³ to 290,000 m³). Disproportionate loss of warm epilimnetic water resulted in a 2.6°C lower mean volume-weighted temperature of the reservoir in 2022 compared to 2021 during the month following drawdown (July 2021: 23.1 ± 0.6°C; July 2022: 20.5 ± 0.8°C; Figure 4c). Conversely, surface-water temperature was similar between the two years (July 2021: 28.3 ± 1.28°C; July 2022: 27.4 ± 1.37°C; Figure 4b).

Meteorological conditions were similar between the reference and drawdown years. Mean air temperature was 21.3 ± 4.2°C (±1 S.D.) between 19 May and 28 June in 2021 and 22.1 ± 4.9°C during the same interval in 2022 (Figure 4a). Likewise, wind speeds were similar between the two years, with a mean of 1.7 ± 1.1 m/s between 19 May and 28 June in 2021 and 1.9 ± 1.4 m/s during the same interval in 2022 (Figure S3b in Supporting Information S1). Total precipitation was slightly greater in 2022 than in 2021, particularly during the first several days of drawdown (Figure S3a in Supporting Information S1). Specifically, mean daily precipitation was 0.8 ± 2.9 mm between 19 May and 28 June in 2021 and 4.2 ± 8.7 mm during the same interval in 2022, though annual mean daily precipitation was similar between the two years (2.3 ± 7.1 mm/d in 2021, 3.4 ± 8.1 mm/d in 2022; Figure S3a in Supporting Information S1).

3.1. Stratification Strength

Maximum buoyancy frequency and Schmidt stability responded in contrasting ways to reservoir drawdown. While July buoyancy frequency was 25% higher in 2022 (0.013 ± 0.002 1/s) than in 2021 (0.010 ± 0.001 1/s), Schmidt stability plateaued immediately after the start of drawdown, resulting in 44% lower Schmidt stability

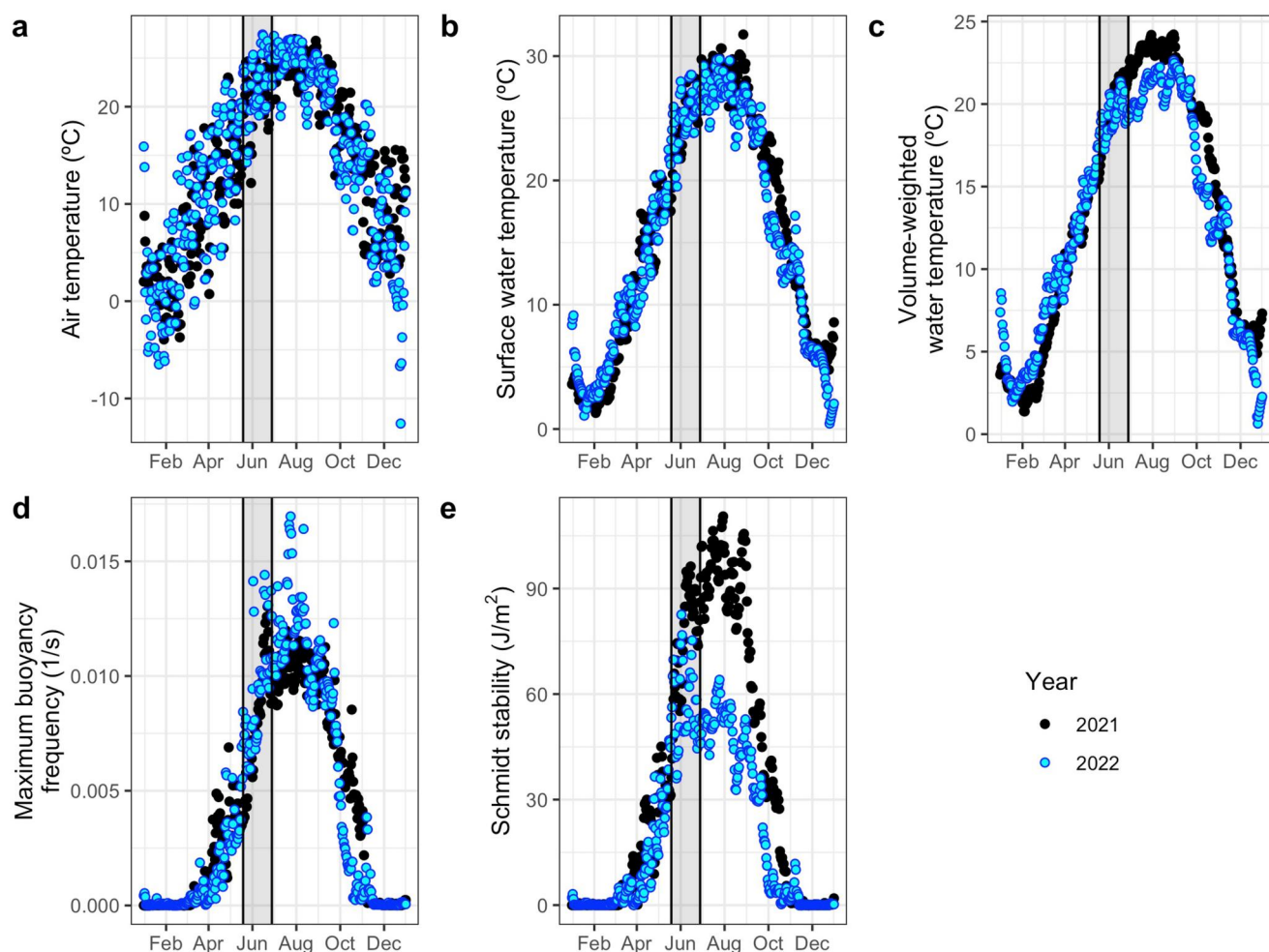


Figure 4. Air temperatures (a) and surface water temperatures (b) were similar between 2021 and 2022. Conversely, drawdown was associated with decreased volume-weighted water temperature of the entire reservoir (c), increased maximum buoyancy frequency (d), and decreased Schmidt stability (e) in 2022, compared to 2021. Shaded intervals indicate the 2022 drawdown period.

values in July 2022 ($54 \pm 5 \text{ J/m}^2$) relative to July 2021 ($97 \pm 7 \text{ J/m}^2$; Figures 4d and 4e). Correspondingly, fall turnover was 18 days earlier in 2022 (19 October) relative to 2021 (6 November).

3.2. Phytoplankton and Biogeochemical Dynamics

Water level drawdown was associated with substantial changes in the magnitude and timing of reservoir biogeochemistry and phytoplankton dynamics. In 2022, surface water TN, TP, phytoplankton biomass, DOC, dissolved CO_2 , and NH_4^+ all exhibited concentrations substantially higher than the range of conditions observed in 2021 (Figure 5). Peaks of TP, TN, and phytoplankton biomass on 27 June were preceded by a peak in SRP on 20 June. Surface water DOC concentrations peaked 8 days after phytoplankton (5 July), followed by peaks in dissolved CO_2 (11 July) and NH_4^+ (18 July). A comparison of maximum concentrations between the two years reveals that in 2022 (vs. 2021), peak TP concentrations were 77% higher (by $15.1 \mu\text{g/L}$), TN concentrations were 271% higher (by $1059 \mu\text{g/L}$), phytoplankton concentrations were 147% higher (by $29.5 \mu\text{g/L}$), DOC concentrations were 177% higher (by $6.9 \mu\text{g/L}$), dissolved CO_2 concentrations were 257% higher (by $43 \mu\text{mol/L}$), and NH_4^+ concentrations were 2273% higher (by $250 \mu\text{g/L}$) than in 2021 (Figure 5).

Changes in the underwater light environment due to drawdown altered depth distributions of phytoplankton biomass across the water column. Turbidity increased sharply following the onset of drawdown in 2022, with a peak 1100% higher than the maximum observed turbidity in 2021 (24.7 NTU higher; Figure 6). Coincident with this peak, the euphotic zone depth (defined as 1% of surface light) reached a minimum value of 1.5 m, which was

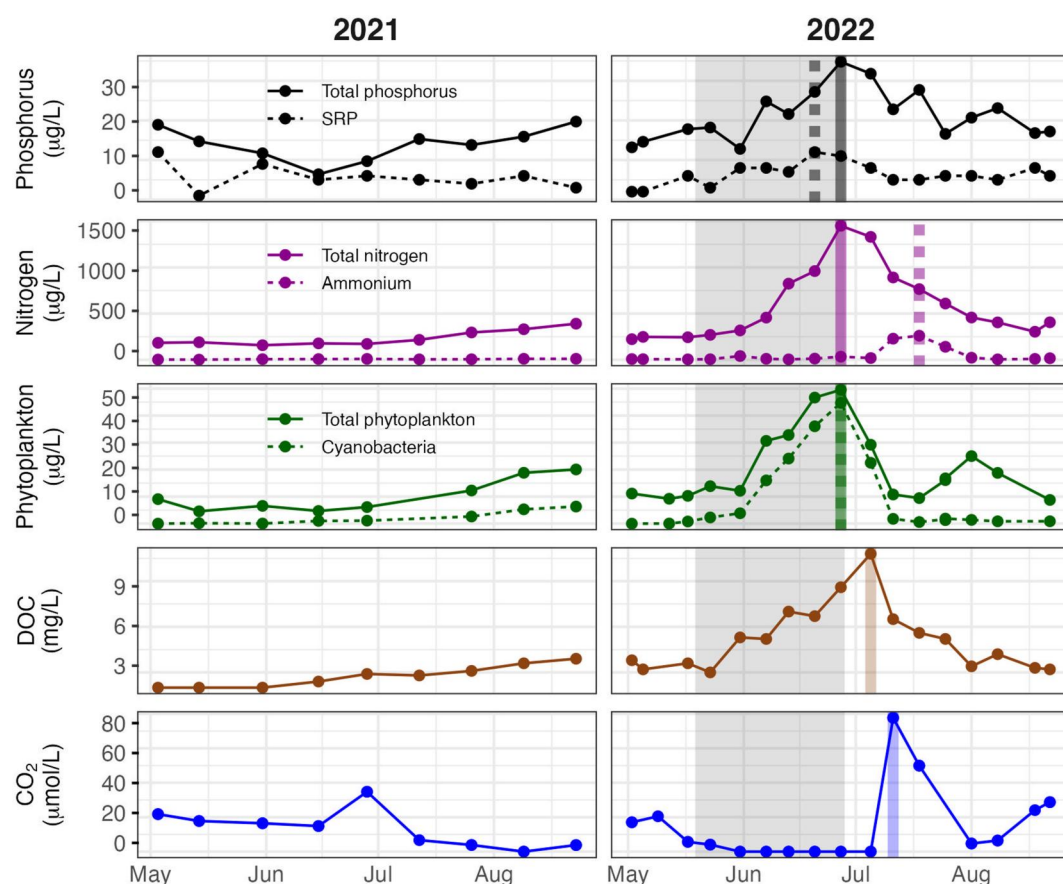


Figure 5. Time series of select water chemistry and biological variables at 0.1 m depth in Beaverdam Reservoir during summers 2021 (left panels) and 2022 (right panels). A June 2022 peak in surface soluble reactive phosphorus (SRP) was followed by peaks in total phosphorus, total nitrogen, total phytoplankton, and cyanobacteria. Dissolved organic carbon (DOC) peaked 8 days later, followed by a peak in dissolved carbon dioxide (CO_2), and finally a peak in ammonium. Colored vertical lines indicate the timing of the observed maximum concentration for each variable in 2022. Points represent discrete sampling visits. Gray shading indicates the drawdown period in 2022.

2.9 m shallower than the shallowest euphotic zone depth observed in 2021. The depth of maximum phytoplankton biomass was shallower and peak widths were narrower for both total biomass and cyanobacteria during the drawdown in 2022 than in 2021. In 2022, the shallowest C_{max} depth for cyanobacteria coincided with the date of maximum turbidity (5 July, just after the drawdown ended), while the shallowest C_{max} depth for total phytoplankton and the narrowest peak width for both total phytoplankton and cyanobacteria occurred mid-drawdown, 2–3 weeks earlier (Figure 6).

3.3. Dissolved Oxygen

Both surface DO concentrations and depth-resolved DO profiles differed substantially before and after drawdown, which was associated with changes in the concentrations of other redox-sensitive solutes in surface waters. Following drawdown, surface DO concentrations decreased to a minimum of 41% saturation (3.5 mg/L), 43% lower than in 2021 (Figures 3b and 7). Loss of oxic epilimnetic water also resulted in increased anoxic extent as a proportion of the water column in 2022 (Figure 3b). Comparing between years, total Fe concentrations reached a peak 54% higher (by 0.34 $\mu\text{g/L}$) and 29 days earlier than in 2021, and soluble Fe concentrations reached a peak 144% higher (by 0.42 $\mu\text{g/L}$) and 49 days earlier than in 2021 (Figure 7). Percent changes in Mn concentrations from 2021 to 2022 were even more substantial than those of Fe. Total Mn concentrations reached a peak 201% higher (by 0.07 $\mu\text{g/L}$) and 29 days earlier than in 2021, and soluble Mn concentrations reached a peak 266% higher (by 0.02 $\mu\text{g/L}$) and 1 day earlier than in 2021 (Figure 7).

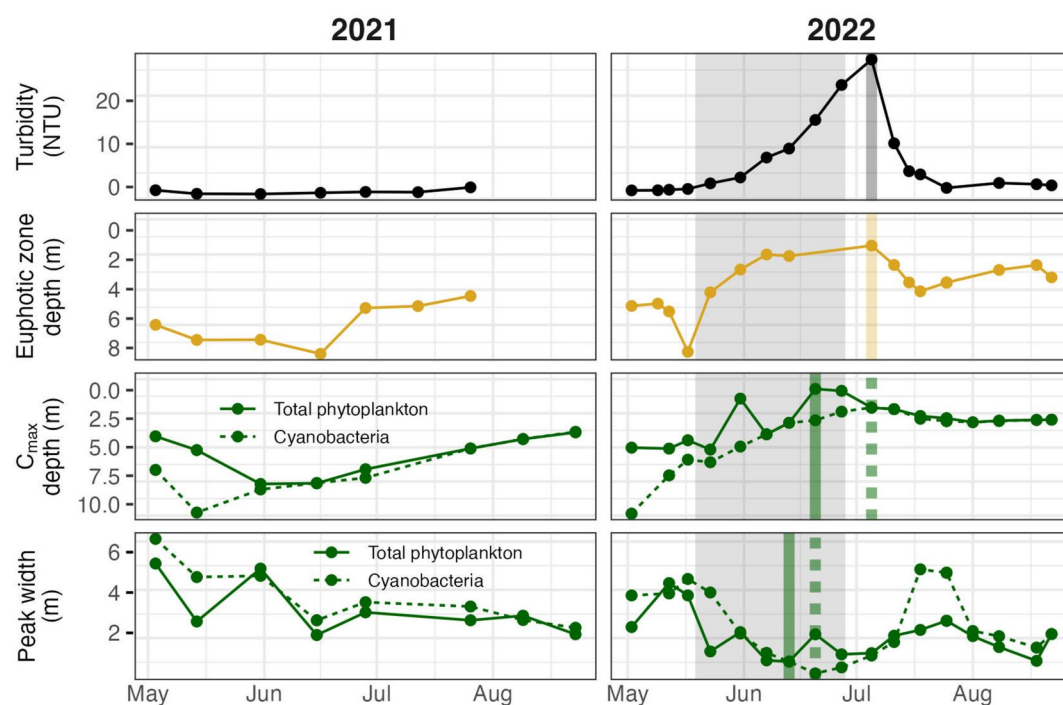


Figure 6. Turbidity peaked and euphotic zone depth was shallowest just after the drawdown at Beaverdam Reservoir in 2022. Chlorophyll maximum (C_{\max}) depth and peak width of total phytoplankton (solid) and cyanobacteria (dotted) also reached a minimum on or before this date. Colored vertical lines indicate observed maxima (Turbidity) or minima (Euphotic zone depth, Total phytoplankton and Cyanobacteria C_{\max} depth and Peak width) for each variable in 2022. Points represent discrete sampling visits. Gray shading indicates the drawdown period in 2022. Note reversed y-axes for euphotic zone depth and C_{\max} depth, with 0 m corresponding to the reservoir surface.

4. Discussion

The month-long drawdown at Beaverdam Reservoir provided a unique opportunity to investigate the emergent responses that arise from multiple, interconnected ecosystem changes during drawdown. Coincident with drawdown, both stratification strength at the thermocline and surface SRP concentrations increased. These initial changes were followed by a substantial surface cyanobacterial bloom and sequential peaks in several biogeochemical variables associated with degradation of the bloom (e.g., DOC, dissolved CO_2). Our intensive monitoring during this management-driven drawdown provides an informative case study illustrating how changes in water level can have emergent effects on reservoir physics, chemistry, and biology in small, thermally stratified reservoirs, which are under-represented in the drawdown literature (Table S1).

4.1. Drawdown Increased Thermocline Strength

Drawdown in Beaverdam Reservoir altered multiple aspects of reservoir physics (e.g., buoyancy frequency, Schmidt stability, epilimnion depth), with important implications for biogeochemical processing. Interestingly, our work highlighted the potential for drawdown to increase the local strength of thermal stratification at the thermocline (i.e., maximum buoyancy frequency; Figure 4). Maximum buoyancy frequency characterizes the likelihood of mixing between surface and bottom layers in a stratified waterbody (e.g., Foley et al., 2012; Mackay et al., 2014), which will affect depth profiles of water chemistry (Bush et al., 2017; MacIntyre et al., 1999; Osborn, 1980) and phytoplankton (Cullen, 2015; Leach et al., 2018; Lofton et al., 2020, 2022). Consequently, changes in thermocline strength have the potential to play an important role in modulating the effect of drawdowns on reservoir chemistry and biology, particularly during smaller drawdowns (i.e., those that do not result in destratification), like in Beaverdam Reservoir. These smaller drawdowns are common worldwide as a result of changes in climate and land use (Cooley et al., 2021; Kraemer et al., 2020; Ye et al., 2017; Zhao et al., 2022), but are not well-characterized across existing literature (Table S1).

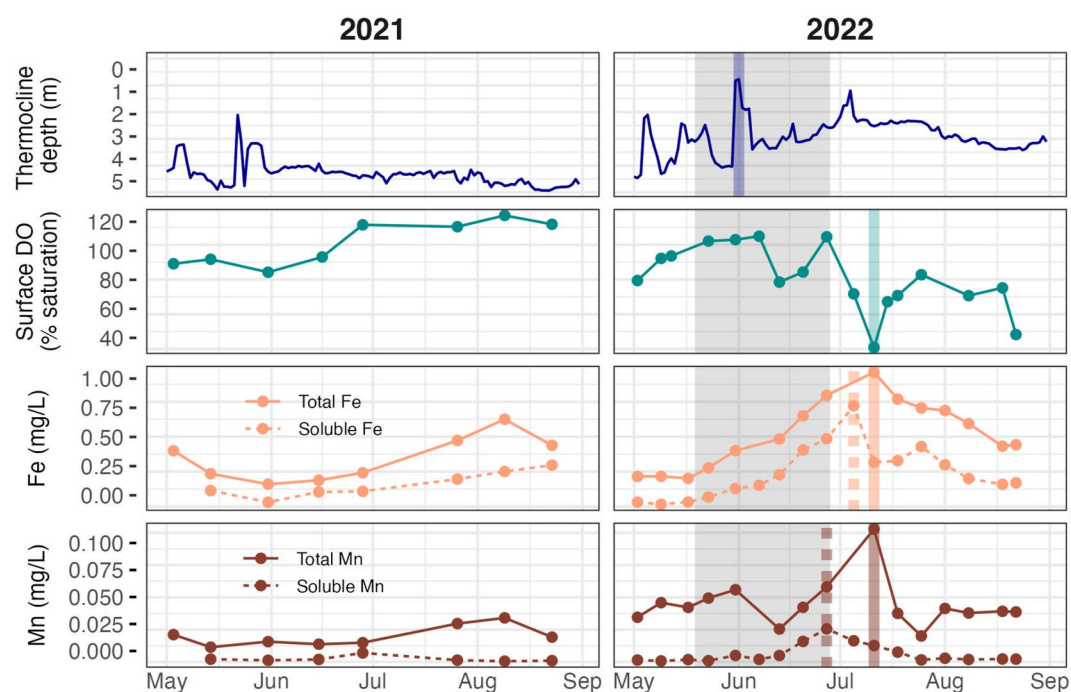


Figure 7. Time series of thermocline depth (m), surface dissolved oxygen (DO) % saturation, surface total iron (Fe; mg/L) and surface total manganese (Mn; mg/L) at 0.1 m depth in Beaverdam Reservoir during summers 2021 and 2022. Gray shading indicates the drawdown period in 2022. Colored vertical lines indicate the observed maximum or minimum for each variable in 2022. Points represent discrete sampling visits, while the continuous line for thermocline depth was derived from high-frequency in situ sensors. Note reversed y-axis scale for thermocline depth, with 0 m corresponding to the reservoir surface.

The observed increase in buoyancy frequency at the thermocline during drawdown could have resulted from multiple mechanisms. Decreased residence time of water in the epilimnion during drawdown (due to increased outflow rates from this layer) could reduce thermal exchange between the epilimnion and hypolimnion, thereby steepening the temperature gradient at the thermocline (Wang et al., 2012). Additionally, decreased epilimnetic volume could also increase surface temperatures by allowing solar radiation and atmospheric heat to warm a smaller volume of water (e.g., Pilla et al., 2018), and this higher temperature differential between surface and bottom waters could increase maximum buoyancy frequency.

Across the drawdown literature, changes in local stratification strength at the thermocline have received less attention than the susceptibility to full water column mixing during drawdown (Table S1), despite the importance of thermocline strength for regulating reservoir chemistry and biology (e.g., Leach et al., 2018; MacIntyre et al., 1999). Importantly, changes in buoyancy frequency and Schmidt stability have different implications for biogeochemical processing. Increases in buoyancy frequency limit mixing of solutes between the epilimnion and hypolimnion, whereas decreases in Schmidt stability can (but do not always) lead to mixing events that homogenize solutes throughout the water column (Bush et al., 2017; MacIntyre et al., 1999; Osborn, 1980; Wetzel, 2001). Decreased water depth inherently reduces the amount of energy required to mix the full water column, thereby resulting in decreased Schmidt stability, documented here and elsewhere (see Table S1). In Beaverdam Reservoir, decreased Schmidt stability during drawdown did not result in full water column mixing or substantial hypolimnion deepening, though it may have contributed to earlier fall turnover in 2022 relative to 2021. Conversely, increased buoyancy frequency was likely more relevant in controlling biogeochemical dynamics during the summer stratified period. Ultimately, our work highlights the importance of calculating multiple metrics of thermal stratification to understand the complex effects of drawdown on reservoir physical processes.

4.1.1. Surface Nutrient and Metal Concentrations Increased, Despite Increased Thermocline Strength

Although drawdown increased maximum buoyancy frequency, surface SRP concentrations increased during drawdown, likely contributing to a substantial surface phytoplankton bloom shortly thereafter (Figure 5). We also

observed peaks of total and soluble Fe and Mn in surface waters, which occurred several weeks after the increase in SRP and coincided with the minimum surface DO (41% saturation) observed during this period (Figure 7). These effects are somewhat counterintuitive, as higher maximum buoyancy frequency would be expected to decrease solute flux rates across the thermocline, thus resulting in lower solute concentrations in the epilimnion (Bush et al., 2017). Our results suggest that alternative mechanisms may be responsible for increased nutrient concentrations during and after drawdown. These mechanisms could include shallowing of the epilimnion, which may concentrate nutrients in a smaller epilimnetic layer (Chapra & Reckhow, 1983; Snodgrass, 1977), increased ebullition, which may allow for solute transport out of sediment (Deemer & Harrison, 2019; Delwiche et al., 2020; Schwarz et al., 2023), and enhanced wave action on newly exposed sediments during drawdown, which may contribute to inputs of nutrients and metals from littoral areas (Furey et al., 2004). Because soluble Fe and Mn concentrations peaked earlier than total Fe and Mn concentrations (Figure 7), it seems likely that these metals were entrained from the anoxic hypolimnion in their reduced (soluble) state, before being oxidized in the epilimnion (Davison, 1993; Krueger et al., 2020; Lewis et al., 2023; Munger et al., 2019). In contrast, the earlier peak in SRP is more likely to have resulted from littoral sediment inputs or ebullition at the start of drawdown, though we note that direct attribution of any mechanisms requires additional fine-scale measurements and/or mechanistic modeling in future studies. Importantly, our results highlight that increases in surface nutrients during drawdown, which are often documented in drawdowns that exhibit decreases in thermal stability (Baldwin et al., 2008; Geraldine & Boavida, 2005; Naselli-Flores, 2003), can occur even when the local strength of stratification at the thermocline increases.

4.2. Phytoplankton Biomass and Distribution Were Altered by Nutrient and Light Dynamics

Drawdown in Beaverdam Reservoir resulted in simultaneous decreases in euphotic depth (Figure 6) and increases in nutrient availability (Figure 5), with relatively consistent surface water temperature (Figure 4). Consequently, the net effect of drawdown on phytoplankton biomass was challenging to predict a priori, as decreased light can decrease phytoplankton growth, while increased nutrient availability can increase phytoplankton growth. Altogether, we observed a substantial increase in surface phytoplankton biomass during the drawdown, with a peak in phytoplankton biomass occurring approximately 7 days after a peak in SRP (Figure 5). Consequently, our work demonstrates that the nutrient increases associated with drawdown can offset decreased light availability to result in an emergent increase in phytoplankton biomass, at least in some cases. Additional studies are needed to test the robustness of this response to drawdown in other reservoirs.

The vertical distribution of phytoplankton in the water column during the drawdown differed from the distribution exhibited in the previous year, potentially in response to the decreased light availability, shallowing of the thermocline, and increased surface nutrient concentrations that occurred during drawdown. Notably, the decrease in C_{\max} depth observed in this study (Figure 6) was correlated with the euphotic zone depth becoming shallower during drawdown (Figure S4 in Supporting Information S1). In previous summers, Beaverdam Reservoir has experienced cyanobacterial blooms in the hypolimnion at depths with $\leq 1\%$ of surface light, resulting in C_{\max} depths deeper than 7 m (Hamre et al., 2018). The bloom that occurred after the 2022 drawdown was much closer to the surface than previous years, with maximum phytoplankton concentrations occurring at C_{\max} depths of ≤ 3 m (Figure 6). Interestingly, due to the altered light environment (i.e., shallower euphotic zone depth) in the reservoir during drawdown, C_{\max} depth was associated with approximately the same light availability in 2022 as in previous years ($\sim 1\%$ of surface light), though at much shallower depths (Figure 6, Figure S4 in Supporting Information S1). Our results support previous work in a nearby reservoir that observed the reciprocal effect, in which thermocline deepening led to a deepening of C_{\max} depth (Lofton et al., 2022). Ultimately, these results highlight the substantial plasticity of phytoplankton to adapt to changing physical conditions, optimizing their location at the depth that best matches their nutrient and light requirements.

We observed that the peak width of phytoplankton biomass was approximately 2 m thinner during drawdown than during the same time period in the previous year (Figure 6). Declines in peak width could result from a number of factors, as phytoplankton exhibit higher growth rates in layers of the water column with optimal temperature, light, and nutrient conditions (Durham & Stocker, 2012; Moll et al., 1984). The steeper temperature gradient at the thermocline during drawdown may have created a narrow range of depths where conditions were optimal for growth, leading to aggregation of phytoplankton in a thinner layer. Likewise, shallower euphotic zone depth and thermocline depth could have decreased suitable thermal and light habitat (Hamilton et al., 2010; Leach et al., 2018; Varela et al., 1994). Ultimately, it is likely that multiple factors collectively contributed to the

development of thinner peak width of phytoplankton biomass during drawdown. Altered spatial distribution of phytoplankton (i.e., decreased peak width) could potentially lead to heterogeneity in phytoplankton-driven biogeochemical processing across the entire water column (e.g., Heini et al., 2014; Levine & Lewis, 1985) or affect zooplankton grazing dynamics (Moeller et al., 2019; Pilati & Wurtsbaugh, 2003; Wang et al., 2020). In addition, concentration of phytoplankton in a narrower layer of the water column could have potential water quality implications if these aggregations occur at a depth from which water is withdrawn for drinking water treatment.

High-frequency profiles of phytoplankton spectral groups were essential to our analysis of how changes in water column depth due to drawdown may alter the depth distribution of phytoplankton. However, without additional sampling and microscopy analyses, we were unable to assess the response of specific phytoplankton taxonomic groups to water level changes. While a lack of phytoplankton samples pre-drawdown precluded a more taxonomically resolved analysis of changes in phytoplankton community structure at Beaverdam Reservoir, future drawdown studies would benefit from such analyses. Importantly, the responses of specific taxa of cyanobacteria and other phytoplankton have substantial implications for the effect of drawdown on water quality, as taxa have varying potential to release toxins (Chorus & Welker, 2021), clog treatment plant filters (Henderson et al., 2008), and cause water taste and odor concerns (Watson, 2004).

4.2.1. The Phytoplankton Bloom Was Associated With Cascading Effects on Carbon and Nutrient Cycling

The surface cyanobacterial bloom observed in 2022 was temporally associated with marked changes in the dynamics of multiple biogeochemical variables (Figure 5). TN and TP increased concurrently with phytoplankton, likely reflecting continuing nutrient inputs and incorporation of N and P into phytoplankton biomass (Li et al., 2012). The subsequent peak in DOC likely resulted from both leaching from live phytoplankton during the bloom and decomposition of senescing phytoplankton after the bloom collapsed (Bartosiewicz et al., 2021; Søndergaard et al., 2000). Dissolved CO₂ concentrations remained very low while phytoplankton and DOC were at their highest—likely due to fixation into phytoplankton biomass—but peaked 6 days after the peak in DOC, when respiration rates likely surpassed fixation rates. Finally, the peak in NH₄⁺ 3 weeks after peak bloom conditions likely reflected ammonification from decomposing organic matter (Gardner et al., 2017; Tezuka, 1986). In sum, the drawdown-associated cyanobacterial bloom was associated with multiple changes in water chemistry, substantially affecting coupled C, N, and P cycles in the reservoir.

Our results follow the findings of other studies with respect to the effects of phytoplankton blooms on reservoir physics and biogeochemistry. Similar to our observations that DOC, dissolved CO₂, and NH₄⁺ peaked shortly (8–21 days) after peak cyanobacterial biomass occurred, other researchers have documented that phytoplankton cell degradation and subsequent leaching can occur rapidly, on the scale of hours to days (Hansen et al., 1986). Previous studies have also similarly found that bloom degradation is associated with increases in dissolved organic matter and dissolved CO₂ (Bartosiewicz et al., 2021; Søndergaard et al., 2000; Zhang et al., 2022), as well as mineralization of both N (Gardner et al., 2017; Tezuka, 1986) and P (Carey et al., 2014; Hałemejko & Chrost, 1984). While we did not collect microbial community data, degradation of phytoplankton blooms is also associated with substantial changes in microbial community structure as microbes decompose senescing phytoplankton cells (Fukami et al., 1983; Grossart & Simon, 1998). Finally, dense growth of phytoplankton cells in surface water during blooms can lead to increased light attenuation and, while not quantified in this study, heat absorption, both affecting the underwater light environment and potentially prolonging or stabilizing thermal stratification (Mesman et al., 2021; Robarts & Zohary, 1984; Zhang et al., 2022). In sum, our work highlights that phytoplankton blooms due to reservoir drawdowns are likely to have cascading effects on multiple aspects of reservoir ecosystem functioning.

4.3. Decreases in Surface DO Caused by Bloom Degradation and Epilimnetic Water Loss

Despite atmospheric exchange, surface DO concentrations decreased substantially following drawdown, which can have important consequences for higher trophic levels in the reservoir. The magnitude of decline in surface water DO observed in our study (41% saturation at 0.1 m depth) is remarkable in comparison to other drawdowns (Table S1). This decrease was likely mediated in part by high oxygen demand due to decomposition of the decaying phytoplankton bloom in surface water and oxidation of reduced solutes within the epilimnion (see Section 4.1.1). Additionally, loss of epilimnetic water volume during drawdown decreased the total epilimnetic

oxygen mass amidst this high oxygen demand. Consequently, we anticipate that low DO saturation may be particularly pronounced during the 2022 drawdown in Beaverdam Reservoir (i.e., compared to other drawdowns) due to the synergistic effects of bloom degradation and epilimnetic water loss (Figures 3, 5 and 7). While zooplankton and fish dynamics were not monitored in this study, the depth at which DO dropped below 3 mg/L (a threshold below which many fish and zooplankton taxa cannot survive; e.g., Missaghi et al., 2017; Stefan et al., 2001) was 3 m shallower in the drawdown year than the non-drawdown year, and the temperature at which DO crossed this threshold was 7.5°C higher in 2022 than 2021 (Figure S5 in Supporting Information S1). Combined, these factors could force fish and zooplankton to congregate within a shallower surface layer (McLaren et al., 2023), increase habitat overlap between zooplankton and predatory fish (Dillon et al., 2021), and/or potentially eliminate habitat for coldwater fish species (Missaghi et al., 2017; Stefan et al., 2001).

Interactions of physical, chemical, and biological variables make changes in surface DO concentrations difficult to predict a priori as an emergent response of drawdown. A synthesis of the previous literature on drawdowns (Table S1) indicates that surface DO can sometimes decrease (Benejam et al., 2008; Cott et al., 2008; DeBoer et al., 2016; Naselli-Flores, 2003; Saber et al., 2020), increase (Sánchez-Carrillo et al., 2007; Yang et al., 2016), or exhibit no change during drawdown (Baldwin et al., 2008; Brasil et al., 2016; Gerales & Boavida, 2005; Magbanua et al., 2015), with potential downstream effects (Hamilton et al., 2022; Schenk & Bragg, 2021). In general, surface water DO declines are more frequently reported for management or experimental drawdowns and less frequently reported for natural drawdowns, potentially due to correlated increases in surface primary production during many natural drawdowns (Table S1). Consequently, our investigation of the effects of a management drawdown in Beaverdam Reservoir provides a useful case study highlighting the emergent effects of simultaneous changes in reservoir physics and biology driving DO dynamics in surface water.

4.4. Strengths and Limitations of Whole-Ecosystem Drawdown Experiment

Our intensive monitoring before, during, and after the management-driven drawdown in Beaverdam Reservoir allowed us to identify potential effects of water level change on reservoir physics, chemistry, and biology. Importantly, the substantial changes we observed in water quality were not associated with corresponding increases in air temperature or decreases in precipitation, as is typical of drought-driven drawdowns (Table S1), helping us to isolate the impacts of water level separate from these other drivers. Still, this analysis is limited to one drawdown and one waterbody, limiting inference into how time of year, lake type (e.g., dimictic vs. polymictic, oligotrophic vs. eutrophic), or legacy effects of previous drawdowns may have altered the results observed here. Without detailed mechanistic modeling, we are unable to conclusively identify the mechanisms responsible for the changes observed in this study. Furthermore, our data collection program precluded analysis of alternative drivers of change during drawdown, including changes in fish populations, littoral plants, and littoral macro-invertebrates (e.g., see White et al., 2011; White et al., 2010; Leira & Cantonati, 2008; McLaren et al., 2023; Hirsch et al., 2017), motivating the need for future studies that include both intensive littoral and pelagic monitoring. Ultimately, the magnitude of change observed during Beaverdam's drawdown relative to the previous non-drawdown year (e.g., phytoplankton concentrations 147% higher, NH_4^+ concentrations 2273% higher) and intuitive mechanistic connections between the variables of interest (e.g., a DOC increase coincident with bloom senescence) provide support for substantial drawdown-driven effects on reservoir physics, chemistry, and biology. Our work contributes to an emerging body of research on the effects of drawdowns (Table S1) and motivates additional research to characterize these events across a broader range of environmental conditions.

4.5. Emergent Effects of Drawdown Vary Among Reservoirs and Drawdowns

Altogether, our study highlights how the emergent effects of drawdown are likely influenced by characteristics of an individual waterbody. At Beaverdam Reservoir, drawdown was insufficient to allow light penetration to hypolimnetic sediment, likely due to the depth and turbidity of the reservoir. However, if sufficient amounts of light did reach the sediments, we may have observed warmed hypolimnetic water and increased benthic algae and/or macrophyte growth, with consequent increases in whole-ecosystem DO, rather than the observed decrease (Figure 1a). As a eutrophic reservoir, Beaverdam Reservoir already had high phytoplankton biomass and hypolimnetic nutrient concentrations, which likely contributed to the observed phytoplankton bloom that occurred during drawdown (Figure 1b). Similarly, presence of an anoxic hypolimnion likely played a role in increasing nutrient fluxes to surface water and decreasing surface DO concentrations following drawdown (Figure 2c). Altogether, our findings and the results of previous research (Table S1) suggest that the volume of

water lost during drawdown, waterbody depth, clarity, outflow depth, and trophic state are likely all critical factors for predicting the emergent effects of drawdown.

Our results provide a useful complement to previous research by demonstrating how loss of epilimnetic water has the potential to substantially worsen, rather than improve, water quality in some reservoirs. Previous management-driven drawdowns have often improved water quality, as indicated by decreased phytoplankton biomass (Ejankowski & Solis, 2015; Matsuzaki et al., 2023; Table S1), likely because these management interventions have removed hypolimnetic water, increased light penetration to sediments, or destratified the waterbody. Removal of hypolimnetic water releases nutrients from the ecosystem, and increased light penetration and destratification can increase DO concentrations in bottom waters, thereby reducing internal nutrient loads (e.g., Matsuzaki et al., 2023; Nürnberg, 2020). Conversely, removal of epilimnetic water at Beaverdam Reservoir increased the surface concentrations of nutrients, contributing to increased phytoplankton growth. As such, our results at Beaverdam Reservoir align more closely with the effects of seasonal or drought-induced drawdowns than management-driven or experimental drawdowns across the published literature. Seasonal and drought-induced drawdowns have often resulted in increased phytoplankton biomass and worsening water quality, though these effects have been difficult to disentangle from correlated seasonal changes in temperature and hydrology (Table S1). Importantly, as climate change and water management continue to increase the frequency and intensity of all types of drawdowns across lakes and reservoirs worldwide, our results highlight the importance of characterizing how drawdown can alter complex in-lake processes, thus affecting water quality.

Data Availability Statement

All data analyzed for this study are published in the Environmental Data Initiative repository (Carey & Breef-Pilz, 2023; Carey, Breef-Pilz, Bookout, et al., 2023; Carey, Breef-Pilz, & Lofton, 2023; Carey, Breef-Pilz, Wander, et al., 2023; Carey, Lewis, et al., 2022; Carey, Lewis, & Breef-Pilz, 2023; Carey, Lewis, Niederlehner, et al., 2023; Carey, Wander, et al., 2023; Schreiber et al., 2023). Analysis code to reproduce the results in this manuscript is available in a Zenodo repository (Lewis et al., 2024).

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Erratum

In the originally published version of this article, the legend for Figure 3 was omitted. The legend explains the color gradients used in the figure. Figure 3 has been corrected, and this may be considered the authoritative version of record.