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

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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

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 two 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 the 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 one 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

59 fluctuations on daily to annual timescales due to management for flood control, hydropower, fish
60 passage, irrigation, and drinking water provision (Fergus et al., 2022; Jiang et al., 2018; Keller et
61 al., 2021; Wada et al., 2014; Hamilton et al. 2022). The seasonal variability of water level in
62 managed reservoirs is, on average, more than four times greater than in natural waterbodies
63 (Cooley et al., 2021), and extreme, non-seasonal water level fluctuations may also be more
64 common in these managed systems. As just one example, water level fluctuated by ~50 m over
65 two years in Lake Shasta, a reservoir in California, USA (Zohary and Ostrovsky 2011). As the
66 frequency of water level drawdowns increases due to both climate change and water
67 management (Cooley et al., 2021; Kraemer et al., 2020; Ye et al., 2017; Zhao et al., 2022), it is
68 critical to determine the ecosystem-level effects of water level change on the interconnected
69 biological, chemical, and physical processes that shape water quality.

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

93   Changes in reservoir physical properties due to drawdown may cascade to alter chemical
94 and biological dynamics, but the net effects of multiple interacting ecosystem processes remain
95 unresolved (Figure 1). If hypolimnetic water is withdrawn from the reservoir (e.g., for water
96 quality management or downstream temperature regulation), nutrient and metal concentrations
97 may decrease at the whole-ecosystem scale (Nürnberg, 2007, 2020). However, if epilimnetic
98 water is withdrawn (e.g., for some drinking water, irrigation, and hydroelectric purposes), or if
99 hypolimnetic withdrawal weakens thermal stratification, epilimnetic nutrients may increase as a
100 result of increased entrainment from the hypolimnion (Zohary & Ostrovsky, 2011). Littoral
101 erosion and sediment drying due to water level fluctuations may lead to inputs of nitrogen (N),
102 phosphorus (P), and carbon (C) from littoral sediments, further increasing surface concentrations
103 during drawdown (Klotz & Linn, 2001). Likewise, methane ebullition may increase during
104 drawdown due to decreased hydrostatic pressure (Beaulieu et al., 2018; Harrison et al., 2017;

105 Deemer and Harrison, 2019), potentially increasing the suspension of bottom sediments and/or
106 increasing cyanobacterial recruitment to the water column (Delwiche et al. 2020; Schwarz et al.
107 2023; Deemer and Harrison, 2019). Increased nutrient concentrations can subsequently also lead
108 to increased phytoplankton biomass (e.g., Baldwin et al., 2008; Naselli-Flores & Barone, 2005).
109 However, the effect of increased nutrient concentrations could be tempered by expected declines
110 in light availability resulting from increased turbidity (e.g., Perrin et al., 2000). Taken together,
111 these divergent changes in nutrient and light availability could result in positive or negative net
112 effects on total phytoplankton biomass (Ma et al., 2023; Figure 1b). Moreover, alteration of
113 thermal stratification by drawdown could also alter the distribution of phytoplankton biomass
114 throughout the water column (Leach et al., 2018; Lofton et al., 2020, 2022). Drawdown could
115 alter biomass distributions either by inducing mixing, thereby homogenizing biomass across
116 depths (Kasprzak et al., 2017; Planas & Paquet, 2016; Rinke et al., 2009; Wu et al., 2015), or by
117 facilitating the formation of deep maxima of biomass if thermal stratification increases post-
118 drawdown (Alldredge et al., 2002; Cullen, 2015; Lewis et al., 2017).
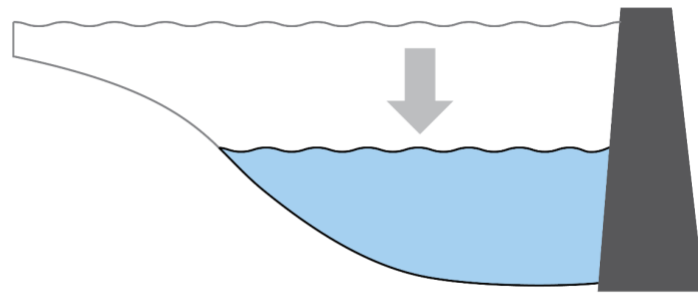
119   Among freshwater ecosystem variables, the net effect of drawdown on dissolved oxygen
120 (DO) concentrations is particularly difficult to predict, as DO is modulated by interacting
121 physical (e.g., stratification dynamics), chemical (e.g., oxygen demand by reduced solutes), and
122 biological conditions (e.g., production and respiration; Figure 1c). DO may increase in surface
123 waters if primary productivity increases, or decrease if primary productivity decreases (Odum,
124 1956). Likewise, decomposition of phytoplankton biomass and inputs of allochthonous organic
125 carbon due to littoral erosion could potentially stimulate epilimnetic respiration, thereby
126 decreasing DO concentrations and increasing the production of carbon dioxide (CO_2) (e.g.,
127 McLaren et al. 2023; Naselli-Flores 2003). Decreased stratification strength could cause whole-
128 ecosystem DO concentrations to increase with mixing of well-oxygenated surface waters into the
129 hypolimnion, or loss of oxic epilimnetic water from the reservoir could cause whole-ecosystem
130 DO concentrations to decrease (e.g., Matsuzaki et al., 2023). Depending on the direction and
131 magnitude of change in DO, further cascading effects on other ecosystem processes (e.g.,
132 dissolved metals concentrations, greenhouse gas production, etc.) may be expected. Overall,
133 while the effects of drawdown on reservoir physics, chemistry, and biology are increasingly
134 being examined (e.g., Deemer & Harrison, 2019; Matsuzaki et al., 2023), less is known about the
135 emergent responses to drawdown that arise from changes in multiple, interconnected ecosystem
136 processes (Figure 1). Here, we adapt the definition of 'emergent' from the complex systems
137 literature to refer to reservoir responses to drawdown that arise from multiple ecosystem
138 interactions, which cannot be easily predicted from the dynamics of one response variable in
139 isolation of the larger ecosystem (*sensu* Artime and De Domenico 2022).

140   Characterizing the effects of management-driven drawdown events may be particularly
141 important in small, thermally-stratified waterbodies, which are common in many regions of the
142 world (Downing et al., 2006). In the United States, over 90% of reservoirs are less than 1 km^2 in
143 surface area (Figure S1; U.S. Army Corps of Engineers, 2021). However, previous whole-
144 ecosystem studies examining the effects of water level changes have often focused on large lakes
145 and reservoirs (e.g., Nakanishi et al., 2022; Ouyang et al., 2021; Table S1) or very shallow,
146 weakly-stratified or fully-mixed waterbodies (e.g., Coops et al., 2003; Matsuzaki et al., 2023;
147 Table S1). Other studies have been conducted in mesocosms that cannot encompass all
148 interacting factors occurring on a whole-ecosystem scale (e.g., Matsuzaki et al., 2023).
149 Moreover, much of the existing literature examining the whole-ecosystem effects of water level
150 drawdown has focused on seasonal or drought-induced changes (see Table S1), which co-occur

151   with changes in temperature and precipitation. Thus, as opportunities to perturb whole
152   ecosystems and examine the couplings between lake and reservoir physics, chemistry, and
153   biology are rare (Barley & Meeuwig, 2017), management-driven drawdowns provide an
154   excellent opportunity for whole-ecosystem experimentation.

155   Here, we intensively monitored a month-long drawdown in a small eutrophic reservoir to
156   analyze the emergent effects of water level change on reservoir physics, chemistry, and biology
157   (Figure 1). Specifically, our study aimed to assess the effects of drawdown on three focal
158   variables: thermal stratification strength, phytoplankton biomass and depth distribution, and DO
159   concentrations. We expected that changes in these three focal variables would be mediated by
160   concurrent changes in water temperature, light penetration, and nutrient concentrations that result
161   from multiple ecosystem interactions during drawdown (Figure 1).

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163

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

169   **2 Methods**

170   2.1 Study site

171   Beaverdam Reservoir is a small, dimictic reservoir located in Vinton, Virginia, USA
172   (37.3128° N, 79.8160° W; Figure 2) that is owned and operated as a secondary drinking water
173   source by the Western Virginia Water Authority. When the reservoir is at full pond it has a
174   maximum depth of 13.4 m, surface area of 0.39 km^2, and residence time of ~0.9 y (Hamre et al.,
175   2018). The catchment area of the reservoir is 3.69 km^2, and consists primarily of deciduous
176   forest (Hamre et al., 2018). The reservoir is typically thermally stratified from May through
177   October, and experiences hypolimnetic anoxia throughout the summer stratified period (Doubek
178   et al., 2018).

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180
181   **Figure 2:** A drawdown in summer 2022 substantially decreased water level in Beaverdam
182   Reservoir. (a) Photos of the reservoir before (top, 9 May 2022) and after (bottom, 5 July 2022)
183   the month-long drawdown. (b) The spatial extent of the reservoir surface area change from pre-
184   drawdown in May (orange) to post-drawdown in July (teal), traced from satellite imagery. The
185   background map shows the location of the reservoir within North America. (c) Change in
186   epilimnetic and hypolimnetic water volume in 2021 and 2022. Vertical lines indicate when the
187   outtake pipe was opened and closed, with the shaded month noting the drawdown interval.

188   2.2 Water level drawdown (2022) and reference year (2021)

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

201   2.3 Monitoring program

202   2.3.1 *In situ* sensors

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

211   In addition to the in-water sensors, we also measured air temperature, wind speed, and
212 precipitation using a research-grade Campbell Scientific meteorological station that collected
213 data every minute (Carey & Breef-Pilz, 2023). The station was located at 37.3027º N, 79.8369º
214 W, 2.17 km from the sampling site at Beaverdam Reservoir. Air temperature was measured
215 using a HC2S3 Temperature and Relative Humidity probe by Rotronic Instrument Corp
216 (Hauppauge, NY, USA). Wind speed was measured using a R.M. Young Wind Monitor Model
217 05103 (RM Young Company, Traverse City, MI, USA), which averaged wind speeds over the
218 minute. Precipitation was measured using a TE525WS-L Rain Gage (Texas Electronics Inc.,
219 Dallas, TX, USA), which measures rainfall in 0.254 mm increments (Carey & Breef-Pilz, 2023).

220   2.3.2 Field sampling

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

224   2.3.2.1 Sensor profiles

225   Full water-column profiles of DO (concentration and percent saturation),
226 photosynthetically active radiation (PAR), and turbidity were collected using a SeaBird 19plus
227 V2 SeaCAT Profiler Conductivity, Temperature, and Depth (CTD) profiler (Sea-Bird Scientific,
228 Bellevue, WA, USA). These profiles were collected approximately weekly during the summer

229 stratified periods of 2021 and 2022, and monthly during the fall, winter, and spring. A YSI
230 ProODO Optical Dissolved Oxygen Instrument (YSI Inc., Yellow Springs, OH, USA) was used
231 to record DO concentrations at 1 m depth intervals in the reservoir from July - December 2021
232 during CTD maintenance; a comparison of the CTD and YSI DO sensors shows very strong
233 correspondence (Carey et al., 2022a).

234   We used a FluoroProbe (bbe Moldaenke, Schwentinental, Germany) to measure
235 phytoplankton biomass and depth distribution in the reservoir. FluoroProbes are submersible, *in-*
236 *situ* fluorometers that estimate biomass of four spectral groups using fluorescence of a suite of
237 photosynthetic pigments (Catherine et al., 2012; Kring et al., 2014): (1) green algae, which is
238 largely correlated with chlorophyll-*a* and chlorophyll-*b* fluorescence; (2) cyanobacteria
239 (phycocyanin); (3) brown algae (xanthophyll, fucoxanthin, and peridinin); and (4) cryptophytes
240 or mixed algae (phycoerythrin; Beutler et al., 2002). Biomass of the four spectral groups at each
241 measured depth was then summed to produce depth-specific total phytoplankton biomass
242 concentrations (Carey et al., 2023d).

243   *2.3.2.2 Water chemistry grab samples*

244   We used a 4-L Van Dorn sampler (Wildco, Yulee, FL, USA) to collect water chemistry
245 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,
246 we collected samples to all of the routine monitoring depths possible and also from ~1 m above
247 the sediments. At each depth, subsamples were taken for dissolved CO_2, dissolved organic
248 carbon (DOC), total and soluble N and P, and total and soluble iron (Fe) and manganese (Mn)
249 concentrations.

250   Water samples for dissolved CO_2 were collected from the Van Dorn sampler and
251 immediately sealed in 20-mL glass vials with crimped septum caps and no headspace. These
252 samples were kept on ice, then refrigerated in the lab and analyzed within 24 hr (Carey et al.,
253 2023b).

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

260   Water samples for analysis of Fe and Mn were collected in 15-mL centrifuge tubes.
261 Unfiltered samples were analyzed for total Fe and Mn. A separate aliquot was filtered
262 immediately upon collection with a 0.45-μm nylon membrane for analysis of soluble Fe and Mn.
263 Samples for metals analysis were preserved with trace metal grade nitric acid in the field to pH
264 <2 (Schreiber et al., 2023).

265   2.4 Laboratory analysis

266   2.4.1 Dissolved carbon dioxide

267   Dissolved CO_2 concentrations were measured on a Shimadzu Nexis GC-2030 Gas
268 Chromatograph (GC; Shimadzu, Kyoto, Japan) with a Flame Ionization Detector (FID) and
269 Thermal Conductivity Detector (TCD) following McClure et al. (2018). Prior to analysis, a 2-mL

270 headspace was created with Helium (He) by displacing 2-mL of sample water and equilibrated
271 by shaking each sample at 300 rpm for 15 minutes. The 2-mL headspace was then injected into
272 the GC at a temperature of 35 degrees C and a carrier gas (He) flow rate of 15 mL/min.
273 Dissolved concentrations of CO_2 in water were calculated using the observed head-space
274 concentrations and Henry's Law (Carey et al., 2023b; McClure et al., 2018).

275 2.4.2 Carbon, nitrogen, and phosphorus

276 Water column depth profiles of C, N, and P concentrations were measured following
277 collection in the field. DOC samples were poured into glass vials which had been acid-washed
278 and combusted at 550°C. These samples were analyzed on an Elementar vario TOC cube
279 (Elementar Analysensysteme GmbH, Hanau, Germany) using the persulfate catalytic method
280 (Brenton & Arnett, 1993). The detection limit for DOC was 0.76 mg/L. Samples for NH_4^+, NO_3^-,
281 and SRP were analyzed colorimetrically using flow injection analysis (APHA 2005) on a Lachat
282 Instruments XYZ Autosampler ASX 520 Series and QuikChem Series 8500 (Lachat ASX 520
283 Series, Lachat Instruments, Loveland, Colorado, USA). Method detection limits were 4.3 µg/L
284 (NH_4^+), 3.8 µg/L (NO_3^-), and 3.0 µg/L (SRP), determined following Carey et al. (2023e).
285 Samples for TN and TP were digested with alkaline persulfate and then analyzed
286 colorimetrically using flow injection analysis. Method detection limits were 56 µg/L (TN) and
287 3.5 µg/L (TP). Additional analytical methodology can be found in the data publication (Carey et
288 al., 2023e).

289 2.4.3 Fe and Mn

290 Samples for total and soluble Fe and Mn were analyzed by ICPMS (inductively coupled
291 plasma mass spectrometry; Thermo Electron iCAP RQ). Detection limits were 0.80 µg/L (Fe)
292 and 0.004 µg/L (Mn).

293 2.5 Data analysis

294 2.5.1 Thermal Stratification

295 We calculated multiple metrics to quantify how thermal conditions changed in
296 Beaverdam Reservoir following drawdown. Schmidt stability (Idso, 1973), a measure of total
297 water column stability; maximum buoyancy frequency, a measure of local stability at the
298 thermocline; and thermocline depth were calculated using the R package *rLakeAnalyzer* (Read et
299 al., 2011) using *in situ* high-frequency thermistor data. Thermocline depth was calculated using a
300 minimum density difference of 0.1 kg/m^3 (Lewis et al., 2024b; following Wilson et al., 2020).
301 For simplicity, we refer to all volume above the thermocline as the epilimnion and all volume
302 below the thermocline as the hypolimnion. Schmidt stability was calculated with dynamic
303 bathymetry as the reservoir volume changed during drawdown by updating the depth of each
304 hypsometric layer of the reservoir with daily water level data (Lewis et al., 2024b). We
305 determined the date of fall turnover as the first day surface and bottom temperatures were within
306 1 °C, following McClure et al. (2020).

307 2.5.2 Phytoplankton depth distribution metrics

308 We calculated two metrics from the FluoroProbe data to characterize the depth
309 distributions of fluorescence-based phytoplankton biomass in Beaverdam Reservoir following

310 Lofton et al. (2020, 2022). First, we calculated the chlorophyll maximum (C_{max}) depth as the
311 depth at which the maximum concentration of fluorescence-based biomass of each spectral group
312 (green algae, brown algae, cyanobacteria, mixed algae, and total phytoplankton) was observed.
313 Second, we calculated the width of the biomass peak (peak width) for each spectral group and
314 for total phytoplankton biomass. To determine peak width, we identified the depths above and
315 below the maximum observed biomass where observed biomass was nearest to the mean
316 biomass concentration across the water column. The distance between these two depths in meters
317 was assigned as the peak width (see Figure S2). While we calculated C_{max} depth and peak width
318 for all four spectral groups and total phytoplankton, we focus our reporting on fluorescence-
319 based biomass of cyanobacteria and total phytoplankton, as cyanobacteria exhibited the highest
320 biomass concentrations of any spectral group on 64% of $n = 25$ total sampling days between 1
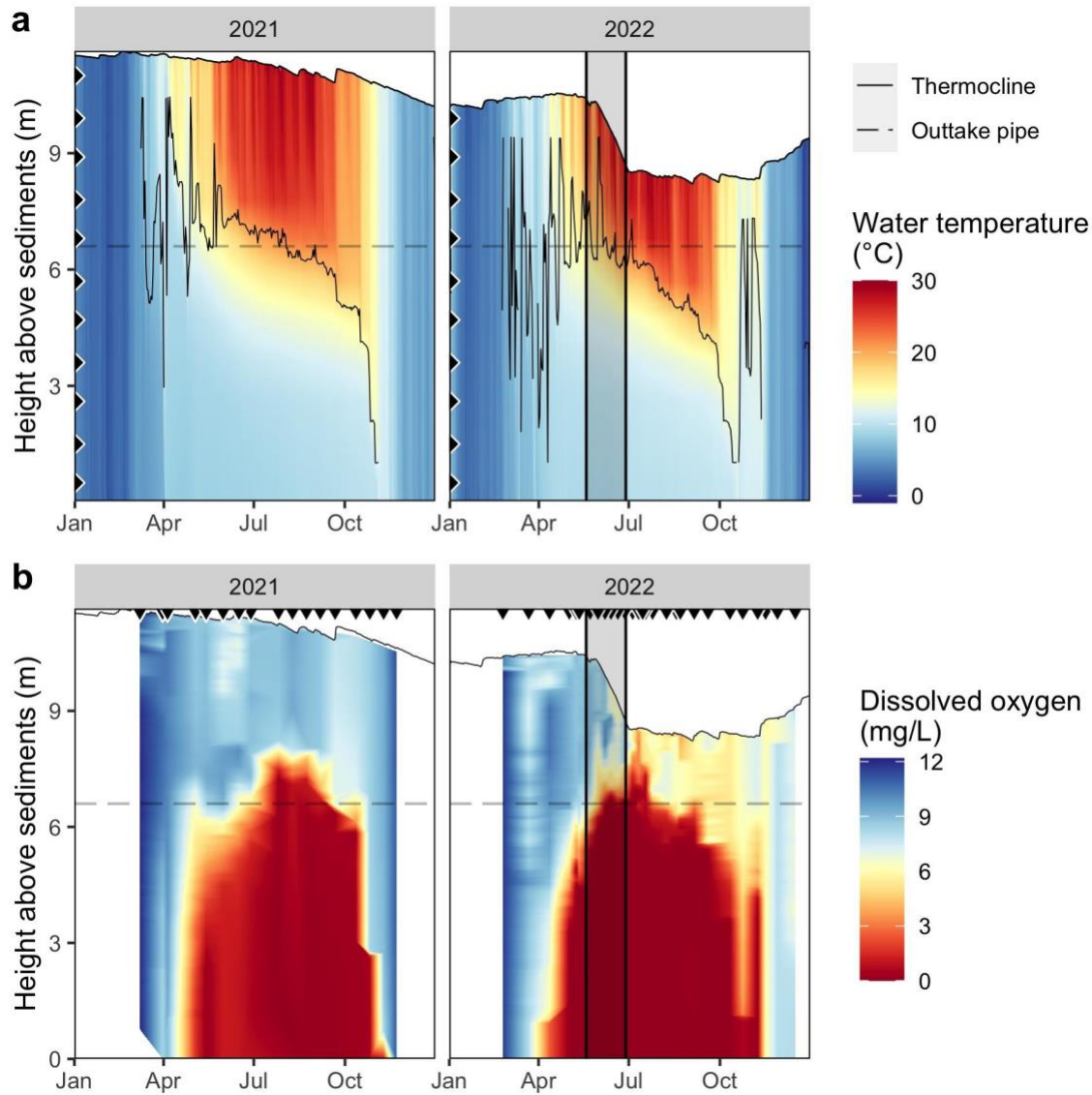321 May–1 September in 2021 and 2022.

322   2.5.3 Temporal comparison

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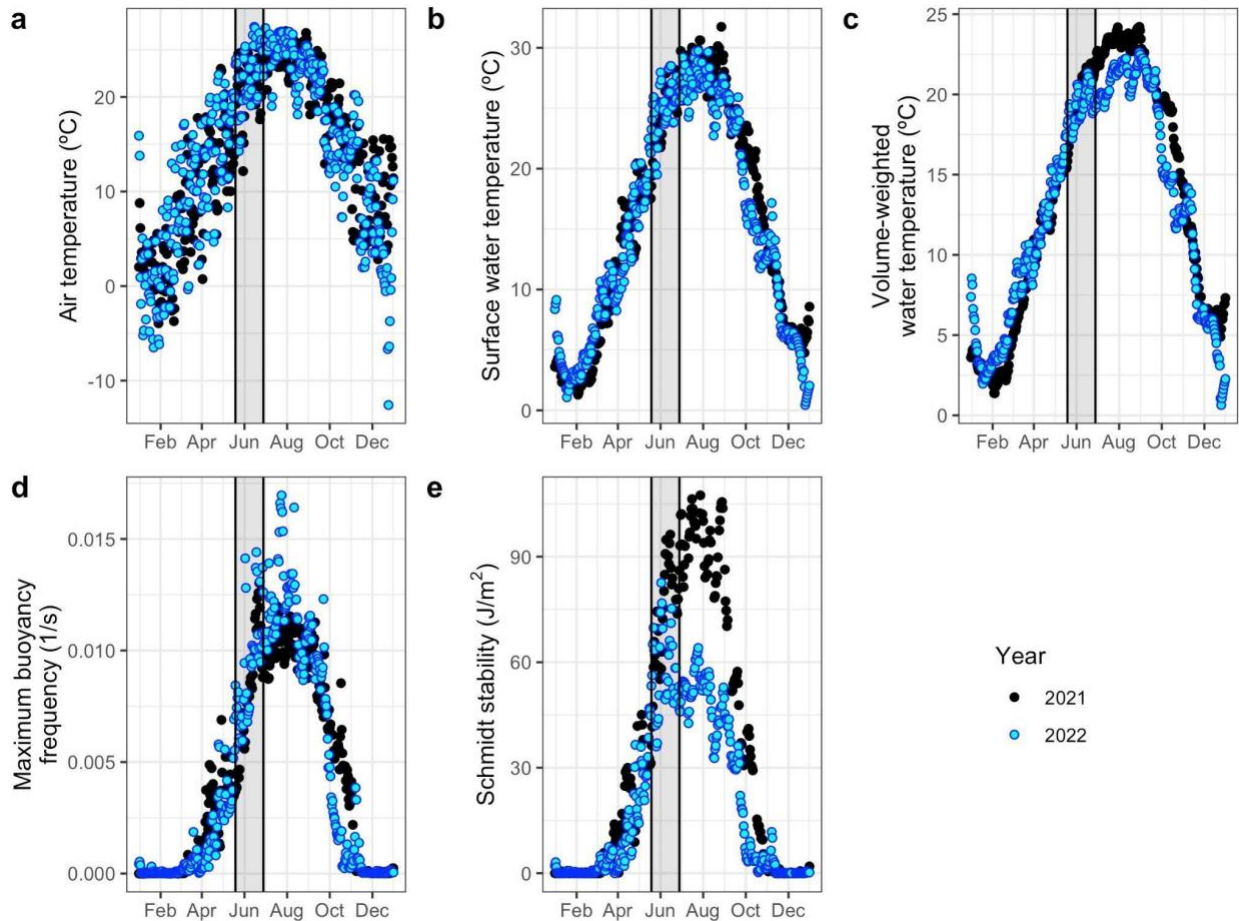329 coincident with drawdown in 2022.

3 Results

331   Water level changed substantially during drawdown, altering Beaverdam Reservoir's
332 physics, chemistry, and biology. From the beginning (19 May) to the end (28 June) of the 2022
333 drawdown, the total volume of Beaverdam Reservoir decreased by 36% (from 795,000 m^3 to
334 508,000 m^3; Figure 2c). In comparison, during the same time period in the reference year (2021),
335 water volume was relatively constant (0.2% increase from 989,000 m^3 to 991,000 m^3), exhibiting
336 typical seasonal fluctuations in the reservoir's water budget (Figure 2c). Drawdown in 2022
337 resulted in a loss of 69,000 m^2 of reservoir surface area and reduced maximum reservoir depth
338 by 1.7 m, from 10.4 m to 8.7 m (Figure 2a, 2b).

339   Due to epilimnetic water extraction, the majority (61%) of the observed change in the
340 reservoir's volume during the drawdown resulted from a loss of epilimnetic water (Figure 2c,
341 Figure 3a). Total epilimnetic volume decreased by 37% (from 462,000 m^3 to 290,000 m^3).
342 Disproportionate loss of warm epilimnetic water resulted in a 2.6 ℃ decrease in mean volume-
343 weighted temperature of the reservoir in 2022 compared to 2021 during the month following
344 drawdown (July 2021: 23.1 ± 0.6 ℃; July 2022: 20.5 ± 0.8 ℃; Figure 4c). Conversely, surface-
345 water temperature was similar between the two years (July 2021: 28.3 ± 1.28 ℃; July 2022: 27.4
346 ± 1.37 ℃; Figure 4b).

347

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 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.

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.

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). Total precipitation was slightly greater in 2022 than in 2021, particularly during the first several days of drawdown (Figure S3a). 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 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).
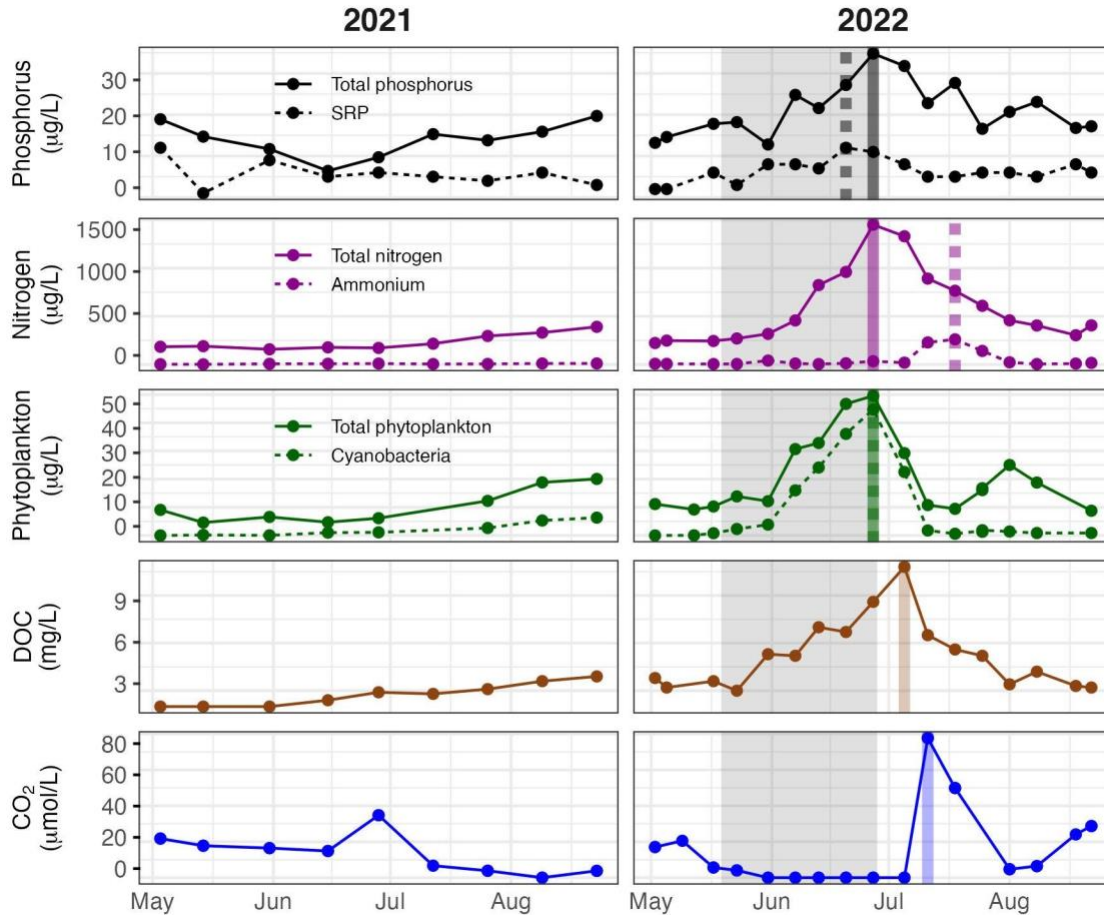
3.1 Stratification strength

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

377 drawdown, resulting in 44% lower Schmidt stability values in July 2022 (54 ± 5 J/m^2) relative to

378 July 2021 (97 ± 7 J/m^2; Figure 4d, 4e). Correspondingly, fall turnover was 18 days earlier in

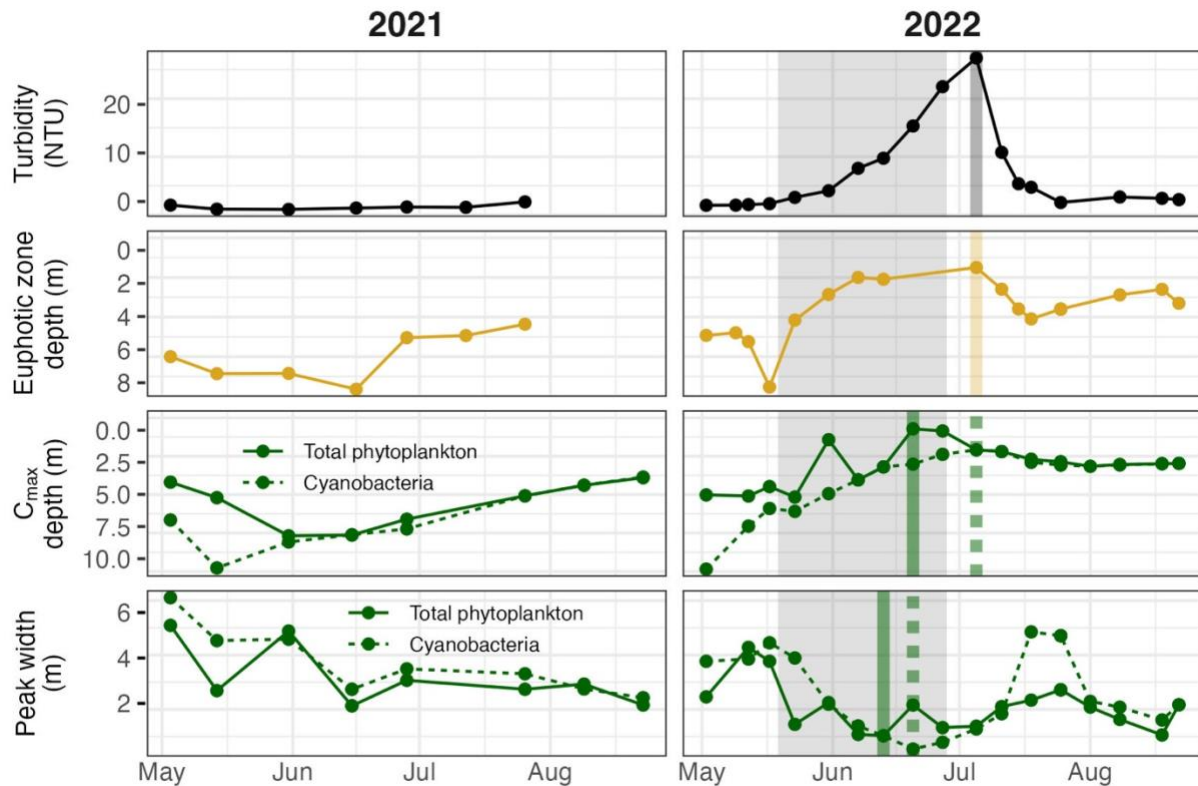379 2022 (19 October) relative to 2021 (6 November).

380   3.2 Phytoplankton and biogeochemical dynamics

381   Water level drawdown was associated with substantial changes in the magnitude and

382 timing of reservoir biogeochemistry and phytoplankton dynamics. In 2022, surface water TN,

383 TP, phytoplankton biomass, DOC, dissolved CO_2, and NH_4^+ all exhibited concentrations

384 substantially higher than the range of conditions observed in 2021 (Figure 5). Peaks of TP, TN,

385 and phytoplankton biomass on 27 June were preceded by a peak in SRP on 20 June. Surface

386 water DOC concentrations peaked 8 days after phytoplankton (5 July), followed by peaks in

387 dissolved CO_2 (11 July) and NH_4^+ (18 July). A comparison of maximum concentrations between

388 the two years reveals that in 2022 (vs. 2021), peak TP concentrations were 77% higher (by 15.1

389 µg/L), TN concentrations were 271% higher (by 1059 µg/L), phytoplankton concentrations were

390 147% higher (by 29.5 µg/L), DOC concentrations were 177% higher (by 6.9 µg/L), dissolved

391 CO_2 concentrations were 257% higher (by 43 µmol/L), and NH_4^+ concentrations were 2273%

392 higher (by 250 µg/L) than in 2021 (Figure 5).

393

394

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, 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. Grey shading indicates the
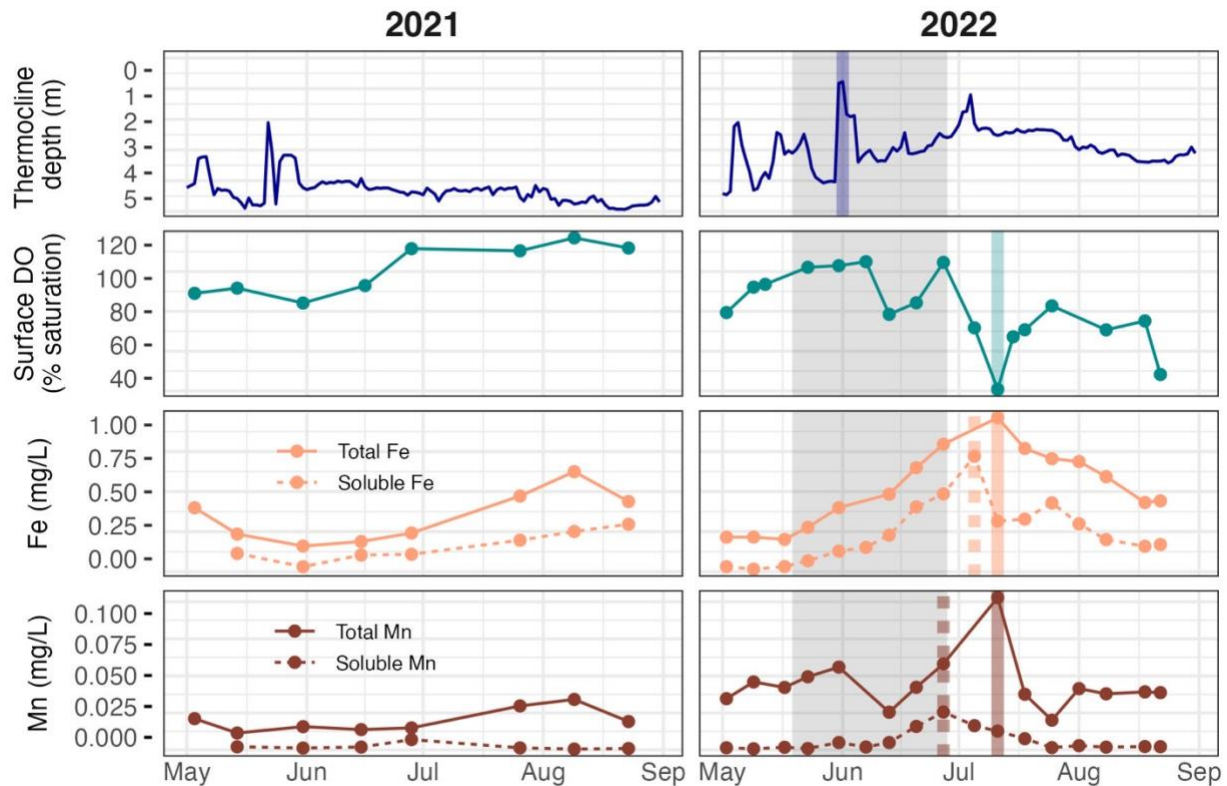drawdown period in 2022.

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 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).

414

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Figure 6: Turbidity peaked and euphotic zone depth was shallowest just after the drawdown at
Beaverdam Reservoir in 2022. 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.

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 (Figure 3b,
Figure 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 µg/L) and 29 days earlier than in 2021, and soluble Fe
concentrations reached a peak 144% higher (by 0.42 µg/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 µg/L) and 29
days earlier than in 2021, and soluble Mn concentrations reached a peak 266% higher (by 0.02
µg/L) and 1 day earlier than in 2021 (Figure 7).

436

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Figure 7: Time series of thermocline depth (m), surface dissolved oxygen (DO; % saturation), surface total Fe (mg/L) and surface total 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.

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).

456   4.1 Drawdown increased thermocline strength

457   Drawdown in Beaverdam Reservoir altered multiple aspects of reservoir physics (e.g.,
458 buoyancy frequency, Schmidt stability, epilimnion depth), with important implications for
459 biogeochemical processing. Interestingly, our work highlighted the potential for drawdown to
460 increase the local strength of thermal stratification at the thermocline (i.e., maximum buoyancy
461 frequency; Figure 4). Maximum buoyancy frequency characterizes the likelihood of mixing
462 between surface and bottom layers in a stratified waterbody (e.g., Foley et al., 2012; Mackay et
463 al., 2014), which will affect depth profiles of water chemistry (Bush et al., 2017; MacIntyre et
464 al., 1999; Osborn, 1980) and phytoplankton (Cullen, 2015; Leach et al., 2018; Lofton et al.,
465 2020, 2022). Consequently, changes in thermocline strength have the potential to play an
466 important role in modulating the effect of drawdowns on reservoir chemistry and biology,
467 particularly during smaller drawdowns (i.e., those that do not result in destratification), like in
468 Beaverdam Reservoir. These smaller drawdowns are common worldwide as a result of changes
469 in climate and land use (Cooley et al., 2021; Kraemer et al., 2020; Ye et al., 2017; Zhao et al.,
470 2022), but are not well-characterized across existing literature (Table S1).

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

479   Across the drawdown literature, changes in local stratification strength at the thermocline
480 have received less attention than the susceptibility to full water column mixing during drawdown
481 (Table S1), despite the importance of thermocline strength for regulating reservoir chemistry and
482 biology (e.g., MacIntyre et al., 1999; Leach et al., 2018). Importantly, changes in buoyancy
483 frequency and Schmidt stability have different implications for biogeochemical processing.
484 Increases in buoyancy frequency limit mixing of solutes between the epilimnion and
485 hypolimnion, whereas decreases in Schmidt stability can (but do not always) lead to mixing
486 events that homogenize solutes throughout the water column (Bush et al., 2017; MacIntyre et al.,
487 1999; Osborn, 1980; Wetzel, 2001). Decreased water depth inherently reduces the amount of
488 energy required to mix the full water column, thereby resulting in decreased Schmidt stability,
489 documented here and elsewhere (see Table S1). In Beaverdam Reservoir, decreased Schmidt
490 stability during drawdown did not result in full water column mixing or substantial hypolimnion
491 deepening, though it may have contributed to earlier fall turnover in 2022 relative to 2021.
492 Conversely, increased buoyancy frequency was likely more relevant in controlling
493 biogeochemical dynamics during the summer stratified period (Lewis et al., 2024a). Ultimately,
494 our work highlights the importance of calculating multiple metrics of thermal stratification to
495 understand the complex effects of drawdown on reservoir physical processes.

496   4.1.1 Surface nutrient and metal concentrations increased, despite increased thermocline
497   strength

498   Although drawdown increased maximum buoyancy frequency, surface SRP
499 concentrations increased during drawdown, likely contributing to a substantial surface

500   phytoplankton bloom shortly thereafter (Figure 5). We also observed peaks of total and soluble
501   Fe and Mn in surface waters, which occurred several weeks after the increase in SRP and
502   coincided with the minimum surface DO (41% saturation) observed during this period (Figure
503   7). These effects are somewhat counterintuitive, as higher maximum buoyancy frequency would
504   be expected to decrease solute flux rates across the thermocline, thus resulting in lower solute
505   concentrations in the epilimnion (Bush et al., 2017). Our results suggest that alternative
506   mechanisms may be responsible for increased nutrient concentrations during and after
507   drawdown. These mechanisms could include shallowing of the epilimnion, which may
508   concentrate nutrients in a smaller epilimnetic layer (Chapra & Reckhow, 1983; Snodgrass,
509   1977), increased ebullition, which may allow for solute transport out of sediment (Delwiche et
510   al. 2020; Schwarz et al. 2023; Deemer and Harrison, 2019), and enhanced wave action on newly
511   exposed sediments during drawdown, which may contribute to inputs of nutrients and metals
512   from littoral areas (Furey et al., 2004). Because soluble Fe and Mn concentrations peaked earlier
513   than total Fe and Mn concentrations (Figure 7), it seems likely that these metals were entrained
514   from the anoxic hypolimnion in their reduced (soluble) state, before being oxidized in the
515   epilimnion (Davison, 1993; Krueger et al., 2020; Munger et al., 2019; Lewis et al., 2023). In
516   contrast, the earlier peak in SRP is more likely to have resulted from littoral sediment inputs or
517   ebullition at the start of drawdown, though we note that direct attribution of any mechanisms
518   requires additional fine-scale measurements and/or mechanistic modeling in future studies.
519   Importantly, our results highlight that increases in surface nutrients during drawdown, which are
520   often documented in drawdowns that exhibit decreases in thermal stability (Baldwin et al., 2008;
521   Geraldes & Boavida, 2005; Naselli-Flores, 2003), can occur even when the local strength of
522   stratification at the thermocline increases.

523   4.2 Phytoplankton biomass and distribution were altered by nutrient and light dynamics

524   Drawdown in Beaverdam Reservoir resulted in simultaneous decreases in euphotic depth
525   (Figure 6) and increases in nutrient availability (Figure 5), with relatively consistent surface
526   water temperature (Figure 4). Consequently, the net effect of drawdown on phytoplankton
527   biomass was challenging to predict *a priori*, as decreased light can decrease phytoplankton
528   growth, while increased nutrient availability can increase phytoplankton growth. Altogether, we
529   observed a substantial *increase* in surface phytoplankton biomass during the drawdown, with a
530   peak in phytoplankton biomass occurring approximately seven days after a peak in SRP (Figure
531   5). Consequently, our work demonstrates that the nutrient increases associated with drawdown
532   can offset decreased light availability to result in an emergent increase in phytoplankton biomass,
533   at least in some cases. Additional studies are needed to test the robustness of this response to
534   drawdown in other reservoirs.
535   The vertical distribution of phytoplankton in the water column during the drawdown
536   differed from the distribution exhibited in the previous year, potentially in response to the
537   decreased light availability, shallowing of the thermocline, and increased surface nutrient
538   concentrations that occurred during drawdown. Notably, the decrease in C_{max} depth observed in
539   this study (Figure 6) was correlated with the euphotic zone depth becoming shallower during
540   drawdown (Figure S4). In previous summers, Beaverdam Reservoir has experienced
541   cyanobacterial blooms in the hypolimnion at depths with ≤1% of surface light, resulting in C_{max}
542   depths deeper than 7 m (Hamre et al., 2018). The bloom that occurred after the 2022 drawdown
543   was much closer to the surface than previous years, with maximum phytoplankton
544   concentrations occurring at C_{max} depths of ≤3 m (Figure 6). Interestingly, due to the altered light

545 environment (i.e., shallower euphotic zone depth) in the reservoir during drawdown, C_{max} depth
546 was associated with approximately the same light availability in 2022 as in previous years (~1%
547 of surface light), though at much shallower depths (Figures 6, S4). Our results support previous
548 work in a nearby reservoir that observed the reciprocal effect, in which thermocline deepening
549 led to a deepening of C_{max} depth (Lofton et al., 2022). Ultimately, these results highlight the
550 substantial plasticity of phytoplankton to adapt to changing physical conditions, optimizing their
551 location at the depth that best matches their nutrient and light requirements.
552 We observed that the peak width of phytoplankton biomass was approximately 2 m
553 thinner during drawdown than during the same time period in the previous year (Figure 6).
554 Declines in peak width could result from a number of factors, as phytoplankton exhibit higher
555 growth rates in layers of the water column with optimal temperature, light, and nutrient
556 conditions (Durham & Stocker, 2012; Moll et al., 1984). The steeper temperature gradient at the
557 thermocline during drawdown may have created a narrow range of depths where conditions were
558 optimal for growth, leading to aggregation of phytoplankton in a thinner layer. Likewise,
559 shallower euphotic zone depth and thermocline depth could have decreased suitable thermal and
560 light habitat (Hamilton et al., 2010; Leach et al., 2018; Varela et al., 1994). Ultimately, it is
561 likely that multiple factors collectively contributed to the development of thinner peak width of
562 phytoplankton biomass during drawdown. Altered spatial distribution of phytoplankton (i.e.,
563 decreased peak width) could potentially lead to heterogeneity in phytoplankton-driven
564 biogeochemical processing across the entire water column (e.g., Heini et al., 2014; Levine &
565 Lewis Jr., 1985) or affect zooplankton grazing dynamics (Moeller et al., 2019; Pilati &
566 Wurtsbaugh, 2003; Wang et al., 2020). In addition, concentration of phytoplankton in a narrower
567 layer of the water column could have potential water quality implications if these aggregations
568 occur at a depth from which water is withdrawn for drinking water treatment.
569 High-frequency profiles of phytoplankton spectral groups were essential to our analysis
570 of how changes in water column depth due to drawdown may alter the depth distribution of
571 phytoplankton. However, without additional sampling and microscopy analyses, we were unable
572 to assess the response of specific phytoplankton taxonomic groups to water level changes. While
573 a lack of phytoplankton samples pre-drawdown precluded a more taxonomically resolved
574 analysis of changes in phytoplankton community structure at Beaverdam Reservoir, future
575 drawdown studies would benefit from such analyses. Importantly, the responses of specific taxa
576 of cyanobacteria and other phytoplankton have substantial implications for the effect of
577 drawdown on water quality, as taxa have varying potential to release toxins (Chorus & Welker
578 2021), clog treatment plant filters (Henderson et al. 2008), and cause water taste and odor
579 concerns (Watson 2004).

580 4.3.1 The phytoplankton bloom was associated with cascading effects on carbon and
581 nutrient cycling

582 The surface cyanobacterial bloom observed in 2022 was temporally associated with
583 marked changes in the dynamics of multiple biogeochemical variables (Figure 5). TN and TP
584 increased concurrently with phytoplankton, likely reflecting continuing nutrient inputs and
585 incorporation of N and P into phytoplankton biomass (Li et al., 2012). The subsequent peak in
586 DOC likely resulted from both leaching from live phytoplankton during the bloom and
587 decomposition of senescing phytoplankton after the bloom collapsed (Bartosiewicz et al., 2021;
588 Søndergaard et al., 2000). Dissolved CO_2 concentrations remained very low while phytoplankton
589 and DOC were at their highest—likely due to fixation into phytoplankton biomass—but peaked

590   6 days after the peak in DOC, when respiration rates likely surpassed fixation rates. Finally, the
591   peak in NH_4^+ three weeks after peak bloom conditions likely reflected ammonification from
592   decomposing organic matter (Gardner et al., 2017; Tezuka, 1986). In sum, the drawdown-
593   associated cyanobacterial bloom was associated with multiple changes in water chemistry,
594   substantially affecting coupled C, N, and P cycles in the reservoir.

595   Our results follow the findings of other studies with respect to the effects of
596   phytoplankton blooms on reservoir physics and biogeochemistry. Similar to our observations that
597   DOC, dissolved CO_2, and NH_4^+ peaked shortly (8–21 days) after peak cyanobacterial biomass
598   occurred, other researchers have documented that phytoplankton cell degradation and subsequent
599   leaching can occur rapidly, on the scale of hours to days (Hansen et al., 1986). Previous studies
600   have also similarly found that bloom degradation is associated with increases in dissolved
601   organic matter and dissolved CO_2 (Bartosiewicz et al., 2021; Søndergaard et al., 2000; Zhang et
602   al., 2022), as well as mineralization of both N (Gardner et al., 2017; Tezuka, 1986) and P (Carey
603   et al., 2014; Hałemejko & Chrost, 1984). While we did not collect microbial community data,
604   degradation of phytoplankton blooms is also associated with substantial changes in microbial
605   community structure as microbes decompose senescing phytoplankton cells (Fukami et al., 1983;
606   Grossart & Simon, 1998). Finally, dense growth of phytoplankton cells in surface water during
607   blooms can lead to increased light attenuation and, while not quantified in this study, heat
608   absorption, both affecting the underwater light environment and potentially prolonging or
609   stabilizing thermal stratification (Mesman et al., 2021; Robarts & Zohary, 1984; Zhang et al.,
610   2022). In sum, our work highlights that phytoplankton blooms due to reservoir drawdowns are
611   likely to have cascading effects on multiple aspects of reservoir ecosystem functioning.

612   4.3 Decreases in surface DO caused by bloom degradation and epilimnetic water loss

613   Despite atmospheric exchange, surface DO concentrations decreased substantially
614   following drawdown, which can have important consequences for higher trophic levels in the
615   reservoir. The magnitude of decline in surface water DO observed in our study (41% saturation
616   at 0.1 m depth) is remarkable in comparison to other drawdowns (Table S1). This decrease was
617   likely mediated in part by high oxygen demand due to decomposition of the decaying
618   phytoplankton bloom in surface water and oxidation of reduced solutes within the epilimnion
619   (see Section 4.1.1). Additionally, loss of epilimnetic water volume during drawdown decreased
620   the total epilimnetic oxygen mass amidst this high oxygen demand. Consequently, we anticipate
621   that low DO saturation may be particularly pronounced during the 2022 drawdown in
622   Beaverdam Reservoir (i.e., compared to other drawdowns) due to the synergistic effects of
623   bloom degradation and epilimnetic water loss (Figures 3, 5, 7). While zooplankton and fish
624   dynamics were not monitored in this study, the depth at which DO dropped below 3 mg/L (a
625   threshold below which many fish and zooplankton taxa cannot survive; e.g., Missaghi et al.,
626   2017; Stefan et al., 2001) was 3 m shallower in the drawdown year than the non-drawdown year,
627   and the temperature at which DO crossed this threshold was 7.5 °C higher in 2022 than 2021
628   (Figure S5). Combined, these factors could force fish and zooplankton to congregate within a
629   shallower surface layer (McLaren et al., 2023), increase habitat overlap between zooplankton
630   and predatory fish (Dillon et al., 2021), and/or potentially eliminate habitat for coldwater fish
631   species (Missaghi et al., 2017; Stefan et al., 2001).

632   Interactions of physical, chemical, and biological variables make changes in surface DO
633   concentrations difficult to predict *a priori* as an emergent response of drawdown. A synthesis of

634 the previous literature on drawdowns (Table S1) indicates that surface DO can sometimes
635 decrease (Benejam et al., 2008; Cott et al., 2008; DeBoer et al., 2016; Naselli-Flores, 2003;
636 Saber et al., 2020), increase (Sánchez-Carrillo et al., 2007; Yang et al., 2016), or exhibit no
637 change during drawdown (Baldwin et al., 2008; Brasil et al., 2016; Geraldes & Boavida, 2005;
638 Magbanua et al., 2015), with potential downstream effects (Hamilton et al. 2022, Schenk and
639 Bragg 2021). In general, surface water DO declines are more frequently reported for
640 management or experimental drawdowns and less frequently reported for natural drawdowns,
641 potentially due to correlated increases in surface primary production during many natural
642 drawdowns (Table S1). Consequently, our investigation of the effects of a management
643 drawdown in Beaverdam Reservoir provides a useful case study highlighting the emergent
644 effects of simultaneous changes in reservoir physics and biology driving DO dynamics in surface
645 water.

646   4.4 Strengths and limitations of whole-ecosystem drawdown experiment

647   Our intensive monitoring before, during, and after the management-driven drawdown in
648 Beaverdam Reservoir allowed us to identify potential effects of water level change on reservoir
649 physics, chemistry, and biology. Importantly, the substantial changes we observed in water
650 quality were not associated with corresponding increases in air temperature or decreases in
651 precipitation, as is typical of drought-driven drawdowns (Table S1), helping us to isolate the
652 impacts of water level separate from these other drivers. Still, this analysis is limited to one
653 drawdown and one waterbody, limiting inference into how time of year, lake type (e.g., dimictic
654 vs. polymictic, oligotrophic vs. eutrophic), or legacy effects of previous drawdowns may have
655 altered the results observed here. Without detailed mechanistic modeling, we are unable to
656 conclusively identify the mechanisms responsible for the changes observed in this study.
657 Furthermore, our data collection program precluded analysis of alternative drivers of change
658 during drawdown, including changes in fish populations, littoral plants, and littoral
659 macroinvertebrates (e.g., see White et al. 2011, White et al. 2010, Leira and Cantonati 2008,
660 McLaren et al. 2023, Hirsch et al. 2016), motivating the need for future studies that include both
661 intensive littoral and pelagic monitoring. Ultimately, the magnitude of change observed during
662 Beaverdam's drawdown relative to the previous non-drawdown year (e.g., phytoplankton
663 concentrations 147% higher, NH_4^+ concentrations 2273% higher) and intuitive mechanistic
664 connections between the variables of interest (e.g., a DOC increase coincident with bloom
665 senescence) provide support for substantial drawdown-driven effects on reservoir physics,
666 chemistry, and biology. Our work contributes to an emerging body of research on the effects of
667 drawdowns (Table S1) and motivates additional research to characterize these events across a
668 broader range of environmental conditions.

669   4.5 Emergent effects of drawdown vary among reservoirs and drawdowns

670   Altogether, our study highlights how the emergent effects of drawdown are likely
671 influenced by characteristics of an individual waterbody. At Beaverdam Reservoir, drawdown
672 was insufficient to allow light penetration to hypolimnetic sediment, likely due to the depth and
673 turbidity of the reservoir. However, if sufficient amounts of light did reach the sediments, we
674 may have observed warmed hypolimnetic water and increased benthic algae and/or macrophyte
675 growth, with consequent increases in whole-ecosystem DO, rather than the observed decrease
676 (Figure 1a). As a eutrophic reservoir, Beaverdam Reservoir already had high phytoplankton
677 biomass and hypolimnetic nutrient concentrations, which likely contributed to the observed

678   phytoplankton bloom that occurred during drawdown (Figure 1b). Similarly, presence of an
679   anoxic hypolimnion likely played a role in increasing nutrient fluxes to surface water and
680   decreasing surface DO concentrations following drawdown (Figure 2c). Altogether, our findings
681   and the results of previous research (Table S1) suggest that the volume of water lost during
682   drawdown, waterbody depth, clarity, outflow depth, and trophic state are likely all critical factors
683   for predicting the emergent effects of drawdown.

684   Our results provide a useful complement to previous research by demonstrating how loss
685   of epilimnetic water has the potential to substantially worsen, rather than improve, water quality
686   in some reservoirs. Previous management-driven drawdowns have often improved water quality,
687   as indicated by decreased phytoplankton biomass (Ejankowski & Solis, 2015; Matsuzaki et al.,
688   2023; Table S1), likely because these management interventions have removed hypolimnetic
689   water, increased light penetration to sediments, or destratified the waterbody. Removal of
690   hypolimnetic water releases nutrients from the ecosystem, and increased light penetration and
691   destratification can increase DO concentrations in bottom waters, thereby reducing internal
692   nutrient loads (e.g., Matsuzaki et al., 2023; Nürnberg, 2020). Conversely, removal of epilimnetic
693   water at Beaverdam Reservoir increased the surface concentrations of nutrients, contributing to
694   increased phytoplankton growth. As such, our results at Beaverdam Reservoir align more closely
695   with the effects of seasonal or drought-induced drawdowns than management-driven or
696   experimental drawdowns across the published literature. Seasonal and drought-induced
697   drawdowns have often resulted in increased phytoplankton biomass and worsening water quality,
698   though these effects have been difficult to disentangle from correlated seasonal changes in
699   temperature and hydrology (Table S1). Importantly, as climate change and water management
700   continue to increase the frequency and intensity of all types of drawdowns across lakes and
701   reservoirs worldwide, our results highlight the importance of characterizing how drawdown can
702   alter complex in-lake processes, thus affecting water quality.

Acknowledgments

Open Research

718   All data analyzed for this study are published in the Environmental Data Initiative
719   repository (Carey et al., 2022b, 2023a, 2023b, 2023c, 2023d, 2023e; Carey & Breef-Pilz, 2023;

720 Schreiber et al., 2023). Analysis code to reproduce the results in this manuscript is available in a
721 Zenodo repository (Lewis et al., 2024b).

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